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Review

Towards effective biocontrol of Phytophthora root rot in annual crops: A meta-analysis

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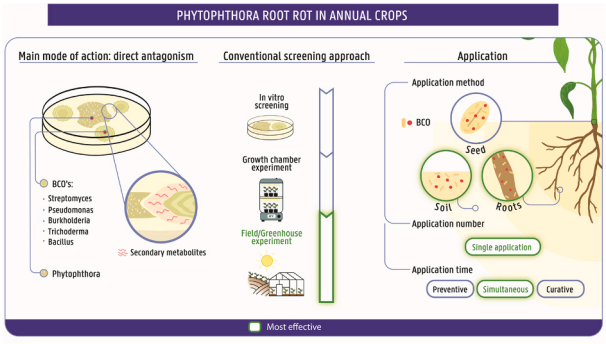
HIGHLIGHTS

- Meta-analysis reveals focus on biocontrol organisms in *Phytophthora capsici*/pepper.
- Diverse biocontrol organism genera reduce *Phytophthora* root rot effectively.
- Biocontrol organisms exhibit activity mainly through direct antagonism.
- Simultaneous BCO application outperforms preventive and curative treatments.
- Multivariate analysis links root/soil biocontrol organism treatments to best efficacy.

GRAPHICAL ABSTRACT



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ABSTRACT

Phytophthora comprise the most destructive plant pathogens, affecting over 1,000 plant species and causing severe diseases such as root rot. Traditional chemical control methods may pose environmental risks and can contribute to resistance development, making alternative strategies such as the implementation of biological control organisms (BCOs) essential. This study presents a meta-analysis evaluating factors that influence the success of BCOs against Phytophthora root rot in annual crops. Systematic data collection and statistical analyses of 49 studies comprising 355 BCO treatments resulted in key insights into the most effective BCO application methods. Root and soil treatments were significantly more effective than seed treatments. Co-application of BCOs with pathogen inoculation enhanced efficacy, likely due to direct antagonism, particularly when specialized metabolites were delivered alongside bacterial BCOs. Strikingly, greenhouse and field trials demonstrated higher BCO efficacy than growth chamber experiments, emphasizing the importance of trial environments. Factor Analysis of Mixed Data (FAMD) and Hierarchical Clustering on Principal Components (HCPC) identified distinct clusters of BCO treatments, revealing clear associations between BCO application methods and efficacy. These

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findings highlight the need for optimized application methods and formulations to maximize BCO stability and efficacy, potentially enhancing their role in integrated pest management strategies.

1. Introduction

Oomycetes, a group of eukaryotic microorganisms within the kingdom of the Straminipila, are well-known as devastating plant pathogens (Beakes et al., 2012; Pettitt, 2015). Unlike fungi, oomycetes exhibit distinct features such as diploidy for most of their life cycle, aseptate hyphae, and primarily β-glucan-based cell walls (Latijnhouwers et al., 2003; Werner et al., 2002). Among these, the genus *Phytophthora* comprises filamentous microorganisms classified into 13 clades based on molecular analyses (Abad et al., 2023; Bollmann et al., 2016). With 223 described species, *Phytophthora* pathogens infect over 1000 plant species, causing diseases such as late blight, root rot, crown rot, and stem dieback (Abad et al., 2023; Batuman et al., 2020; Cacciola and di San Lio, 2008; Yang et al., 2017). The most notorious and extensively described *Phytophthora* species is the late blight pathogen *P. infestans*, mainly infecting tomato and potato plants. Potato late blight resulted in the Irish potato famine in the 1840s, leading to an estimated 750,000 deaths in Europe (Zadoks, 2008). Many *Phytophthora* species, such as *P. cinnamomi* and *P. ramorum*, primarily infect trees and shrubs. These pathogens pose significant challenges to the conservation of forests and shrublands due to the lack of effective management strategies. The impact of *P. ramorum*, causing sudden oak death for the Californian and Oregon forests, has had a permanent effect on the American forest ecosystems, as millions of trees such as tanoak and oak were affected (Garbelotto et al., 2001; Henricot and Prior, 2004; Rizzo and Garbelotto, 2003; Yang et al., 2017). Among control approaches of these tree-infecting species, biological control methods and genetics or breeding programmes have received most attention, while chemical and silvicultural methods are less studied (López-García et al., 2024). Regarding biocontrol measures, a systematic review on biocontrol strategies targeting *P. cinnamomi,* a pathogen affecting diverse tree species such as avocado and chestnut, highlighted the potential of biological management in these ecosystems (de Andrade Lourenço et al., 2022).

While the biocontrol of *Phytophthora* species affecting trees and shrubs has been extensively reviewed, to our knowledge no comprehensive study has specifically reviewed the biocontrol of *Phytophthora* species causing root rot in annual crops. This lack of dedicated analyses was the rationale behind this study, as understanding effective biocontrol strategies for these pathogens is essential given the significant impact of root rot-inducing *Phytophthora* species in annual crops. For instance, *P. nicotianae* and *P. sojae* are among the most destructive pathogens in tobacco and soybean, respectively, causing significant yield losses, sometimes reaching 100% (Robideau et al., 2011; Sugimoto et al., 2011; Yang et al., 2017). Other significant root-rot causing *Phytophthora* species, such as *P. cinnamomi*, *P. cryptogea*, and *P. cactorum,* infect ornamental plants including rhododendron, gerbera, azalea, and petunia (Ferrin and Kabashima, 1991; Grasso et al., 2003; Hwang and Benson, 2005; Linderman and Zeitoun, 1977; Liu et al., 2022b). Some species, such as *P. cryptogea*, infect a wide range of plants; others, such as *P. erythroseptica*, have a narrow host range, with *P. sojae* exclusively infecting soybean (Erwin and Ribeiro, 1998; Kroon et al., 2012). An overview of all *Phytophthora* spp. inducing root rot in annual crops is provided in Supplementary **Table S1**, including their clade classification, host range, sex determination, and survival structures, as reported by Cline et al. (2008) and Erwin and Ribeiro (1996).

Under favorable conditions, typically in moist soils at 25–30°C, the infection cycle of soilborne Phytophthora root rot species initiates by the germination of oospores or chlamydospores, the survival structures present in soil and plant debris, followed by the release of biflagellate zoospores (Giachero and Marquez, 2022). The motile zoospores navigate both in waterlogged soils and hydroponic systems by responding to molecular, chemical, and electrical stimuli (Bassani et al., 2020; Moruzzi et al., 2017). Upon reaching the root tissue, zoospores encyst and adhere to the root surface through the release of adhesive compounds. During cyst germination, a germ tube penetrates the root epidermis, growing intercellularly along anticlinal cell walls. In cortical cells, haustoria form to allow nutrient uptake, while chlamydospores and multinucleate sporangia develop on the root surface. The sporangia then undergo cytokinesis, releasing zoospores back into the soil (Hardham, 2001). Haustoria may play a critical role in sustaining the biotrophic phase of the pathogen by delivering pathogenicity factors and effectors that regulate host defense responses, thereby maintaining host cell viability (Judelson and Ah-Fong, 2019). During this stage, *Phytophthora* spp. actively suppress the hypersensitive response (HR), a plant defense mechanism characterized by localized programmed cell death at the site of pathogen invasion (Dong et al., 2012).

