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Biological and chemical products alter plant growth and control *Pythium aphanidermatum* in coriander

Eveline Mendes da Silva · Poliana Prates de Souza Soares · Naasoom Luiz Santos Mesquita · Natália Deniz Brito · Leandro Dias da Silva · Quelmo Silva de Novaes · Armínio Santos · Rafael José Vilela de Oliveira

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Abstract *Pythium aphanidermatum* is an important pathogen in several coriander (*Coriandrum sativum*)–producing regions, as it causes damping-off in seedlings and stem and root rot, often leading to plant death. Therefore, this study evaluated biological and chemical products for the control of root rot in coriander. An in vitro paired-culture assay was conducted using two *Trichoderma* species (*Trichoderma* sp. and *Trichoderma harzianum*) against *P. aphanidermatum*. In addition, effects of potassium phosphite, *Melaleuca alternifolia* extract, fosetyl-Al, *Bacillus subtilis*, and *Lactobacillus plantarum* + *Saccharomyces cerevisiae* were assessed at concentrations of 0, 10, 100, 500, and 1000 mg L^{-1} in PDA medium on mycelial growth of the oomycete. Experiments followed a completely randomized design. Subsequently, a greenhouse experiment was performed using coriander plants inoculated with *P. aphanidermatum* as a control and plants treated with the biological and chemical products evaluated in vitro. Selected morphophysiological variables were then analyzed. Both *Trichoderma* species and all tested products significantly inhibited mycelial growth of *P. aphanidermatum*. Among treatments, *Melaleuca alternifolia* extract showed the greatest efficacy, reducing disease incidence and post-emergence damping-off while enhancing gas exchange, resulting in greater plant growth and increased fresh mass accumulation in roots and shoots.

Keywords Biological control · *Coriandrum sativum* · Soil pathogen · Oomycetes · Plant health · Physiology

E. M. da Silva (✉) · P. P. de Souza Soares · N. L. S. Mesquita · N. D. Brito · Q. S. de Novaes · A. Santos
Departamento de Fitotecnia E Zootecnia, Universidade Estadual Do Sudoeste da Bahia, Vitória da Conquista, Bahia, Brazil
e-mail: silvameveline@gmail.com

L. D. da Silva
Universidade do Estado da Bahia, Juazeiro, Bahia, Brazil

R. J. V. de Oliveira
Centro de Tecnologias Estratégicas Do Nordeste - CETENE, Recife, Pernambuco, Brazil

R. J. V. de Oliveira
Universidade Federal Do Agreste de Pernambuco, Garanhuns, Pernambuco, Brazil

Introduction

Brazil ranks among the world's leading producers of vegetables, including coriander, which provides leaves and fruits widely used in culinary applications. Among leafy vegetables, coriander occupies the sixth place in national production, following lettuce, cabbage, broccoli, and cauliflower, with a production volume of 1,109,063 tons cultivated over 73,938 hectares (IBGE, 2017). Beyond its economic relevance, coriander cultivation also holds substantial social importance due to its extensive production scale.

However, coriander yield has declined markedly because of phytosanitary constraints. The oomycete *Pythium aphanidermatum* causes significant production losses by inducing necrotic lesions in stem and root tissues, leading to wilting of aerial parts, followed by damping-off and, in severe cases, plant death (Silva et al., 2024). Repeated cultivation in the same area increases disease incidence, often forcing growers to seek pathogen-free fields to avoid yield losses.

Management of diseases caused by *Pythium* spp. relies on multiple strategies, including preventive measures such as the use of healthy seeds to limit pathogen introduction, selection of well-drained soils, appropriate irrigation management, and crop rotation with non-host species. However, because *Pythium* spp. are soilborne pathogens with a wide host range and saprophytic capability, crop rotation alone may be ineffective. In addition, these organisms produce resistance structures that enable long-term survival in soil (Nzungize et al., 2012).

Beyond preventive approaches, chemical and biological control strategies are commonly adopted. Chemical management primarily involves fungicides such as phenylamides and phosphonates. Phenylamides inhibit RNA synthesis by interfering with polymerase activity involved in rRNA production (Sierotzki et al., 2019). Phosphonates exhibit a complex and not fully elucidated mode of action; however, they have been shown to act directly on pathogens through phosphorous acid formation and indirectly by inducing host defense responses (Dann & McLeod, 2020).

Efficient and sustainable management of *P. aphanidermatum* requires an integrated approach that combines and alternates products with distinct modes of action, including chemical and biological agents (Dethoup et al., 2022). Nevertheless, compatibility between these control strategies remains a critical concern. Fungicides such as phenylamides and phosphonates may exert toxic effects on beneficial microorganisms, including *Trichoderma* spp., thereby reducing their biocontrol potential and their ability to induce systemic resistance in host plants (Carro-Huerga et al., 2021; Dethoup et al., 2022).

Species of *Trichoderma* rank among the most extensively studied and widely applied biological control agents, with numerous reports demonstrating their effectiveness against *Pythium* spp. across different crops (Elshahawy & El-Mohamedy, 2019; Liu et al., 2022; Pimentel et al., 2022). In parallel, alternative disease control strategies, including use of phosphites and plant extracts, have gained attention. These agents may act directly by inhibiting mycelial growth and spore production or by disrupting pathogen metabolism through toxic effects (King et al., 2010; Mantil et al., 2015). Additionally, they can act indirectly by stimulating plant defense mechanisms, promoting phytoalexin synthesis, reactive oxygen species production, and antioxidant enzyme activity (Lobato et al., 2010).

Therefore, identifying effective control strategies for diseases caused by *P. aphanidermatum* in coriander remains essential to reduce yield losses. Accordingly, this study aimed to evaluate in vitro and in vivo effects of different products on coriander (*Coriandrum sativum* L.) growth, suppression of *P. aphanidermatum*, and associated morphophysiological plant responses.

Materials and methods

Sources of *Pythium aphanidermatum* and *Trichoderma* spp. isolates

The *Pythium aphanidermatum* isolates (OQ845776 and OQ851471) were obtained from coriander plants exhibiting root rot symptoms in commercial fields located in Vitória da Conquista, Bahia, Brazil (Silva et al., 2024). A voucher specimen was deposited in the Arnaldo Gomes Medeiros Collection at CEPEC/CEPLAC, Ilhéus, Bahia, under registration number 3035 (code 02900). An unidentified *Trichoderma* species, designated *Trichoderma* sp., was isolated from soil samples collected in the same production areas. Identification was based on laboratory observation of hyphal morphology, conidiophores, conidia, and characteristic green colony pigmentation (Samuels, 2006). In addition, an isolate of *Trichoderma harzianum* obtained from a commercial biological product was included in the experiment.

In vitro antagonism of *Trichoderma* spp. against *Pythium aphanidermatum*

In vitro antagonism was evaluated using a paired-culture assay, in which *Trichoderma* sp. and *Trichoderma harzianum* were confronted with an isolate of

P. aphanidermatum. The experiment followed a completely randomized design. Antagonism assays comprised seven technical replicates (plates) per treatment, all prepared from the same parental cultures of the fungal isolates. The entire assay was conducted as a single biological replicate. Control treatments consisted of plates containing a single mycelial disk of *P. aphanidermatum* placed at the center, also with seven technical replicates.

Seven-millimeter-diameter agar disks containing *Trichoderma* sp. or *T. harzianum* were individually placed on one side of a 90-mm Petri dish containing potato dextrose agar (PDA). A disk of equal diameter containing *P. aphanidermatum* was placed on the opposite side to establish paired colonies. All disks were positioned approximately 1.5 cm from the edge of the plate.

