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Systematic Review

Current Progress in Microbial Biocontrol of Banana *Fusarium* Wilt: A Systematic Review

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Abstract: *Fusarium oxysporum* f. sp. *cubense* (*Foc*) poses a significant threat to global banana production. This systematic review updates current knowledge on the efficacy of various antagonistic microorganisms in controlling *Foc*, considering the recent spread of this disease to new regions. The studies were systematically analyzed, focusing on methodologies, results, and conclusions to provide a comprehensive overview of current research and its practical implications. A total of 118 studies were reviewed, covering the use of antagonistic microorganisms such as *Trichoderma* spp., *Bacillus* spp., *Streptomyces* spp., and *Pseudomonas* spp., both in pure cultures and in consortia. Most studies focused on controlling *Foc* TR4 in Cavendish subgroup bananas and originated from Asia. Microbial consortia demonstrated a higher control percentage with lower variability, particularly in genera such as Pseudomonas. In contrast, pure cultures were more commonly used for Streptomyces. The choice between consortia and pure cultures depends on the genus and the experimental context, as each approach has distinct advantages. Although the reviewed studies were generally of high quality, long-term research is still lacking. Antagonistic microorganisms represent a promising alternative for *Foc* control, although their efficacy depends on the specific strain and environmental conditions. It has been observed that inoculating these microorganisms onto seedlings before transplantation or in combination with organic matter enhances their effectiveness. Localized testing and formulation optimization are recommended to improve their application as preventive and suppressive tools in soil against infections. The review highlights a vast diversity of microbial agents with high efficacy rates, various modes of action, and additional benefits for plant development beyond *Foc* biocontrol. Furthermore, some studies achieved 100% control at the plant level under controlled conditions. These findings demonstrate that biological control is a viable alternative for integrated *Foc* management. Future research should prioritize new approaches that facilitate the widespread adoption of these methodologies, including microbial formulation, field application, and integration with other control methods.

Keywords: *Fusarium oxysporum* f. sp. *cubense*; *Fusarium* wilt of banana; antagonist microorganisms

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1. Introduction

During the past century, the banana *Fusarium* wilt (BFW) epidemic, caused by *Fusarium oxysporum* f. sp. *cubense* (*Foc*) race 1 (R1), led to significant losses in global banana production [1]. The disease predominantly affected commercial varieties such as 'Gros Michel', posing a substantial threat to the banana export industry. The introduction of the *Foc* R1-resistant Cavendish variety facilitated the recovery of the banana sector [2]. However, global banana and plantain production is threatened by the widespread dissemination of tropical race 4 (TR4), now officially reported in 23 countries, with a significant presence in South and Southeast Asia [3]. *Foc* TR4 affects the widely cultivated Cavendish clone and traditional banana varieties [4] and plantains, which serve as a staple food and a vital income source, particularly in Africa, Latin America, and the Caribbean [5]. This *Foc* variant can potentially cause total yield losses in affected banana plantations, reaching up to 100% [6]. As a result, this disease seriously impacts banana production, threatening food and economic security in many tropical and sub-tropical regions [5].

Although tolerant Cavendish somaclones, such as Formosana (GCTCV-218), are used in commercial fields affected by the pathogen in Taiwan, the Philippines, and Mozambique [7], tolerance has been observed to vary depending on soil inoculum levels [8]. However, no widely accepted *Foc* TR4-resistant commercial variety is available [8,9]. Chemical control methods have shown limited success against *Foc* TR4, as exemplified by the fungicide propiconazole [10], the only product currently registered for field use in Australia [11]. Propiconazole inhibits sterol biosynthesis in fungi [12], and due to its xylem mobility [13], it was hypothesized to control *Foc* progression within the xylem of banana plants [14]. However, it fails to prevent *Foc* sporulation. Moreover, herbicide applications such as glyphosate, atrazine, or paraquat/diquat have been shown to exacerbate fungal colonization during plant senescence, with the resulting production of micro- and macroconidia serving as potential inoculum sources for nearby plants [10]. No effective fungicide or strategy exists to eradicate pathogens from contaminated fields currently. Consequently, managing the disease remains exceedingly costly. It poses a significant challenge for global agriculture, particularly for small-scale banana farmers who lack the financial resources to sustain production in the presence of *Foc* TR4.Biological control has garnered increasing attention as a sustainable and effective alternative for managing BFW [15]. Since the 1970s, over 180 studies have investigated the potential of various microbial biological-control agents (MBCAs), including bacteria such as *Pseudomonas* spp. and *Bacillus* spp., as well as fungi like *Trichoderma* spp., among others [16]. These agents have demonstrated significant efficacy under laboratory, greenhouse, and field conditions, achieving 50% to 100% control rates, depending on the microbial genus, formulation, and application conditions [17,18]. Furthermore, innovative strategies such as microbial consortia, synthetic communities, and advanced bioformulations have been explored. These approaches often incorporate organic amendments with various MBCAs or their metabolites to enhance their effectiveness and stability under field conditions [19]. Despite notable progress in this field, significant knowledge gaps persist, limiting the widespread adoption of biological control in banana production systems and its integration into comprehensive disease management plans [8].