Current management strategies for Phytophthora root rot have proven effective within the Integrated Pest Management (IPM) strategy, but exhibit certain drawbacks. IPM emphasizes prevention through disease-free materials and strict phytosanitation (Hong and Moorman, 2005; Jacobsen, 1997). In soilless systems, irrigation mats made from material like polyethylene and polypropylene help prevent the spread of *Phytophthora* by filtering zoospores (Van Der Gaag et al., 2001). Additionally, well-drained soils or raised beds decrease the spread of zoospores and mitigate root rot, as demonstrated by reduced *P. fragariae* incidence in raised-bed raspberry cultivation (Maloney et al., 1993). While effective, these IPM practices are very labour-intensive. One other preventive strategy is the development of resistant host plants through breeding programs. Extensive research has focused on breeding soybean varieties with race-specific and partial resistance to *P. sojae* (Lin et al., 2022; Sugimoto et al., 2011). Efforts to develop crops resistant to Phytophthora root rot have also extended to other pathosystems, such as *P. cactorum*-resistant strawberries and *P. capsici*-resistant peppers (Borrero et al., 2017; Naegele and Hausbeck, 2020). However, the durability of resistance is often compromised by pathogen evolution and environmental factors. Moreover, resistant varieties may produce lower yields than susceptible varieties in the absence of disease pressure (Vyska et al., 2016). Chemical control strategies against *Phytophthora* spp. have traditionally relied on the use of fumigants such as metam sodium and methyl bromide-chloropicrin mixtures. These compounds have demonstrated effectiveness in reducing inoculum levels in susceptible crops including bell pepper and gerbera (Kaewruang et al., 1989; Sánchez-Chávez et al., 2017). However, due to increasing environmental and human health concerns, their regulatory status has changed substantially. Under Regulation (EC) No 1107/2009, both methyl bromide and chloropicrin have been banned in the European Union, whereas metam sodium remains approved for use (European Commission, 2025). Beyond fumigants, conventional fungicides have also been employed with varying degrees of success. While many fungicides are effective, the development of resistance in *Phytophthora* populations presents a growing challenge. For instance, *P. capsici* has developed resistance against metalaxyl (also known as mefenoxam), as described by Wang et al. (2020a). Nevertheless, metalaxyl remains authorized under the same EU regulation and continues to be used against *P. fragariae* in strawberry and *P. capsici* in pepper (European Commission, 2025; Lamour and Hausbeck, 2000; Maloney et al., 1993; Wang et al., 2020a). In addition, membrane-active surfactants have been explored as an alternative means of control. These agents are capable of lysing *Phytophthora* zoospores, but they exhibit limited efficacy against mycelial or encysted zoospores, limiting their utility (Stanghellini et al., 2000; Stanghellini and Tomlinson, 1987). Biological control presents a sustainable and promising option. Biological control organisms (BCOs),

commonly found in the plant rhizosphere, combat pathogens through various mechanisms (Villarreal-Delgado et al., 2018). These include priming plant immunity (Conrath et al., 2015; Pieterse et al., 2014), nutrient and space competition (Spadaro and Droby, 2016), hyperparasitism (Ghorbanpour et al., 2018) and antibiosis by the production of antimicrobial metabolites (Glare et al., 2012; Lahlali et al., 2022).

Several studies have reviewed the potential of BCOs against specific Phytophthora root rot species. de Andrade Lourenço et al. (2022) presented an overview of BCOs active against the tree-infecting *P. cinnamomi*. López-García et al. (2024) discussed the control strategies to manage *Phytophthora* in forestry, highlighting the role of bio-based measures. Quispe-Quispe et al. (2022) demonstrated the activity of *Trichoderma*, *Bacillus*, *Pseudomonas*, and *Streptomyces* against *P. capsici* in *Capsicum* species. However, Wan and Liew (2020) reported that the efficacy of *Bacillus* spp. in controlling *P. capsici* was inconsistent, emphasizing the influence of environmental conditions on BCO performance. Additionally, Yu et al. (2022) reviewed the biocontrol potential of *Bacillus* and *Streptomyces* species against *P. sojae* in soybean, emphasizing the need for more research on underlying molecular mechanisms. Despite these insights, no comprehensive review has specifically examined the biological control of all Phytophthora root rot pathogens in annual crops or how BCOs combat these pathogens. To address this gap, a systematic review was conducted to critically evaluate the factors influencing the success of biological control against Phytophthora root rot. Additionally, a qualitative analysis was conducted to elucidate the mode of action (MOA) by which BCOs suppress *Phytophthora* pathogens.

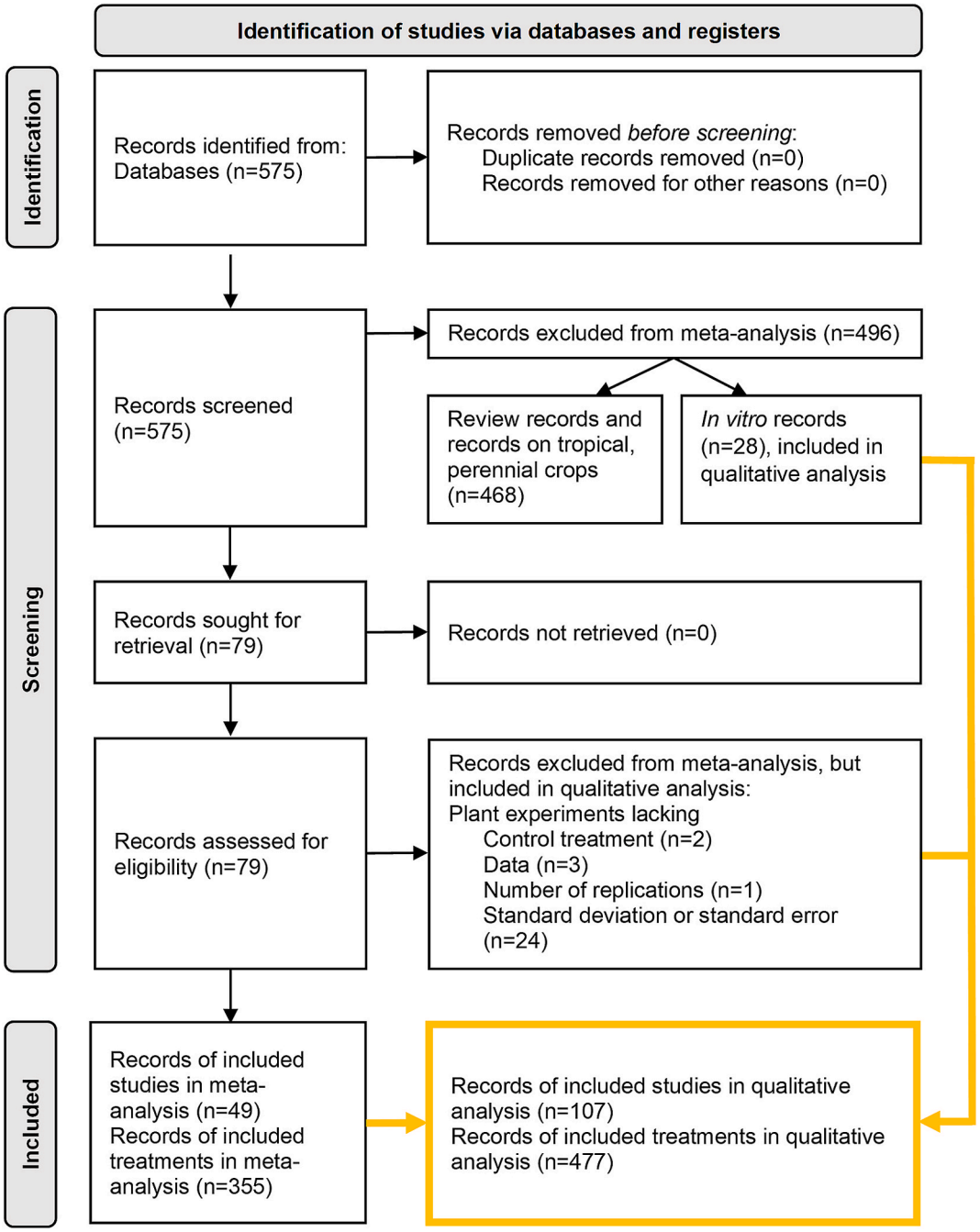

Fig. 1. PRISMA flow diagram illustrating the data collection, selection and processing steps followed in this meta-analysis (adapted from Page et al., 2021). The orange box and arrows represents the studies included in the qualitative analysis of BCO's modes of action. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2. Material and methods