Plates were incubated in a BOD growth chamber at 25 °C under a 12-h photoperiod and evaluated twice daily, at 7:00 a.m. and 7:00 p.m., starting from the onset of incubation. Each plate was considered an experimental unit.

Evaluations were conducted in two stages. First, colony diameter of *P. aphanidermatum* was measured in two perpendicular directions previously marked on the underside of the Petri dish using a millimeter ruler, and mean mycelial growth was calculated. Subsequently, percentage inhibition (I) of *P. aphanidermatum* relative to the control was determined using the following equation:

$$I = ((TC)/C) \times 100$$

where:

I percentage of inhibition;

C mycelial growth diameter in the control;

T mycelial growth diameter in the treatment.

Sensitivity of *Pythium aphanidermatum* to commercial products

Potassium phosphite (Phytogard®, Stoller), *Melaleuca alternifolia* extract (Timorex Gold®, STK Bio-Ag Technologies), fosetyl-Al (Aliette®, Bayer), *Bacillus subtilis* (Serenade®, Bayer), and *Lactobacillus plantarum* + *Saccharomyces cerevisiae* (Embiotic®, Korin) were evaluated (Table 1). Products were serially diluted to final concentrations of 1, 10, 100, 500, and 1000 mg L^{-1} in molten potato dextrose agar (PDA) maintained at 45–50 °C. Subsequently, 20 ml of medium containing each product were poured into 90-mm-diameter Petri dishes.

After solidification, a 7-mm-diameter mycelial disk of *Pythium aphanidermatum* grown on PDA was transferred to the center of each plate. Control treatments consisted of PDA plates inoculated with *P. aphanidermatum* without product addition. Plates were incubated in a BOD growth chamber at 25 °C under a 12-h photoperiod for two days, until mycelial growth reached the edge of the plate (9.0 cm diameter).

The experiment followed a completely randomized design with 26 treatments (five products × five concentrations plus a control) and six replicates, with each Petri dish considered an experimental unit. Analytical procedures were identical to those described for the *Trichoderma* spp. antagonism assay.

Table 1 Products evaluated in the in vitro bioassay for control of *Pythium aphanidermatum* in coriander

Active ingredient (ai)	Class	Formulation type	ai concentration
Potassium phosphite	_	Concentrated suspension	298 g/L
Fosetyl-Al	Systemic fungicide	Wettable powder	800 g/kg
Bacillus subtilis	Microbiological bactericidal fungicide	Concentrated Suspension	13.68 g/L
Lactobacillus plantarum + *Saccharomyces cerevisiae*	_	Homogeneous suspension	10^4 CFU/mL + 10^3 UFC/mL
Melaleuca alternifolia extract	Fungicide and bactericide with contact and mesostemic action	Emulsifiable Concentrate	222.50 g/L

In vivo effect of *Trichoderma* spp. and commercial products on control of *Pythium aphanidermatum* in coriander

The experiment was conducted using one coriander cultivar ('Verdão') in a randomized block design with eight treatments and four replicates. Treatments consisted of: C, control inoculated with *Pythium aphanidermatum* without product application; F, potassium phosphite; EM, *Melaleuca alternifolia* extract; FA, fosetyl-Al; BS, *Bacillus subtilis*; LS, *Lactobacillus plantarum* + *Saccharomyces cerevisiae*; T, *Trichoderma* sp.; and TH, *Trichoderma harzianum*.

Inoculum of *P. aphanidermatum* was prepared from cultures grown on potato dextrose agar (PDA) at 25 °C. Mycelium was scraped from culture plates with distilled water and filtered through an autoclaved nonwoven fabric filter (20 g m^{-2}). The resulting suspension was diluted to a final concentration of 1×10^5 zoospores ml^{-1}, determined using a Neubauer counting chamber (Alfenas & Mafia, 2016). Subsequently, 50 ml of the inoculum suspension were applied to each container.

Suspensions of *Trichoderma* sp. and *T. harzianum* were prepared from cultures grown on PDA at 25 °C and adjusted to a concentration of 1×10^8 spores ml^{-1}, as determined using a Neubauer chamber (Alfenas & Mafia, 2016).

Throughout the experiment, soil was sterilized by autoclaving at 120 °C for 1 h at 1.5 atm on two consecutive cycles, with a 24-h interval between sterilizations. Sterilized soil was then placed in pots with a capacity of 2 dm^3, and 100 ml of the respective product solution were applied. After 24 h, *P. aphanidermatum* was inoculated using a suspension containing 1×10^5 zoospores ml^{-1}. On the following day, 50 coriander seeds were sown per pot. Product applications were repeated at seven-day intervals until the end of the crop cycle.

Morphophysiological evaluations

Seedling emergence, post-emergence damping-off, and disease incidence were monitored throughout the experiment.

Emergence (EME): Seedling emergence was expressed as the percentage of seedlings emerged relative to the number of seeds sown per plot and calculated using the following equation:

$$\text{EME} = (\text{Number of seedlings emerged in the treatment} \times 100)/\text{Number of seeds sown}$$

Post-emergence damping-off (PDO): Post-emergence damping-off was determined as the percentage of plants that collapsed relative to the number of seedlings emerged per plot, according to the following equation:

$$\text{PDO} = (\text{Number of plants collapsed in the treatment} \times 100)/\text{Number of seedlings emerged}$$

Incidence (INC): Disease incidence was calculated as the percentage of plants exhibiting symptoms such as damping-off, root rot, or stem rot relative to the number of plants emerged per plot, using the following equation:

$$\text{INC} = (\text{Number of plants with symptoms in the treatment} \times 100)/\text{Number of plants emerged}$$

At the end of the experiment (35 days after sowing), the following morphophysiological analyses were performed:

Leaf gas exchange: Measurements were made in fully expanded leaves using a portable photosynthesis system (LI-6400 XT; LI-COR Biosciences Inc., Nebraska, USA). Net photosynthetic rate (A), stomatal conductance (g_s), transpiration rate (E), and the intercellular-to-ambient CO_2 ratio (Ci/Ca) were recorded between 8:30 and 11:30 a.m. under saturating artificial light of 1000 µmol photons m^{-2} s^{-1} and an ambient CO_2 concentration (Ca) of approximately 390 µmol mol^{-1}.

Extraction and quantification of chlorophylls and carotenoids: Three 6-mm-diameter leaf disks were excised from fully expanded leaves and placed in light-protected tubes containing 4 ml of 80% (v/v) acetone. Samples were stored for 36 h to allow

extraction of chlorophyll a, chlorophyll b, and carotenoids (Hiscox & Israelstam, 1979). Pigment concentrations were determined by spectrophotometric readings at 480, 646.8, and 663.8 nm, following the method described by Wellburn (1994).

Biometric properties: Plant height (cm) was measured from the stem base to the insertion point of the youngest expanding leaf. Root length (cm) was measured from the stem insertion point to the root apex. Measurements were obtained using a graduated ruler.

Fresh mass of shoots and roots: Shoots were separated from roots at the stem insertion point and weighed separately using a precision scale with four decimal places.

Data were subjected to analysis of variance, and treatment means were compared using the Scott–Knott test at a 5% significance level. Statistical analyses were performed using SISVAR version 5.6 (Ferreira, 2014).