The most recent review of *Foc* biological-control agents was published in 2019, before detecting *Foc* TR4 in Latin America [16]. Since then, *Foc* TR4 has been reported for the first time in Colombia in 2019 [20], Peru in 2021 [21], and Venezuela in 2022 [22]. In Peru, the continued spread of the fungus could result in significant losses in the production of organic bananas for export and conventional bananas for the domestic market [23]. Therefore, the disease has regained prominence and demands renewed attention from the scientific community to develop measures for the prevention, containment, and management of *Foc* TR4.

This article systematically reviews the current knowledge on MBCAs used to manage BFW. It analyzes the main strategies developed to date, including recent studies on the efficacy of microbial consortia, bioformulations, and the impact of various microbial genera on the pathogen and soil microbial communities. Additionally, the article highlights future prospects for addressing existing challenges and explores opportunities for integrating biological control into comprehensive BFW management strategies, aiming to enhance the sustainability and resilience of global banana production.

2. Materials and Methods

2.1. Literature Search and Dataset Construction

A systematic review of the scientific literature was conducted based on adapting the PRISMA methodology (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) [24]. The research question guiding the methodological process was as follows: what are the MBCAs used to manage *Foc* in bananas? The review included only original research articles published in indexed journals available in scientific databases such as Scopus, Web of Science, and PubMed, with full-text access in digital format. Articles published in English, Spanish, and Chinese between 2012 and 2024 were considered, focusing on experimental studies involving MBCAs use for the control of BFW in vitro, in seedling trials, or experimental field plots involving banana (*Musa* spp.) or plantain. To ensure the comprehensiveness of the search process, the following descriptors were derived from the research question: "banana", "*Fusarium*", and "antagonistic microorganisms". Additionally, Boolean operators were applied to refine the systematic search, using the following query: ("*Fusarium oxysporum* f. sp. *cubense*" OR "*Fusarium* wilt" OR "*Foc* TR4" OR "Panama disease" OR "*Fusarium* wilt disease") AND ("banana" OR *Musa* spp.) AND ("antagonistic microorganisms" OR "biocontrol agents" OR *Trichoderma* OR *Bacillus* OR *Pseudomonas* OR Actinomycetes OR "biological control") AND ("efficacy" OR "control" OR "management").

2.2. Article Selection and Exclusion

Figure 1 illustrates the flowchart outlining the article identification and selection process. Among the databases, Web of Science (WoS) contributed the most to the systematic review, accounting for 278 articles (44.7% of the total). Scopus followed this with 251 articles (40.3%) and PubMed with 93 articles (15%).

A total of 622 records (raw data) were retrieved from the three open-access electronic databases used in this search: PubMed, Web of Science, and Scopus (Figure 1). Exclusion criteria were (1) opinion articles, scientific communications, and review studies (313 records excluded); (2) studies on crops other than *Musa* spp., or those unrelated to BWF (169 records excluded); and (3) Exclusion of studies without access to the full paper or those involving the use of purified metabolites (20 records excluded).