2.1. Literature search strategy and data collection

Research articles were collected from the Web of Science platform, searching in the "All fields" option with the keywords "biocontrol and *Phytophthora*" and "biological control and *Phytophthora*", yielding 575 publications from 1990 to 2023. The dataset was refined to include only studies addressing biocontrol of Phytophthora root rot in annual crops. Studies on tropical or perennial crops, studies only describing *in vitro* experiments, and studies unsuited for meta-analysis (e.g. plant experiments lacking control treatments, standard deviation, data, or replication details) were excluded. Finally, 49 studies comprising 355 biocontrol treatments were retained for the meta-analysis (Fig. 1; **Supplementary Note S1**). The raw data can be found in the attached excel file "Meta-analysis raw data.xlsx". A biocontrol treatment is defined as the application of a BCO, regardless of the method, dosage, number of applications within a plant experiment. For qualitative analysis of BCO's MOA, the abovementioned excluded studies that only describe *in vitro* experiments and those unsuited for meta-analysis, were included, yielding 107 studies with 477 treatments.

From each selected study, general information was collected for traceability, including the study's title, reference, and year of publication. Factors that can cause variation in plant response to *Phytophthora* infection were recorded, such as crop type, experimental setup, incubation temperature, and relative humidity. To evaluate whether the type of BCO influences the biocontrol effectiveness against *Phytophthora* infection, data on the tested BCO, including taxonomy and strain name, were collected. Additionally, parameters related to application techniques were documented to assess their potential impact on BCO performance. These parameters included BCO concentration, method of application, frequency of application, site of application on the plant, and timing of application. Information on the *Phytophthora* species, including species and strain names, as well as inoculum source and concentration, was also recorded. Lastly, outcome parameters (*disease incidence, disease severity, infected roots, pathogen presence, plant mortality,* and *seed germination*) reflecting the effectiveness of each BCO in controlling *Phytophthora* were recorded.

2.2. Meta-analysis

Six different outcome parameters were reported: *disease incidence, disease severity, infected roots, pathogen presence, plant mortality,* and *seed germination*. To enable comparison across these parameters, a standardization was performed towards a single *efficacy* parameter. The efficacy was calculated as the relative effect of each treatment compared to the control. For all outcome parameters, except *seed germination*, the efficacy was calculated using Eq. (1), as an increase in efficacy is associated with a reduction in these parameters. In contrast, *seed germination* efficacy was calculated using Eq. (2), since greater BCO efficacy corresponds to enhanced seed germination. The standard deviation of the efficacy was calculated using Eq. (3).

$$efficacy(\%) = 100 - \left[\frac{treatment}{control} * 100\right] \quad (1)$$

$$efficacy(\%) = \left[\frac{treatment}{control} - 1\right] * 10 \quad (2)$$

$$\sigma_{efficacy}(\%) = 100 * \frac{treatment}{control} * \sqrt{\left[\frac{\sigma_{treatment}}{treatment}\right]^2 + \left[\frac{\sigma_{control}}{control}\right]^2} \quad (3)$$

Subsequently, the effect size of each treatment was determined using Hedges' g, representing the standardized difference of means between the treatment and control ($\bar{x}_{Treatment}$-$\bar{x}_{Control}$/SD_{Pooled}) (Hedges, 1981). Compared to the efficacy parameter, the effect size also takes into account the number of repetitions per BCO treatment. The correlation between these two parameters was assessed by calculating the Spearman's Rank correlation coefficient, which was found to be 0.53 (**Supplementary Fig. S1**; Ali and Al-Hameed, 2022).

2.3. Fail-safe number and funnel plots to evaluate data robustness and publication bias, respectively

To assess the robustness of the data, the fail-safe number (FSN) was calculated using Rosenberg's approach and was found to be 125,401, representing the number of non-significant treatments that would need to be added to the meta-analysis to invalidate the observed effects (Rosenberg, 2005). The FSN was calculated in RStudio using the *meta* package (Balduzzi et al., 2019). In addition, to evaluate potential publication bias, funnel plots (**Supplementary Fig. S2**) were generated in RStudio using the *meta* package, following the methods of Sterne and Egger (2001), Balduzzi et al. (2019), and Duval and Tweedie (2000). An asymmetric distribution was found indicating the presence of publication bias, showing that researchers are more likely to publish positive results rather than studies involving inactive BCOs. This indicates that the conclusion of the meta-analysis should be interpreted with caution, as the analysis will emphasize well-performing or highly effective BCOs while underrepresenting poorly performing strains. Despite this bias, the high robustness of the data and the positive correlation analysis confirm the reliability of the data, validating the feasibility of thoroughly conducting a meta-analysis on the impact of different applications on the efficacy of BCOs against Phytophthora root rot species. To further ensure the robustness of the findings, factors that could potentially influence BCO efficacy with fewer than three independent treatments were excluded from the analysis. This threshold was set to minimize biases and avoid drawing conclusions based on insufficient data.

2.4. Statistical analysis

Statistical analyses of factors influencing the BCO's efficacy were conducted at the 5% significance level using an ANOVA test, followed by a post-hoc Games-Howell test. As an additional validation to determine the optimal timing, location, and frequency for adding the BCO to the plants for maximum efficacy, a Factor Analysis of Mixed Data (FAMD) was conducted, together with a Hierarchical Clustering on Principal Components (HCPC). This was performed in RStudio, utilizing the "FacoMineR" and "factoextra" packages (Lê et al., 2008). Significant differences between and within clusters were assessed using a v-test, in which a v-test statistic greater than 1.96 corresponds to a p-value below 0.05, indicating statistical significance. The sign of the v-test value determines whether the cluster mean is higher or lower than the overall mean.

3. Results

3.1. Phytophthora capsici/pepper interactions are the main focus in Phytophthora-biocontrol research

First, the set of pathosystems studied in biocontrol research was identified (Table 1). Most research on *in planta* biocontrol of *Phytophthora* has focused on BCOs targeting *P. capsici* in pepper plants, with 32 out of 49 studies investigating this specific pathosystem, followed by *P. sojae* in soybean and *P. cactorum* in strawberry. In contrast, research on other important Phytophthora root rot pathogens, such as *P. cryptogea*, *P. drechsleri*, *P. medicaginis*, and *P. parasitica*, remains limited.

3.2. Phytophthora root rot species can be controlled by a wide range of biocontrol organisms

Plant-based *Phytophthora*-biocontrol research included in this meta-

Table 1
Phytophthora-crop interaction studies in which BCOs have been tested. For each pathosystem, the number and abundance of studies and biological treatments are provided. Note that the number of studies exceeds the total of 49 independent studies as three studies (Diánez Martínez et al., 2016; Santos et al., 2019, 2023) investigated two different pathosystems.