Results

In vitro inhibition of mycelial growth of *Pythium aphanidermatum*

Paired culture with *Trichoderma* sp. and *Trichoderma harzianum* exerted a clear antagonistic effect on mycelial growth of *Pythium aphanidermatum* isolate (Fig. 1). Mycelial growth inhibition reached 63.33% in the presence of *Trichoderma* sp. and 35.11% with *T. harzianum,* respectively.

Mycelial growth was reduced in the presence of all commercial products, regardless of the active ingredient. However, sensitivity varied among products (Table 2). At a concentration of 1 mg L^{-1}, all

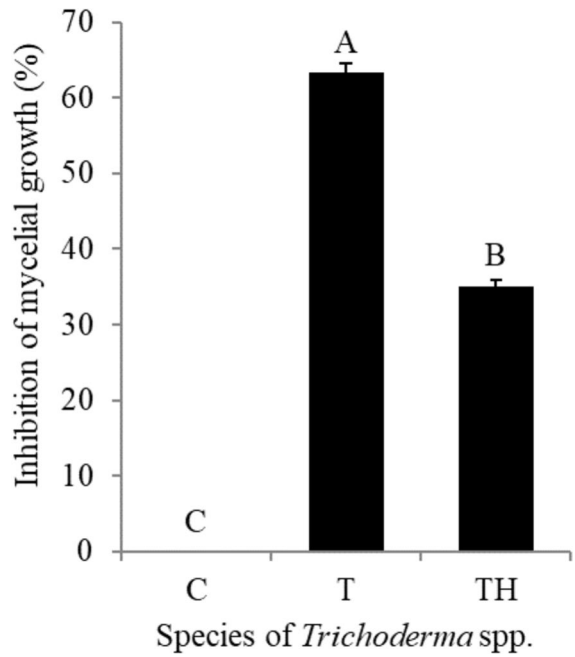


Fig. 1 Antagonistic effect of *Trichoderma* spp. on *Pythium aphanidermatum* isolate in PDA culture medium. C- Control, T- *Trichoderma* sp., TH- *Trichoderma harzianum.* Means followed by the same letter do not differ significantly according to the Scott–Knott test ($p < 0.01$)

Table 2 Inhibition of *Pythium aphanidermatum* mycelial growth by different products at varying concentrations

Product	Concentration (mg L^{-1})					
	0	1	10	100	500	1000
Potassium phosphite	9.0(0.0)*Aa**	9.0(0.0)Aa	9.0(0.0)Aa	6.7(25.7)Bb	3.3(63.2)Dc	2.4(73.7)Cd
Fosetyl-Al	9.0(0.0)Aa	9.0(0.0)Aa	8.9(1.6)Aa	6.2(30.6)Cb	4.5(50.5)Cc	0.8(91.1)Dd
Lactobacillus plantarum + *Saccharomyces cerevisiae*	9.0(0.0)Aa	9.0(0.0)Aa	9.0(0.0)Aa	9.0(0.0)Aa	9.0(0.0)Aa	5.6(37.8)Ab
Bacillus subtilis	9.0(0.0)Aa	8.6(4.8)Ab	4.6(49.2)Bc	2.8(69.0)Dd	0.7(92.2)Ee	0.7(92.2)De
Melaleuca alternifolia extract	9.0(0.0)Aa	9.0(0.0)Aa	9.0(0.0)Aa	8.9(1.6)Aa	5.0(44.3)Bb	3.1(65.3)Bc
CV%	5.73					

* Radial growth (in cm) after 2 days of incubation. Values in parentheses indicate the percentage inhibition of mycelial growth relative to the control

** Means followed by the same lowercase letter within rows and uppercase letter within columns do not differ significantly according to the Scott–Knott test at the 5% probability level

treatments showed low inhibitory activity against mycelial growth of *P. aphanidermatum*. Inhibition was first observed at 10 mg L^{-1} for *Bacillus subtilis*, 100 mg L^{-1} for potassium phosphite and fosetyl-Al, 500 mg L^{-1} for *Melaleuca alternifolia* extract, and 1000 mg L^{-1} for *Lactobacillus plantarum* + *Saccharomyces cerevisiae*.

For the sensitivity assay, regression analyses were performed separately for each product, and the corresponding coefficients of determination and polynomial equations were determined. Significant differences were observed among products in the relationship between concentration and mycelial growth. Increasing product concentrations resulted in a progressive reduction in mycelial growth of *Pythium aphanidermatum* (Fig. 2).

Effect of products on control of *Pythium aphanidermatum* in coriander plants

Higher seedling emergence was observed following application of fosetyl-Al and *Melaleuca alternifolia* extract, with rates of 68% and 64.5%, respectively.