Phytophthora spp.	Crop	Number of studies	Studies abundance (%)	Number of treatments	Treatment abundance (%)
P. cactorum	strawberry	3	6.0	9	2.5
P. capsici	pepper	32	62.0	207	58.3
P. capsici	zucchini	1	2.0	16	4.5
P. capsici	cucumber	1	2.0	13	3.7
P. capsici	tomato	2	4.0	7	2.0
P. cryptogea	tomato	2	4.0	10	2.8
P. drechsleri	gom-chwi	1	2.0	58	16.3
P. drechsleri	cucumber	1	2.0	2	0.6
P. medicaginis	chickpea	1	2.0	6	1.7
P. parasitica	tomato	1	2.0	3	0.8
P. parasitica	pepper	2	2.0	11	3.1
P. sojae	soybean	5	10.0	13	3.7

analysis predominantly focused on *Trichoderma* (69 treatments), *Bacillus* (59 treatments), and *Pseudomonas* (35 treatments) species (Fig. 2A). Various *Trichoderma* species with biocontrol activity against *Phytophthora* have been reported across different clades: the *longibrachiatum* clade (*T. longibrachiatum*, *T. pseudokoningii*, *T. reesei*, and *T. saturnisporum*), the *viride* clade (*T. asperellum, T. hamatum*, and *T. viride*), the *harzianum* clade (*T. aggressivum*), and the *virens* clade (*T. virens*). The strains reported to exhibit both active and inactive properties were *T. asperellum* and *T. saturnisporum*.

Among *Bacillus* species, the most active strains primarily belonged to the *B. subtilis* clade (e.g. *B. aerius*, *B. amyloliquefaciens*, *B. atrophaeus*, *B. licheniformis*, *B. subtilis, B. vallismortis*, and *B. velezensis*). Additionally, *B. altitudinis*, *B. cereus*, and *B. thuringiensis* demonstrated biocontrol activity as well. *Bacillus* strains showing both active and inactive biocontrol properties belonged to *B. megaterium*, which has recently been reclassified as *Priestia megaterium*.

Among *Pseudomonas* species, those exhibiting biocontrol activity primarily belonged to the *P. fluorescens* group (e.g., *P. fluorescens*, *P. putida*) and its subgroup (e.g., *P. corrugata*), as well as the *P. aeruginosa* lineage (e.g., *P. aeruginosa* and *P. otitidis*). Additionally, *P. libanensis* also demonstrated anti-*Phytophthora* activities. *Pseudomonas* strains that displayed both active and inactive biocontrol properties were classified as *P. fluorescens*, *P. otitidis*, and *P. putida*.

In addition to the top three genera previously discussed, other genera

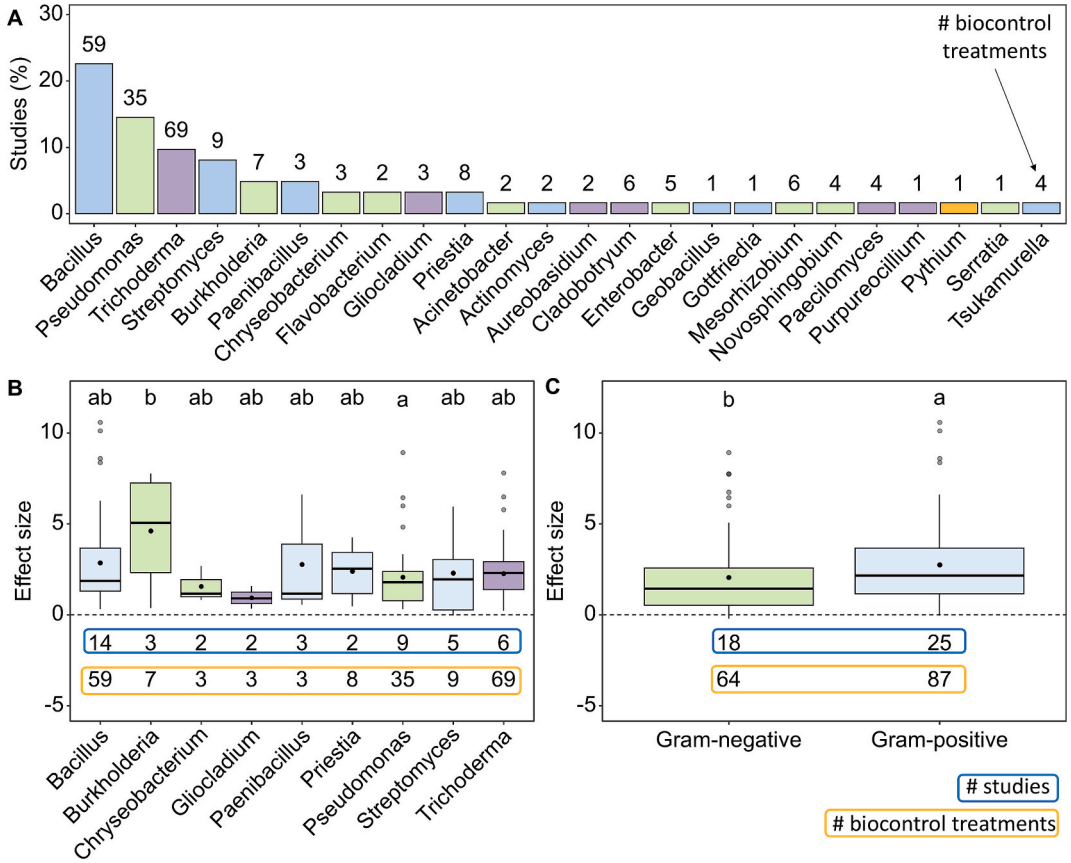

Fig. 2. (A) Number of studies and treatments evaluating different genera as potential biocontrol organisms (BCOs) against *Phytophthora* root rot pathogens. Bar colors indicate microbial groups: blue (Gram-positive bacteria), green (Gram-negative bacteria), purple (fungi), and orange (oomycetes) **(B)** Effect size (Hedges' g) for BCO efficacy by bacterial and fungal genera, and **(C)** comparison of effect sized between Gram-negative and Gram-positive bacteria. Statistical significant was assessed using ANOVA with Games-Howell post-hoc tests. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

demonstrating activity against Phytophthora root rot included species from the genera *Acinetobacter*, *Actinomyces*, *Burkholderia*, *Chryseobacterium*, *Cladobotryum*, *Flavobacterium*, *Geobacillus*, *Lysobacter*, *Paecilomyces*, *Paenibacillus*, *Purpureocillium*, and *Pythium*. Furthermore, strains exhibiting both active and inactive biocontrol properties belonged to the genera *Aureobasidium*, *Enterobacter*, *Gliocladium*, *Streptomyces*, *Novosphingobium*, and *Tsukamurella*. Notably, the only genus exclusively associated with non-active strains was *Serratia*.

The effectiveness of the different BCO genera was compared using a meta-analysis approach. To ensure a robust analysis, genera with fewer than three treatments were excluded. The results showed that all included genera exhibited comparable effect sizes against Phytophthora root rot (Fig. 2B). Additionally, statistical analysis revealed that Gram-positive bacteria (e.g. *Actinomyces*, *Bacillus*, *Geobacillus*, *Streptomyces*, *Paenibacillus*, and *Tsukamurella*) were significantly more effective as BCOs than Gram-negative bacteria (e.g *Acinetobacter*, *Burkholderia*, *Chryseobacterium*, *Enterobacter*, *Flavobacterium*, *Novosphingobium*, and *Pseudomonas*) (Fig. 2C).

3.3. BCOs exhibit their biocontrol activity mainly through direct antagonism

Understanding the MOA of a BCO against Phytophthora root rot species is scientifically valuable, as it facilitates more targeted searches for additional BCOs with similar reported biocontrol traits. In addition to the studies used in the meta-analysis, 58 other studies were included in the MOA study. These comprised 20 publications focusing on *in vitro* antimicrobial assays and 38 other studies. The latter executed plant-based experiments but were excluded from the meta-analysis due to not meeting the necessary quality criteria. In total, 107 studies were used to evaluate the MOAs employed by BCOs against Phytophthora root rot. First, MOAs assessed through *in vitro* assays will be discussed, followed by those evaluated in plant-based experiments.

The majority of *in vitro* studies (63) used a dual culture approach to examine the effects of BCOs on *Phytophthora* mycelial development. Few studies examined BCO effects on zoospore, cyst, and sporangium formation (Agusti et al., 2011; Khatun et al., 2018; Kim et al., 2020; Long et al., 2023; Lu et al., 2017; Segarra et al., 2013; Shen et al., 2002, 2007) or investigated volatile organic compounds (VOCs) as potential MOAs. Several studies investigated the role of antibiosis with 16 studies examining BCO supernatants and 12 focusing on pure metabolites, identifying active compounds from *Bacillus* species and other genera (Table 2). For example, Yu et al. (2023b) found that fusaricidin, a compound produced by *Paenibacillus polymyxa* NX20, inhibited *P. capsici* by suppressing zoospore production and germination. Moreover, two studies utilized BCO mutants with disrupted production of specialized metabolites to assess their role in biocontrol efficacy (Han et al., 2021; Lin et al., 2023). Mutant analysis of *B. velezensis* FZB42 showed that bacilysin, rather than other antimicrobial compounds like lipopeptides and polyketides, is responsible for its antagonistic activity against *P. sojae,* causing significant damage to the pathogen's hyphal structures (Han et al., 2021). Lin et al. (2023) found that the HSAF (Heat-Stable Antifungal Factor)-deficient mutant Δ*lafB* completely lost the antagonistic activity compared to the wild type *Lysobacter enzymogenes* OH11 against *P. sojae* and *P. capsici*. *In vitro* mycoparasitism was investigated by 6 studies, primarily involving *Trichoderma* and *Pythium* species (Table 3). For example, *Pythium oligandrum* was found to penetrate the host cell wall of *P. parasitica* hyphae, likely producing cellulolytic enzymes during this process (Picard et al., 2000).

In planta studies assessing the efficacy of BCOs were often executed phenomenologically, without exploring underlying MOAs. However, several notable studies have specifically investigated the induction of systemic resistance. Cheng et al. (2022) reported a unique finding where

Table 3
BCOs that control *Phytophthora* species *in vitro* by mycoparasitism.

BCO	*Phytophthora* sp.	Reference
Pythium oligandrum 1010	*P. parasitica* 149	Picard et al. (2000)
Streptomyces plicatus B4-7	*P. capsici*	Chen et al. (2016)
Trichoderma asperellum Tv-1	*P. nicotianae*	Liu et al. (2022a)
Trichoderma atroviride Au50	*P. cinnamomi*	Martins et al. (2022)
Trichoderma saturnisporum T2	*P. capsici*	Diánez Martínez et al. (2016)
	P. parasitica	
Trichoderma virens HZA14	*P. capsici* HZ07	Tomah et al. (2020)

Table 2
Examples of pure compounds exhibiting *in vitro* activity or no activity against *Phytophthora* species, along with their producers and the pathogen target processes. If the activity of specialized metabolites was assessed through mutant analysis, this is indicated with "(mutant)". M: mycelium development, SF: sporangium formation, ZP: zoospore production, ZR: zoospore rupture, CG: cyst germination.

Metabolite	Biocontrol organisms	Target	*Phytophthora* sp.	Reference
Antagonistic activity				
1H-pyrrole-2-carboxamide	*Actinomyces* sp. A217	M	*P. capsici*	He et al. (2020)
Aerugine	*Pseudomonas fluorescens* MM-B16	M	*P. capsici*	Lee et al. (2003)
Bacilysin	*Bacillus velezensis* DMW1	M	*P. capsici*, *P. sojae* 6497	Yu et al. (2023a)Han et al. (2021)
	Bacillus velezensis FZB42 (mutant)		*P. sojae*	
Benzoic acid	*Burkholderia cepacia* MPC-7	M	*P. capsici* KACC 40483	Sophearetn et al. (2013)
Diketopiperazine	*Bacillus* sp. N	M, SF, ZP, ZR, CG	*P. capsici*	Kumar & Nambisan (2014)
Fengycin	*Bacillus amyloliquefaciens* KX953161.1	CG	*P. capsici*	Ley-López et al. (2022)
Fusaricidin	*Paenibacillus polymyxa* NX20	M, ZP, CG	*P. capsici*	Yu et al. (2023b)
Gliotoxin	*Trichoderma virens* HZA14	M	*P. capsici* HZ07	Tomah et al. (2020)
Glucanases	*Streptomyces* sp. EF-14	M	*P. fragariae* var. *rubi* L200	Valois et al. (1996)
Macrocyclic lactone	*Serratia plymuthica* A21-4	M, SF, CG	*P. capsici*	Shen et al. (2007)
Phenylacetic acid	*Borkholderia cepacia* MPC-7	M	*P. capsici* KACC 40483	Sophearetn et al. (2013)
	Lysobacter antibioticus HS124			Ko et al. (2009)
Macrolactam	*Lysobacter enzymogenes* OH11 (mutant)	M, CG	*P. sojae* 6497, *P. capsici* T263	Lin et al. (2023)
Stilbenes	*Bacillus* sp. N	M, SF, ZP, ZR, CG	*P. capsici*	Kumar & Nambisan (2014)
Surfactin	*Bacillus amyloliquefaciens* KX953161.1	CG	*P. capsici*	Ley-López et al. (2022)
No antagonistic activity				
Bacillaene	*Bacillus velezensis* DMW1	M	*P. capsici*, *P. sojae* 6497	Yu et al. (2023a)
Difficidin				
Fengycin				
Macrolactin				
Surfactin				
Iturin A	*Bacillus vallismortis* EXTN-1	M	*P. capsici*	Park et al. (2016)
	Bacillus velezensis DMW1	M	*P. capsici*, *P. sojae* 6497	Yu et al. (2023a)

Pythium oligandrum induced ferroptosis, a form of cell death accompanied by iron accumulation and lipid peroxidation, in soybean, thereby enhancing resistance against *P. sojae*. Plett et al. (2021) showed the role of *Mesorhizobium ciceri* in triggering induced resistance in chickpea against *P. medicaginis*. Furthermore, treatment of soybean with *Bacillus altitudinis* JSCX-1 increased reactive oxygen species (ROS) production and callose deposition in leaves, effectively reducing *P. sojae* infection (Lu et al., 2017). Xu and Kim (2016) demonstrated an increase in the activity of defense-related enzymes, including phenylalanine ammonia-lyase (PAL), peroxidase (PO), polyphenol oxidase (PPO), and superoxide dismutase (SOD) in pepper seedlings treated with *Paenibacillus polymyxa* SC09-21, significantly reducing disease severity. Similarly, Wu et al. (2022) observed enhanced activity of PAL, PO, SOD, and catalase (CAT) in *Serendipita indica*-treated seedlings, improving resistance to *P. cryptogea*-induced root rot in gerbera. A spraying treatment with an iturin A analog, a cyclic lipopeptide produced by *Bacillus vallismortis* EXTN-1, led to the upregulation of defense marker genes in pepper plants leading to a significant disease reduction of *P. capsici*, although it did not directly inhibit *P. capsici in vitro* (Park et al., 2016). Aerugin, an antimicrobial compound produced by *Pseudomonas fluorescens* MM-B16, was found to suppress *Phytophthora* disease in pepper plants when applied as a foliar spray one day prior to inoculation with *P. capsici*. This compound also exhibited *in vitro* activity, inhibiting *P. capsici* mycelium development (Lee et al., 2003).