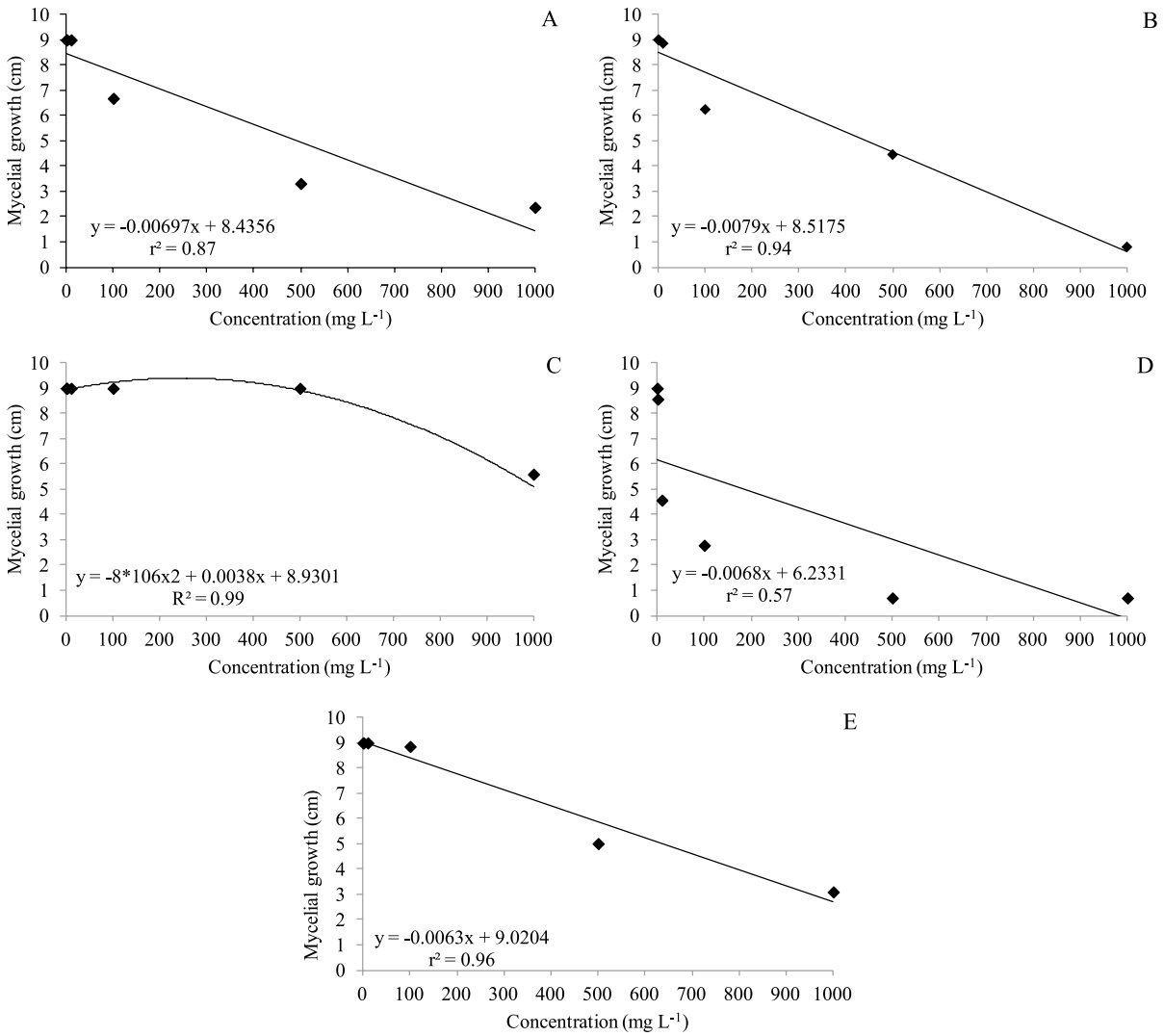


Fig. 2 Effect of different product concentrations on inhibition of mycelial growth of *Pythium aphanidermatum.* (**A**) Potassium phosphite, (**B**) fosetyl-Al, (**C**) *Lactobacillus plantarum* + *Saccharomyces cerevisiae*, (**D**) *Bacillus subtilis*, and (**E**) *Melaleuca alternifolia* extract. Statistical analysis at 5% probability

Both treatments increased emergence by approximately 30% compared to the control (Fig. 3).

Higher post-emergence damping-off was observed in the control, *Trichoderma harzianum*, and potassium phosphite treatments, with values of 58.91%, 54.70%, and 50.37%, respectively. In contrast, the remaining treatments reduced the number of collapsed plants (Figs.4 and 5).

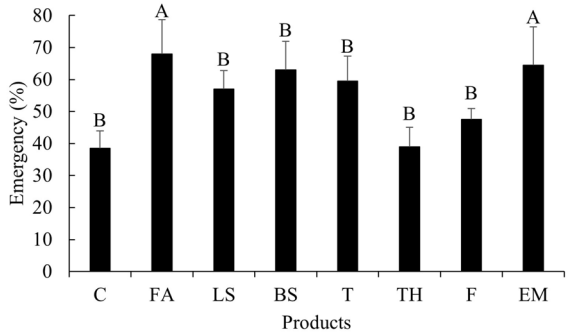


Fig. 3 Emergence of coriander seedlings as a function of different products and species of *Trichoderma*. (C) Control, (FA) fosetyl-Al, (LS) *Lactobacillus plantarum*+*Saccharomyces cerevisiae*, (BS) *Bacillus subtilis*, (T) *Trichoderma* sp., (TH) *Trichoderma harzianum*, (F) potassium phosphite, and (EM) *Melaleuca alternifolia* extract. Bars represent the standard error of the mean (n = 4). Means followed by the same letter do not differ significantly according to the Scott–Knott test ($p < 0.05$)

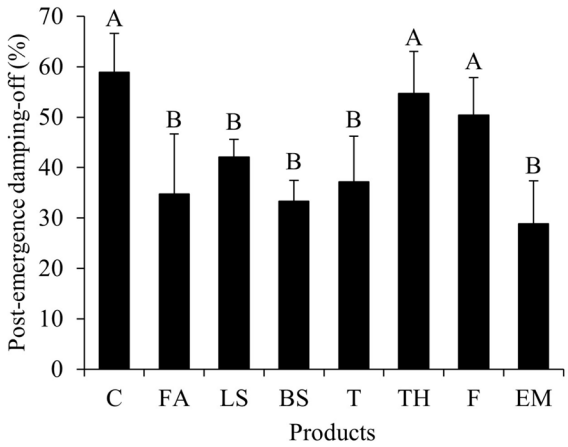


Fig. 4 Post-emergence damping-off in coriander plants exposed to different products and *Trichoderma* species. (C) Control, (FA) fosetyl-Al, (LS) *Lactobacillus plantarum*+*Saccharomyces cerevisiae*, (BS) *Bacillus subtilis*, (T) *Trichoderma* sp., (TH) *Trichoderma harzianum*, (F) potassium phosphite, and (EM) *Melaleuca alternifolia* extract. Bars represent the standard error of the mean (n = 4). Means followed by the same letter do not differ significantly according to the Scott–Knott test ($p < 0.05$)

No significant differences in disease incidence among treatments. Nevertheless, *Melaleuca alternifolia* extract and *Bacillus subtilis* reduced incidence by 26.33% and 25.54%, respectively, compared to the control (Fig. 6).

Application of *Bacillus subtilis* and *Melaleuca alternifolia* extract promoted greater plant height and root system development (Fig. 7).

Significant differences were observed in shoot and root fresh mass among treatments. Application of *Bacillus subtilis* and *Melaleuca alternifolia* extract increased shoot fresh mass by 477.10% and 428.61% and root fresh mass by 404.17% and 398.21%, respectively, compared with the control (Fig. 8).

Significant differences were observed in photosynthetic pigment levels among treatments (Fig. 9). Treatments with *Trichoderma* sp., *Trichoderma harzianum*, and potassium phosphite showed lower total chlorophyll contents than the remaining treatments (Fig. 9a). In contrast, carotenoid content was reduced only under potassium phosphite application when compared with the other treatments (Fig. 9b).

Significant differences were observed in leaf gas exchange parameters among treatments (Fig. 10). Plants treated with *Melaleuca alternifolia* extract, *Bacillus subtilis*, and *Trichoderma harzianum* exhibited higher photosynthetic rates than those receiving the remaining treatments. In addition, treatments with *Lactobacillus plantarum*+*Saccharomyces cerevisiae*, fosetyl-Al, and *Trichoderma* sp. showed higher photosynthetic rates than the control and potassium phosphite treatments (Fig. 10a).

Lower stomatal conductance values of 0.10, 0.12, and 0.16 mol m^{-2} s^{-1} were recorded in control plants and in plants treated with *Trichoderma* sp. and potassium phosphite, respectively (Fig. 10b). The highest transpiration rates were observed under application of *Melaleuca alternifolia* extract, *T. harzianum*, *B. subtilis*, and *Lactobacillus plantarum*+*S. cerevisiae*, with values of 3.96, 3.39, 2.97, and 2.64 mmol H_2O m^{-2} s^{-1}, respectively (Fig. 10c). Moreover, the highest Ci/Ca ratio was detected in plants treated with potassium phosphite, whereas the lowest value was observed under *Trichoderma* sp. treatment (Fig. 10d).

Discussion

The control strategies evaluated in this study included biological agents with antagonistic activity and chemical products based on different active ingredients.

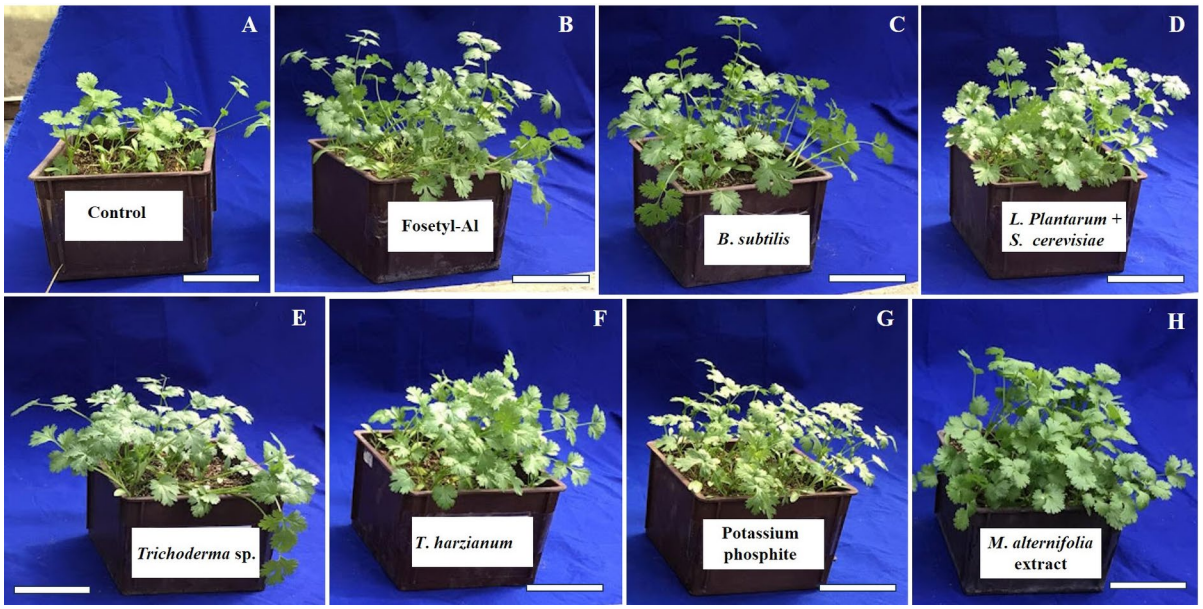


Fig. 5 Effect of different treatments on growth of coriander plants (*Coriandrum sativum*) inoculated with *Pythium aphanidermatum*. (C) Control, (FA) Fosetyl-Al, (LS) *Lactobacillus plantarum* + *Saccharomyces cerevisiae*, (BS) *Bacillus subtilis*, (T) *Trichoderma* sp., (TH) *Trichoderma harzianum*, (F) Potassium phosphite, and (EM) *Melaleuca alternifolia* extract

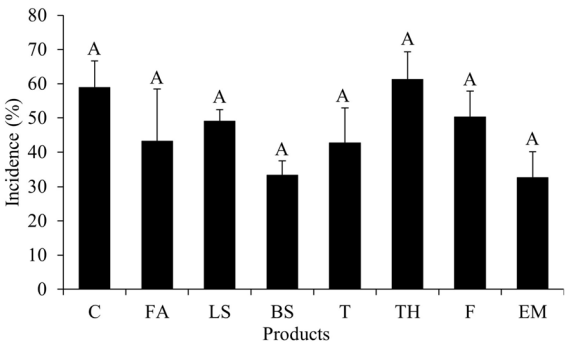


Fig. 6 Disease incidence in coriander plants treated with different products and *Trichoderma* species. (C) Control, (FA) fosetyl-Al, (LS) *Lactobacillus plantarum* + *Saccharomyces cerevisiae*, (BS) *Bacillus subtilis*, (T) *Trichoderma* sp., (TH) *Trichoderma harzianum*, (F) potassium phosphite, and (EM) *Melaleuca alternifolia* extract. Bars represent the standard error of the mean (n = 4). Means followed by the same letter do not differ significantly according to the Scott–Knott test ($p < 0.05$)

Under in vitro conditions, *Bacillus subtilis* and fosetyl-Al exhibited the greatest inhibitory effects. In vivo, treatments with fosetyl-Al, *Lactobacillus plantarum* + *Saccharomyces cerevisiae*, *Bacillus subtilis*, *Trichoderma* sp., and *Melaleuca alternifolia* extract significantly reduced post-emergence damping-off. Moreover, application of *Bacillus subtilis* and *Melaleuca alternifolia* extract enhanced leaf gas exchange, resulting in increased shoot and root growth in coriander plants.

Inhibition of *Pythium aphanidermatum* mycelial growth by up to 63.33% in treatments with *Trichoderma* species may be attributed to antibiosis and competitive interactions. Mycoparasitism, involving penetration and infection of the pathogen, likely contributed to antagonism through competition for space and nutrients (Stange et al., 2024). Supporting this interpretation, in vitro assays have shown that isolates of *Trichoderma harzianum*, *Trichoderma asperellum*, and *Trichoderma virens* suppress mycelial growth of *P. aphanidermatum* (Elshahawy & El-Mohamedy, 2019). Additional inhibitory mechanisms involve production of antifungal compounds (Tchameni et al., 2020). Volatile and nonvolatile metabolites produced by *T. harzianum* inhibited 65.6% and 69.3% of *Pythium ultimum* mycelial growth, respectively (Boat et al., 2019). However, metabolite production and fungitoxic activity may vary among species and even among isolates within the same species (Martins and Melo, 1998).

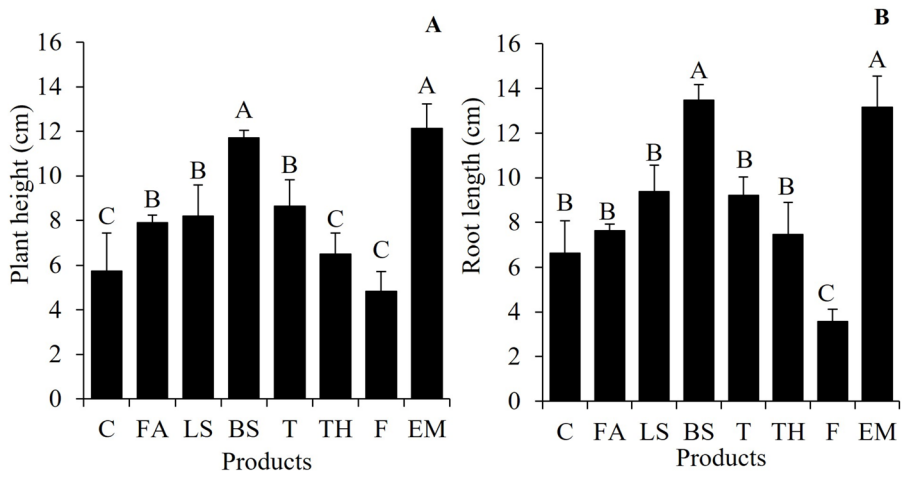


Fig. 7 Plant height (**A**) and root length (**B**) of coriander plants treated with different products and *Trichoderma* species. (**C**) Control, (FA) fosetyl-Al, (LS) *Lactobacillus plantarum* + *Saccharomyces cerevisiae*, (BS) *Bacillus subtilis*, (T) *Trichoderma* sp., (TH) *Trichoderma harzianum*, (F) potassium phosphite, and (EM) *Melaleuca alternifolia* extract. Bars represent the standard error of the mean (n = 4). Means followed by the same letter do not differ significantly according to the Scott–Knott test ($p < 0.05$)