Additionally, the role of specialized metabolites produced by BCOs in controlling *Phytophthora* pathogens in plant-based experiments was evaluated. When comparing the effect sizes of metabolite-free cell suspensions and metabolite-rich cell suspensions, no significant differences were observed (Fig. 3A). However, when the analysis was restricted to bacterial BCOs (excluding fungal and oomycete BCOs), the metabolite-rich cell suspensions demonstrated significantly higher biocontrol efficacy compared to the metabolite-free cell suspensions (Fig. 3B).

3.4. BCOs are more performant under greenhouse and field conditions than under growth chamber environments, likely due to selective testing

In the studies analyzed in this meta-analysis, plant-based experiments were most frequently conducted in greenhouse settings (42%) and controlled environments, such as growth chambers (39%). The remaining experiments were performed in field conditions (14%) and hydroponic systems (5%). BCO efficacy was significantly higher in

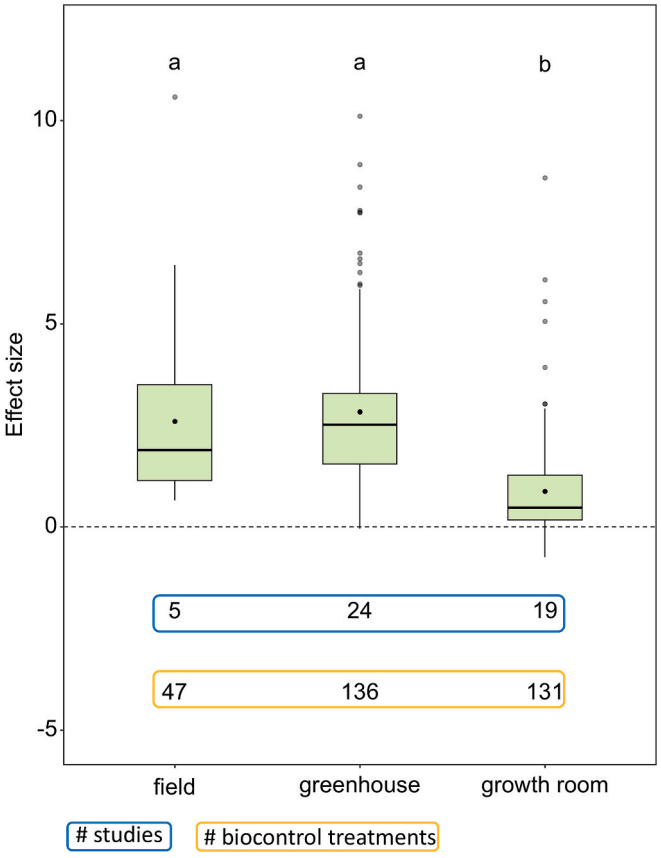

Fig. 4. Effect sizes (Hedges' *g*) for BCO efficacy under field, greenhouse, and growth room conditions. Statistical differences were tested using ANOVA with Games-Howell post-hoc analysis.

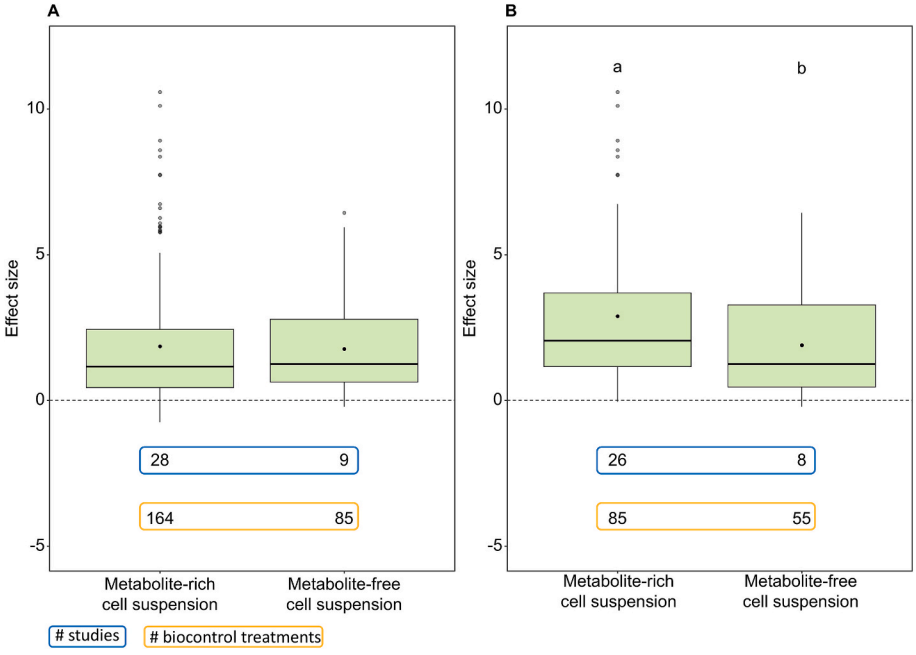

Fig. 3. Effect sizes (Hedges' *g*) for BCO efficacy with and without the use of specialized metabolites, shown for the full dataset **(A)** and for bacterial BCOs only **(B)**. Statistical differences were assessed using ANOVA.

greenhouse and field trials compared to growth chambers (Fig. 4).

3.5. The efficacy of BCO is unaffected by number of treatments, but influenced by the method of application

A major challenge in optimizing the efficacy of BCOs is to determine the most effective application method and timing for plant or soil treatments. The literature review revealed a lack of consensus on the optimal BCO concentration, with studies using different units of measurements across studies. For bacterial BCOs, concentration is typically expressed in colony-forming units per milliliter; however, no significant differences in the BCO effect size were observed across different concentrations. For fungi and oomycetes, concentrations were expressed in terms of sporangia, oospores, zoospores, or hyphae, typically per gram of soil. These inconsistencies made comparisons between studies difficult. In addition, BCOs are mainly applied through root, seed, and soil treatments, but also through water treatments in hydroponic systems. Among these methods, root and soil applications were significantly more effective than seed treatments (Fig. 5A). Additionally, no significant added value was observed for repeated BCO applications over a single treatment (Fig. 5B), indicating that a single application is generally sufficient for optimal control of Phytophthora root rot. Finally, application timing proved critical, with simultaneous BCO treatment where BCOs are applied at the same time as the introduction of the pathogen being the most effective strategy (Fig. 5C).

Additionally, both numeric and nominal data were analyzed using a Factor Analysis of Mixed Data (FAMD), which explained 41.7% of the total variability in the dataset in the first two dimensions. Hierarchical Clustering on Principal Components (HCPC) identified three distinct clusters. Cluster 1 and 3 were associated with significantly higher treatment effects compared to the overall average treatment effect, whereas cluster 2 comprised lower-than-average treatment effects (Fig. 6). Cluster 1 contained a significantly higher number of observations where BCOs were applied through root treatments (v-test = 13.31, $p < 0.001$), while cluster 3 included significantly more observations of BCO applications through soil treatment (v-test = 6.13) and simultaneous application at the time of pathogen introduction (v-test = 14.91, $p < 0.001$). In contrast, cluster 2 contained significantly more observations of BCO application via seed treatment (v-test = 10.30, $p < 0.001$) and significantly fewer observations of root and soil treatments (v-test values of −7.52 and −5.05, respectively). The effect of repeated BCO applications on efficacy could not be conclusively determined, as the HCPC did not include treatments with a single BCO application.