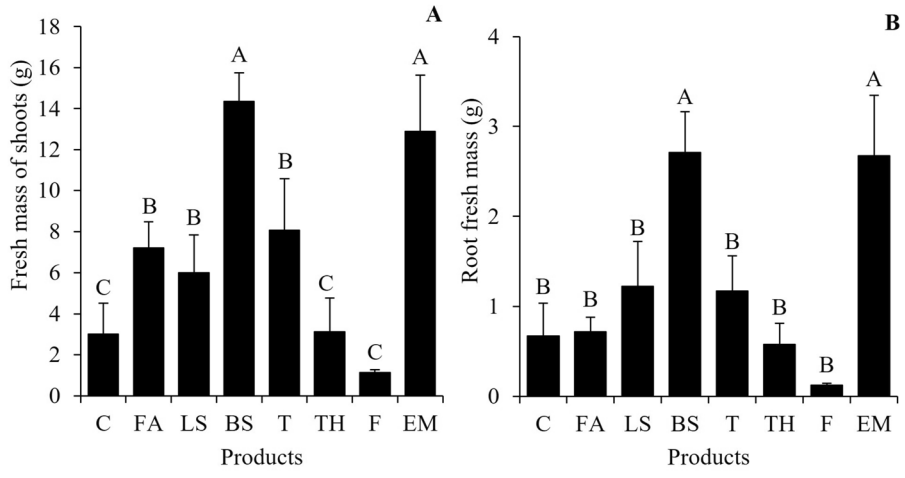


Fig. 8 Shoot (**A**) and root (**B**) fresh masses of coriander plants (cv. Verdão). (C) Control, (FA) fosetyl-Al, (LS) *Lactobacillus plantarum* + *Saccharomyces cerevisiae*, (BS) *Bacillus subtilis*, (T) *Trichoderma* sp., (TH) *Trichoderma harzianum*, (F) potassium phosphite, and (EM) *Melaleuca alternifolia* extract. Bars represent the standard error of the mean (n = 4). Means followed by the same letter do not differ significantly according to the Scott–Knott test ($p < 0.05$)

Seed treatment with *Trichoderma* species has also been shown to protect soybean seedlings against *Pythium* spp., resulting in plant stand and vigor increases of 15–20% compared with untreated controls. In vitro observations further indicate that mycoparasitism represents a key mechanism of antagonism against the Pythium species tested (Pimentel et al., 2022).

Species of *Trichoderma* are widely recognized for establishing mutualistic associations with plants, promoting growth and enhancing resistance to pathogens (Khan et al., 2023). Growth promotion is mediated by modulation of phytohormone signaling pathways and improved nutrient uptake and bioavailability in soil. In addition, root colonization by *Trichoderma* spp. can activate plant defense responses, characterizing

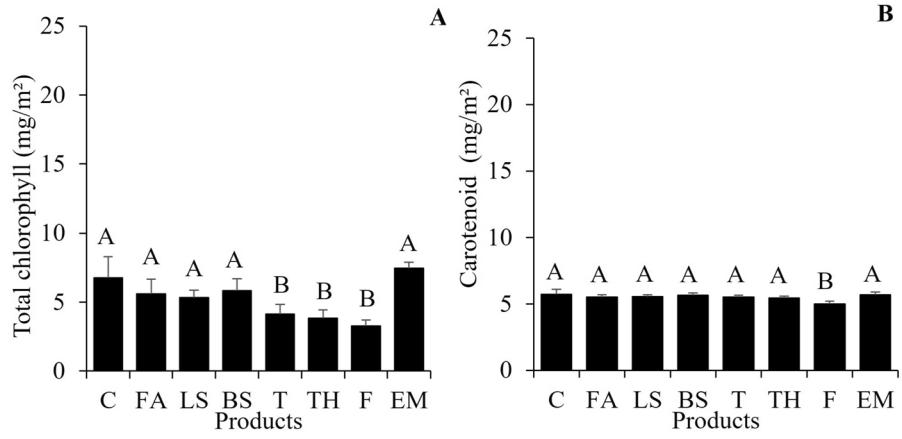


Fig. 9 Total chlorophyll (**A**) and carotenoid (**B**) contents in coriander leaves treated with different products and *Trichoderma* species. (C) Control, (FA) fosetyl-Al, (LS) *Lactobacillus plantarum* + *Saccharomyces cerevisiae*, (BS) *Bacillus subtilis*, (T) *Trichoderma* sp., (TH) *Trichoderma harzianum*, (F) potassium phosphite, and (EM) *Melaleuca alternifolia* extract. Bars represent the standard error of the mean (n = 4). Means followed by the same letter do not differ significantly according to the Scott–Knott test ($p < 0.05$)

induced systemic resistance (Martínez-Medina et al., 2017).

Several studies demonstrate that *Trichoderma* acts as a modulator of plant hormonal signaling networks involved in resistance induction. For example, a novel strain of *T. longibrachiatum* H9 promoted growth and reduced gray mold severity in cucumber by activating genes and proteins associated with salicylic acid (SA) and jasmonic acid (JA) synthesis and signaling (Yuan et al., 2019). Similarly, *Trichoderma* colonization in tomato plants induced resistance to the root-knot nematode *Meloidogyne incognita* by priming SA- and JA-dependent defense pathways (Martínez-Medina et al., 2017). This dynamic hormonal modulation, which adapts to different stages of parasitism, highlights the integral role of *Trichoderma* in plant immunity.

Phosphite compounds derived from potassium, manganese, or copper have also demonstrated high efficacy against *Pythium* spp., inhibiting up to 100% of mycelial growth at certain concentrations (Santos et al., 2018). However, such inhibition generally occurs at concentrations of approximately 100 mg L^{-1}, indicating that potassium phosphite efficacy is associated with phosphorous acid formation. Phosphorous acid exhibits direct fungicidal activity and can activate plant defense mechanisms, including phytoalexin production (Reuveni, 1997). Similarly, fosetyl-Al, a member of the phosphonate group, exerts its activity through phosphorous acid production. This capacity to suppress mycelial growth is particularly relevant for reducing disease severity after infection has occurred (Matheron & Porchas, 2000).

The ability of *Bacillus subtilis* to inhibit mycelial growth by up to 92.2% can be attributed to its fungitoxic activity mediated by multiple modes of action. Its antagonistic effects are largely associated with production of secondary metabolites with antibiotic properties that play a central role in activating plant defense mechanisms, triggering induced systemic resistance (ISR) and host defense responses (Kai, 2020; Kiesewalter et al., 2021; Zalila-Kolsi et al., 2016). In addition, lipopeptides produced by *B. subtilis* disrupt fungal cell membranes, particularly in reproductive structures, leading to membrane deformation and rupture and, consequently, effective inhibition of mycelial growth (Silveira et al., 2020).

The capacity of *B. subtilis* to suppress mycelial growth of *P. aphanidermatum* and promote plant growth is linked to its function as a plant growth–promoting rhizobacterium operating through multiple mechanisms, as demonstrated by both in vitro and in vivo assays. Antagonistic activity of *B. subtilis* against *P. aphanidermatum* has been reported in vitro in common beans, with growth inhibition reaching 67.95%, primarily attributed to production of volatile compounds, twenty of which were identified (Rashad et al., 2024).

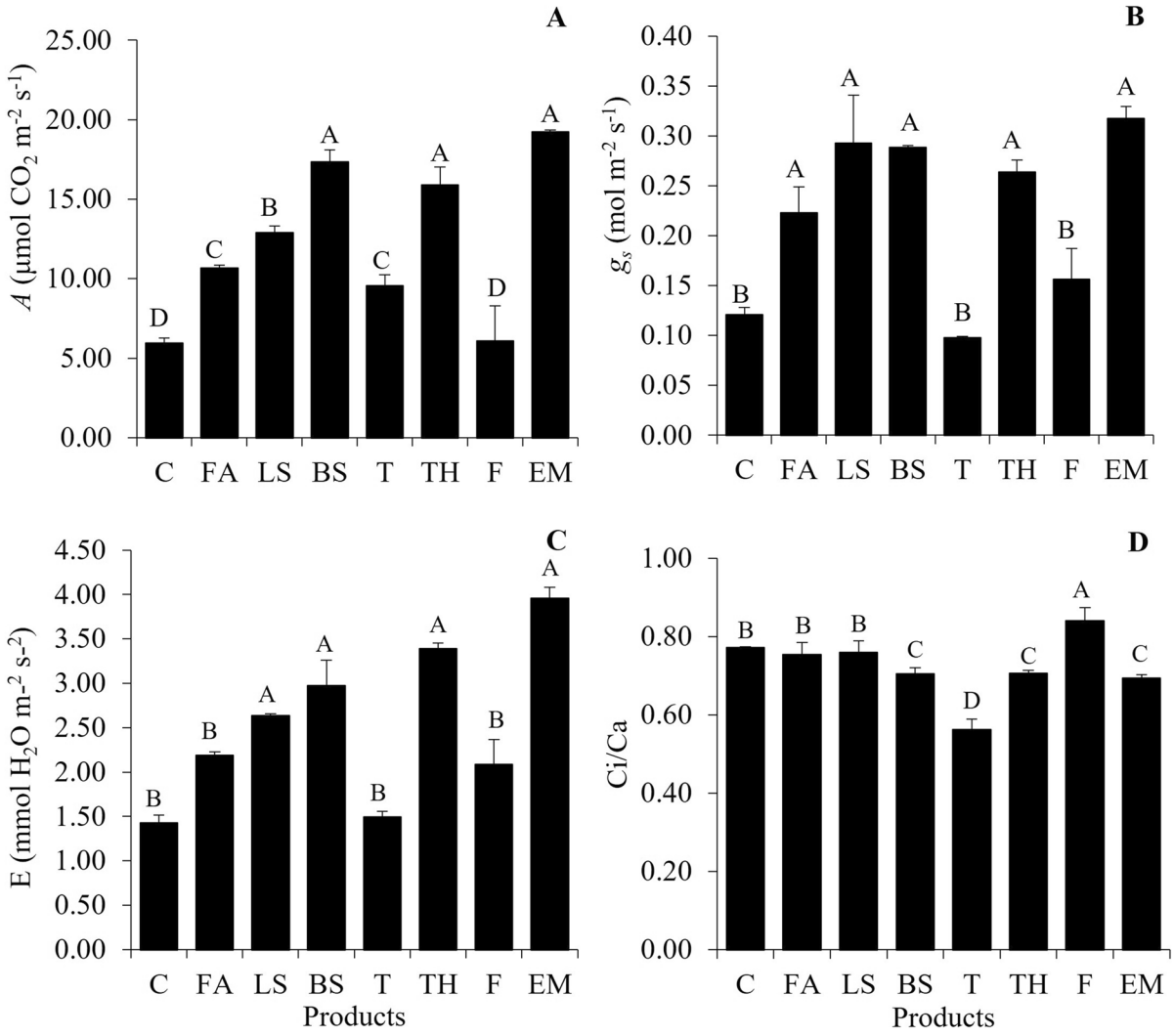


Fig. 10 Leaf gas exchange parameters of coriander plants: (**A**) Photosynthetic rate (*A*), (**B**) stomatal conductance (g_s), (**C**) transpiration (*E*), and (**D**) Ci/Ca ratio of coriander plants. (**C**) Control, (FA) fosetyl-Al, (LS) *Lactobacillus plantarum* + *Saccharomyces cerevisiae*, (BS) *Bacillus subtilis*, (T) *Trichoderma* sp., (TH) *Trichoderma harzianum*, (F) potassium phosphite, and (EM) *Melaleuca alternifolia* extract. Bars represent the standard error of the mean (n = 4). Means followed by the same letter do not differ significantly according to the Scott–Knott test ($p < 0.05$)

Beyond direct pathogen control, Ali et al. (2025) found that application of *Bacillus* species demonstrated potential to mitigate damping-off and enhance plant growth dynamics. Samaras et al. (2021) also noted that *B. subtilis* application significantly increased tomato shoot and root length and was associated with transcriptional activation of auxin-related genes in the host plant. Additional physiological benefits include increased photosynthetic pigment content, enhanced antioxidant enzyme activity, elevated phenolic compound levels, and improved macronutrient accumulation (Ali et al., 2025). Similar responses have been reported in common bean, in which *B. subtilis* application increased shoot height, root length, shoot biomass accumulation, and dry matter content, resulting in higher productivity (Rashad et al., 2024).

The in vivo efficacy of *B. subtilis* against soilborne pathogens such as *Pythium* spp. is further supported by its ability to induce systemic resistance. In tomato plants, *B. subtilis* triggered transcriptional activation

of defense-related genes, including PR-1A and GLUA associated with salicylic acid (SA) signaling, and CHI3, LOXD, and PAL associated with jasmonic acid and ethylene (JA/ET) pathways (Samaras et al., 2021). In common bean infected with *P. aphanidermatum*, *B. subtilis* application enhanced expression of defense genes such as JERF3, GLU, and PR1, while also increasing peroxidase (POD) and polyphenol oxidase (PPO) activity and total phenolic content (Rashad et al., 2024).

This coordinated activation of defense pathways suggests a synergistic response against pathogen infection (Rashad et al., 2024). Root colonization capacity, demonstrated in vivo for *B. subtilis* (Samaras et al., 2021), is critical for sustained induction of systemic resistance and contributes to effective disease suppression, as well as improvements in physiological traits such as increased chlorophyll, carotenoid, and total pigment contents (Ali et al., 2025; Rashad et al., 2024).

Melaleuca alternifolia extract inhibited mycelial growth by 65.3%, an effect likely associated with its antimicrobial properties. Hydrophobic terpene compounds present in the extract interact strongly with microbial membrane lipids, altering membrane permeability and leading to cell death (Cox et al., 2001; Yu et al., 2015). In addition, *M. alternifolia* extract has been reported to induce morphological alterations in mycelia and to inhibit cellular respiration and spore germination (Reuveni & Cohen, 2020). The primary antifungal constituents of *M. alternifolia* extract include terpinen-4-ol, α-terpineol, terpinolene, and 1,8-cineole (Zalila-Kolsi et al., 2016).

Low seedling emergence may be associated with the ability of *Pythium* spp. to induce pre-emergence damping-off. In pepper and eggplant seedlings inoculated with *P. aphanidermatum*, pre-emergence damping-off rates of up to 30.3% and 34.5%, respectively, have been reported because of root system damage (Muthukumar et al., 2010; Subharathinam et al., 2020). In contrast, in cucumber plants inoculated with *P. ultimum*, potassium phosphite application reduced damping-off severity and increased shoot and root fresh and dry mass accumulation (Mofidnakhaei et al., 2016). These beneficial effects intensified with increasing phosphite concentrations. Therefore, the limited effectiveness of potassium phosphite in controlling damping-off caused by *P. aphanidermatum* in the present study may be related to the applied dose. Conversely, fosetyl-Al, Bacillus subtilis, *Lactobacillus plantarum* + *Saccharomyces cerevisiae*, *Trichoderma* sp., and *Melaleuca alternifolia* extract effectively reduced damping-off caused by P. aphanidermatum.

Although treatment with *Trichoderma harzianum* did not reduce *P. aphanidermatum* incidence or seedling damping-off in this study, previous research has demonstrated that microorganisms belonging to this genus can suppress diseases caused by oomycetes (Liu et al., 2022). In turmeric plants, for example, an isolate of *T. harzianum* (TharDOB-31) significantly reduced rhizome rot and leaf blight caused by *P. aphanidermatum*, resulting in increased productivity relative to untreated controls (Vinayarani & Prakash, 2018). In that study, parasitic activity was also observed, with hyphal wrinkling, breakage, and lysis of the pathogen.