4. Discussion

This study offers valuable insights into the potential of BCOs for managing Phytophthora root rot in annual crops. Through a meta-analysis on standardized data, the efficacy of diverse BCOs was evaluated and crucial factors influencing their performance were identified. Our findings suggest that Phytophthora root rot in annual crops can be managed using a diverse array of BCOs, as no significant differences in efficacy were observed among BCO genera reported with biocontrol activity. However, this conclusion should be interpreted with caution, as evidence of publication bias was identified, with a clear tendency to report positive biocontrol results. Nonetheless, the most studied BCO genera included *Trichoderma, Bacillus,* and *Pseudomonas.* These findings align with research on tree-infecting *Phytophthora* species, where *Trichoderma* and *Bacillus* spp. effectively controlled *P. cinnamomi* in avocado and chestnut trees (de Andrade Lourenço et al., 2022). Likewise, *Pseudomonas* species have demonstrated activity against *P. palmivora* in cacao and *P. parasitica* in citrus orchards (Acebo-Guerrero et al., 2015; Steddom et al., 2002). Oomycete pathogens are generally susceptible to biocontrol, particularly in suppressive soils and composts enriched with antagonistic microorganisms. Studies have shown that compost enriched with *Enterobacter, Paenibacillus,* or *Trichoderma* effectively suppress *Phytophthora* in various crops, such as *P. infestans* in tomato and *P. capsici* in pepper and pumpkin (Bahramisharif and Rose, 2019; Bellini et al., 2020, 2021; Cocozza et al., 2021; de Nijs et al., 2023; Diánez et al., 2007; Doungous et al., 2018; Luna-Olvera et al., 2009; Termorshuizen et al., 2006). *Pseudomonas* species isolated from disease-suppressive cocoyam fields have been demonstrated to effectively control the root

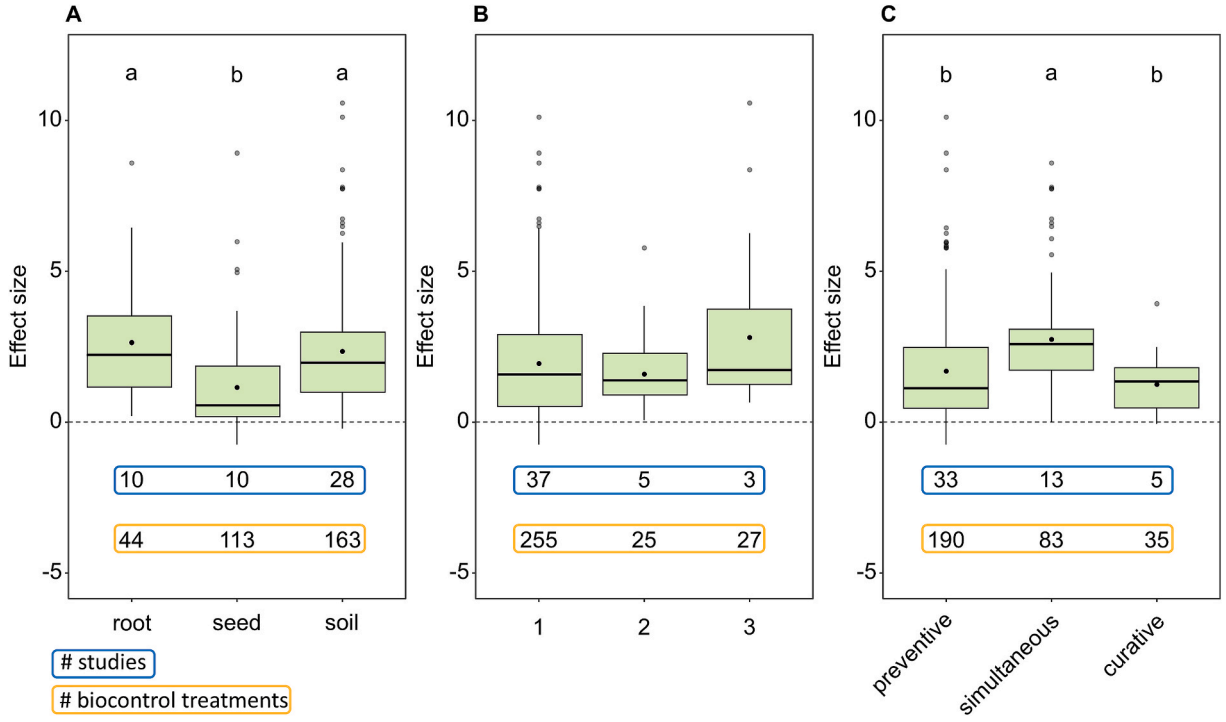

Fig. 5. Effect sizes (Hedges' *g*) for BCO efficacy based on application method (root, seed, soil) **(A)**, number of applications (1, 2, or 3 times) **(B)**, and treatment timing (preventive, simultaneous, curative) **(C)**. Statistical differences were assessed using ANOVA with Games-Howell post-hoc tests.

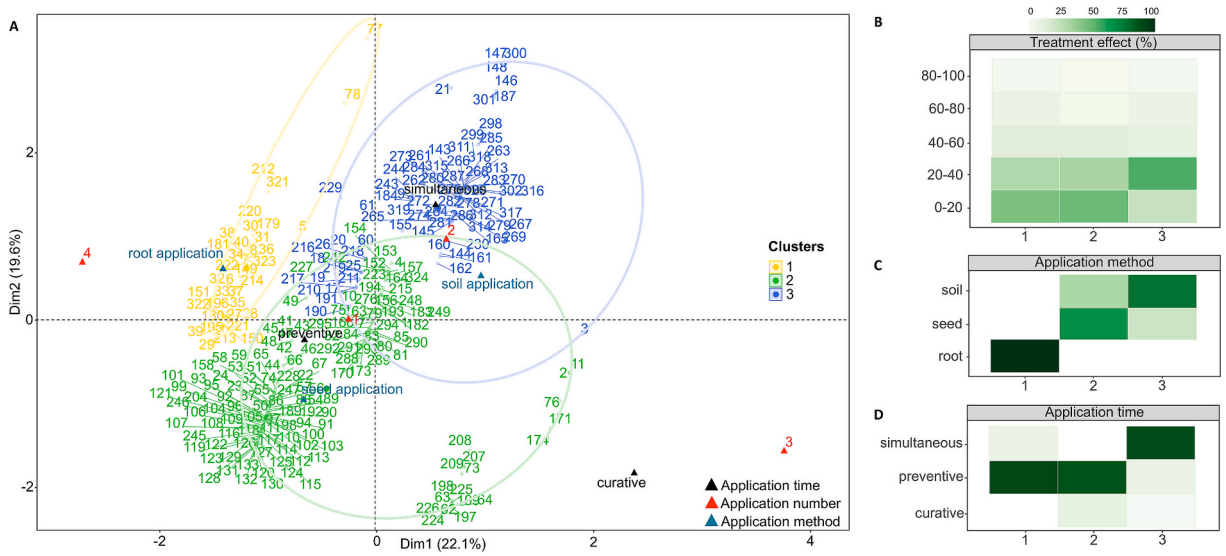

Fig. 6. Factor analysis of mixed data (FAMD). (A) Two-dimensional (Dim1, Dim2; cumulative variance: 41.7%) cluster plot and spatial sample (color triangles) distribution. V-test values of the treatment effect for each cluster is 2.71, −8.29, 7.26, respectively. (B) Relative contributions of the treatment effect, (C) application method, and (D) application time for each cluster (x-axis). The more dark green, the higher the abundance of treatments with a specific parameter.

rot pathogen *Pythium myriotylum* (Oni et al., 2019; Perneel et al., 2007). Other microorganisms, including *Bacillus* species isolated from the rhizosphere of *Arabidopsis thaliana* and a compost mixture, have also demonstrated biocontrol potential against *Phytophthora* species (Syed-Ab-Rahman et al., 2018).