Variation in the performance of microbial treatments may be associated with differences in their capacity to colonize plant tissues. Faster and more efficient colonization increases the likelihood of successful pathogen suppression (Lara-Capistran et al., 2020), likely because beneficial microorganisms must establish within the agroecosystem before exerting effective control.

Application of *Melaleuca alternifolia* extract resulted in a 98.57% increase in root growth compared with the control. This response is agronomically relevant, as enhanced vertical and lateral root development expands the rhizosphere volume, improving water and nutrient uptake and supporting overall plant growth. The positive effects of *M. alternifolia* extract can be attributed to its fungicidal and bactericidal activity through contact and mesostemic action (Arroyo and Henriquez, 2015). Its mode of action involves disruption of membrane integrity, strongly affecting both plasma and mitochondrial membranes (Carson et al., 2006; Shao et al., 2013). In addition, inhibition of cellular respiration has been reported, likely due to direct interference with respiratory enzymes (Cox et al., 2001). In contrast, the more limited increase in root length observed with potassium phosphite may be related to phytotoxic effects at higher application rates, which can restrict plant growth (Achary et al., 2017).

The greater shoot height and fresh mass observed in treatments with *Bacillus subtilis* and *Melaleuca alternifolia* extract are likely associated with effective

suppression of *P. aphanidermatum* and reduced damage to the root system. By enhancing root length and biomass, these treatments improve water and nutrient absorption, which ultimately promotes greater vegetative growth.

Total chlorophyll levels were lowest in treatments with *Trichoderma* sp., *Trichoderma harzianum*, and potassium phosphite, while carotenoid content was lowest under potassium phosphite application. Photosynthetic pigments play a vital role in photosynthesis, as they participate in ATP and NADPH production and carbohydrate synthesis, which support formation of primary metabolites and defense-related hormones such as abscisic acid and ethylene (Lu & Yao, 2018). Adequate pigment concentrations are therefore essential not only for sustaining photosynthesis but also for maintaining plasma membrane integrity (Matsuda et al., 2004).

Reductions in photosynthetic pigment levels have been widely reported in plants challenged by pathogens (El-Sayed et al., 2023; Siddiqui et al., 2021). Such reductions may be associated with increased activity of degradative enzymes, including chlorophyllase, induced during pathogen infection (Javaid et al., 2017).

Photosynthetic rates were lowest in control plants and those treated with potassium phosphite, reaching 5.96 and 6.10 µmol CO_2 m^{-2} s^{-1}, respectively. In general, reduced photosynthetic rates were preceded by lower stomatal conductance and appear to be associated with altered CO_2 assimilation, as Ci/Ca ratios were higher than those observed in treatments with greater photosynthetic activity. Conversely, the negative effects of *Trichoderma* sp. on gas exchange may be attributed to restricted CO_2 influx resulting from stomatal closure, which reduced both Ci/Ca ratio and photosynthetic rate.

Reductions in photosynthetic rate in plants affected by soilborne pathogens have been reported in several studies, including plants infected with *Phytophthora citricola, Fusarium oxysporum* and *Sclerotium rolfsii* (Chowdhury et al., 2023; Du et al., 2022; Fleischmann et al., 2005). By colonizing the root system, these pathogens reduce water transport to the leaves, thereby interfering with photosynthetic metabolism and, consequently, plant growth (Silva et al., 2018). However, the present data indicate that coriander plants may maintain relatively high photosynthetic rates even during *Pythium* infection. In maize, increases in photosynthetic rate and plant growth following inoculation with *Trichoderma harzianum* have been attributed to upregulation of photosynthetic processes and enhanced starch accumulation resulting from root colonization by *Trichoderma* (Harman and Shoresh, 2007). In the present study, although application of *T. harzianum* increased photosynthetic rate in coriander plants, it did not promote plant growth, which may be explained by its limited efficiency in controlling *Pythium aphanidermatum.*

Reduction in stomatal conductance in plants infected with *Pythium aphanidermatum* may result from root system damage caused by the pathogen, which limits water uptake by roots and reduces leaf water content, ultimately leading to stomatal closure and leaf wilting (Ray, 2024). In contrast, plants treated with fosetyl-Al, *Lactobacillus plantarum*+*Saccharomyces cerevisiae*, *Bacillus subtilis*, *Trichoderma harzianum*, or *Melaleuca alternifolia* extract exhibited significantly higher stomatal conductance and transpiration than the control inoculated only with *P. aphanidermatum*. These results indicate that these treatments enhance photosynthetic efficiency in plants under *P. aphanidermatum* infection by facilitating assimilation of photosynthetic carbon.

Transpiration is a key process in plant water balance; however, excessive transpiration can compromise water availability for essential physiological processes, particularly under limited soil moisture. To prevent water loss, plants regulate transpiration primarily through stomatal closure, thereby reducing transpiration rates (Von Caemmerer & Baker, 2007).

Enhanced gas exchange observed following application of *Bacillus subtilis* and *Melaleuca alternifolia* extract is likely related to stimulation of root and shoot growth, which increases water uptake and light interception. Under potassium phosphite application, the Ci/Ca ratio was reduced as a consequence of lower stomatal conductance, which restricted CO_2 influx and decreased its intracellular concentration.

Conclusions

Bacillus subtilis and fosetyl-Al exhibited the highest inhibition of *Pythium aphanidermatum* mycelial growth under in vitro conditions, while *Trichoderma* sp. showed greater inhibitory activity than *Trichoderma harzianum*.

The lowest levels of post-emergence damping-off were observed in treatments with fosetyl-Al, *Lactobacillus plantarum* + *Saccharomyces cerevisiae*, *Bacillus subtilis*, *Trichoderma* sp., and *Melaleuca alternifolia* extract.

Finally, application of *Bacillus subtilis* and *Melaleuca alternifolia* extract enhanced gas exchange in coriander plants, resulting in increased shoot and root growth.

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Authors' contribution All authors contributed to the study conception and design.

Conceptualization: Eveline Mendes da Silva, Quelmo Silva de Novaes, Poliana Prates de Souza Soares, Naasoom Luiz Santos Mesquita, Leandro Dias da Silva, Natália Deniz Brito, Armínio Santos, Rafael José Vilela de Oliveira.

Experimentation: Eveline Mendes da Silva, Poliana Prates de Souza Soares, Natália Deniz Brito, Naasoom Luiz Santos Mesquita.

Data analysis: Eveline Mendes da Silva, Quelmo Silva de Novaes, Leandro Dias da Silva.

Preparation of the manuscript draft: Eveline Mendes da Silva, Quelmo Silva de Novaes, Poliana Prates de Souza Soares, Leandro Dias da Silva, Rafael José Vilela de Oliveira.

Proofreading and Editing: Eveline Mendes da Silva, Poliana Prates de Souza Soares, Quelmo Silva de Novaes, Leandro Dias da Silva.

Approved the version to be published: Eveline Mendes da Silva, Quelmo Silva de Novaes, Poliana Prates de Souza Soares, Natália Deniz Brito, Naasoom Luiz Santos Mesquita, Leandro Dias da Silva, Armínio Santos, Rafael José Vilela de Oliveira.

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Declarations

Conflicts of interest The authors declare no conflicts of interest.

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