The discovery of potential BCOs typically begins with *in vitro* antagonistic assays, where BCOs producing antimicrobial metabolites often show stronger activity. This is largely due to the efficient diffusion of bioactive compounds under controlled conditions, a feature that may not fully translate to natural environments. To address this limitation, screening methods should integrate *in vitro* assays with *in planta* testing under conditions that mimic agricultural environments (Amann et al., 1995; Clardy et al., 2006; Raaijmakers and Mazzola, 2012).

The findings of this study underscore the importance of direct antagonism as an important MOA in controlling Phytophthora root rot. Effective antimicrobial control requires close interaction between the BCO and the pathogen, as evidenced in the meta-analysis by the significantly enhanced efficacy observed with the simultaneous application of BCOs and *Phytophthora* inoculation, compared to preventive or curative BCO treatments. Notably, 62% of reported biological treatments involved preventive BCO applications. This suggests a preference among researchers for preventive application, next to simultaneous application (27%), likely to maximize a direct contact between BCOs and the pathogen. This aligns with the central role of direct antagonism. Moreover, co-introducing specialized metabolites alongside BCO cells has shown to enhance *Phytophthora* suppression in plant-based experiments. However, few studies have evaluated the *in planta* effect of pure specific specialized metabolites showing antagonistic properties against these pathogens, leaving room for further research. In contrast, *in vitro* studies on pure specialized metabolites active against Phytophthora root rot species have been conducted more frequently. Specialized metabolites produced by *Actinomyces*, *Bacillus*, *Burkholderia*, *Lysobacter*, *Paenibacillus*, *Pseudomonas*, *Serratia*, and *Trichoderma* have demonstrated strong *in vitro* antimicrobial properties (Table 2). Several studies, including López-García et al. (2024), report the effectiveness of bacterial and fungal extracts against tree-infecting *Phytophthora* species. Volynchikova and Kim (2022) further support these findings, showing that many of these microorganisms directly antagonize *P. infestans*, and *P. nicotianae* via antimicrobial compounds that inhibit mycelial growth, sporulation, and zoospore germination. The cyclic lipopeptides fengycin B and iturin A, derived from *Bacillus* species, inhibit mycelial growth of *P. infestans* (Wang et al., 2020b, 2020). In addition, leucinostatin A and B, cyclic lipopeptides produced by the beneficial fungus *Purpureocillium lilacinum*, inhibit the growth of *P. infestans*, as shown by *in vitro* mutant analyses (Wang et al., 2016). Similarly, brabantamide A, a cyclic lipopeptide produced by *P. corrugata*, inhibits phospholipases in *P. infestans* (Van Der Voort et al., 2015). The latter two compounds have not specifically been evaluated for their antimicrobial activity against root-rot inducing *Phytophthora* species that infect annual crops.

In addition to direct antagonism, some studies have identified alternative MOAs through which BCO enhance plant resistance to control Phytophthora root rot pathogens in annual crops. Induced resistance mechanisms include the induction of programmed cell death, activation of defense-related enzymes, and reinforcement of structural barriers such as callose deposition. Similar effects have also been observed with other *Phytophthora* species. For example, *Pseudomonas fluorescens* SS101 and *Bacillus pumilus* W-7 produce active compounds (massetolide A and surfactin, respectively) that induce plant resistance against *P. infestans* in tomato and potato, respectively (Tran et al., 2007; Wang et al., 2020b).

This study highlights the enhanced efficacy of BCOs in greenhouse and field trials compared to growth chamber experiments. Initial screenings in growth chambers enable the evaluation of a broad range of BCOs, which increases the possibility of inconsistent or adverse effects of BCOs. Subsequent validation, with only BCOs that were successful in the growth chamber experiments, in larger-scale greenhouse or field trials, improves success rates (Köhl et al., 2011).

Moreover, this study demonstrated that the application method significantly influences the biocontrol activity of BCOs. Root or soil treatments proved more effective than seed treatments, likely due to lower colonization capacity of BCOs when applied to the seed. Soil and root treatments typically have shorter intervals between BCO application and pathogen introduction, increasing the likelihood of BCO survival and activity. Similarly, for the control of *Rhizoctonia solani*, *Bacillus subtilis* RB14-C was more effective when applied to the soil compared to seed treatment, as the latter led to reduced bacterial colonization on tomato roots (Szczech and Shoda, 2006). The effectiveness of seed treatments can be improved by optimizing the seed coating formulations (Kumar et al., 2017). To maximize effectiveness, the application method of BCOs should be optimized for each specific cropping system. For example, in soilless greenhouse tomato cultivation, a BCO substrate

drench is recommended before transplanting seedlings, as tomato is typically grown in substrates. This method is also suitable for other greenhouse crops, such as peppers, cucumbers, and strawberries (López-Aranda et al., 2011). However, substrate choice is critical as BCO efficacy varies depending on the substrate and BCO used. For example, *Streptomyces griseoviridis* performs best in pumice, while *Trichoderma* is more effective in peat for controlling *P. cryptogea* and *Pythium aphanidermatum* in tomato (Khalil et al., 2011). Managing *P. sojae* in field-grown soybean, is particularly challenging due to the pathogen's persistence in plant debris (Giachero and Marquez, 2022). In such cases, BCO seed treatments are often preferred over soil applications, as plant debris can reduce the effectiveness of soil-applied BCOs.

Another finding of the meta-analysis was that increasing the number of BCO applications did not significantly enhance the efficacy. This suggests that *Phytophthora* may not persist after the initial BCO treatment, potentially due to the direct antagonistic activity of the BCO and its successful establishment within the plant environment. In this review, many reported BCOs are known to be highly efficient root colonizers. For example, *Paenibacillus* species are able to thrive in the plant rhizosphere (Langendries and Goormachtig, 2021), while *Trichoderma* species are also recognized for their ability to colonize plant roots (Woo et al., 2023). Similarly, *Bacillus* species can colonize plant roots through the production of surfactin, which promotes biofilm formation and enhances their survival (Anckaert et al., 2024). However, the studies included in this meta-analysis did not quantify the BCO or the *Phytophthora* pathogen between successive treatments nor did they investigate whether the BCOs produce antimicrobial metabolites within the plant environment, highlighting area for further research.

A refined screening approach is proposed for identifying effective BCOs against Phytophthora root rot in annual crops. Screening efforts should emphasize the co-application of BCOs and their metabolites alongside *Phytophthora* inoculation to ensure direct antagonism. Root and soil treatments should be prioritized over seed treatments, but alternative strategies, such as repeated BCO applications or preventive and curative treatments, should also be considered when initial screenings yield inconsistent results. Finally, more research into the modes of action of BCOs is crucial for refining and scaling up their application in sustainable crop protection.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used chatGPT in order to improve the clarity, coherence, and academic tone of the text. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

CRediT authorship contribution statement

Kilian Van Loocke: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Noémie De Zutter:** Writing – review & editing, Validation, Software, Methodology, Conceptualization. **Kris Audenaert:** Writing – review & editing, Validation, Conceptualization. **Barbara De Coninck:** Writing – review & editing, Validation, Supervision, Conceptualization. **Monica Höfte:** Writing – review & editing, Validation, Supervision, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2025.105834.

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