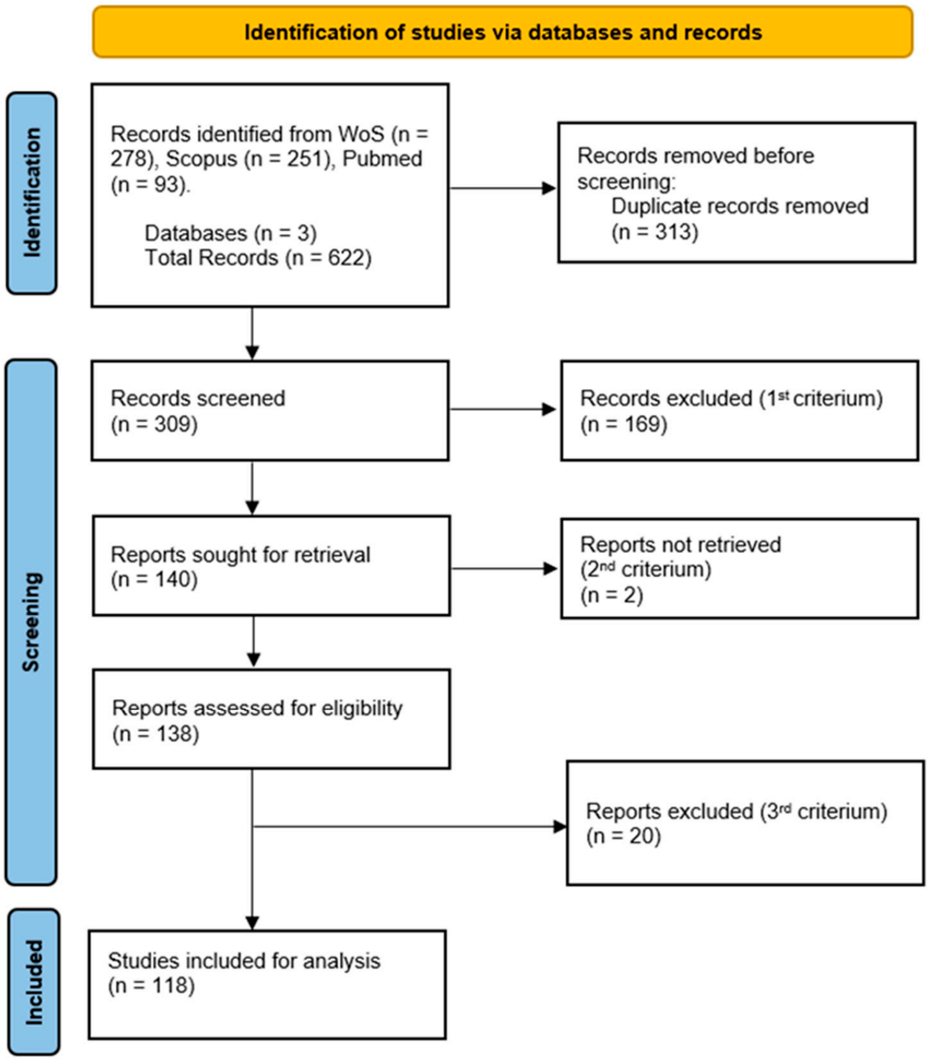

Figure 1. PRISMA flow diagram for the selection of studies included in the present systematic review on microorganisms used as antagonists of the *Foc* strains (R1, R2, and R4) affecting banana cultivars to date.

2.3. Data Extraction and Analysis

Following the selection of studies, the classification and analysis process involved a critical reading of the full texts to extract relevant information and construct a data matrix. Several key variables were analyzed to ensure a comprehensive assessment of the research.

The first variable considered was the microorganism, referring to the species that demonstrated the highest efficacy in controlling *Foc* among the evaluated treatments. This information was either explicitly stated by the authors or inferred based on quantitative data, such as percentage inhibition or control. For results and graph analysis, microorganisms were grouped by genus.

The year of publication was also recorded to assess temporal trends in research. Additionally, the country where each study was conducted was identified to understand geographical research distribution. The race *Foc* studied was classified as Race 1, Race 2, or Race 4 (R4), with the latter including both subtropical (ST4) and tropical (TR4) variants. Another important variable was the origin of the biocontrol microorganism, which referred to the source or environment from which the microorganism was isolated for use against *Foc* at different trial levels.

The experimental level of trial was categorized as dual culture (Petri dish assays), seedling trials (inoculation and pathogen control under controlled conditions), or experimental plots. If a study included multiple levels, a priority order was applied to highlight the most relevant level for the study's objectives, following this sequence: experimental plots, seedling trials, and dual culture.

The dose of the applied microorganism, whether as a pure inoculum or in a consortium, was documented for seedling trials and experimental plots. The control efficacy was assessed based on the pathogen suppression achieved by the microorganism or consortium, expressed as a percentage. For dual-culture trials on Petri dishes, this was represented as the percentage of inhibition, whereas for seedling and experimental-plot studies, the percentage of disease control was reported. If the article did not explicitly provide this value, it was calculated using the following formula:

$$\% \text{ efficacy} = \frac{\text{disease measure (control)} - \text{disease measure (MBCA)}}{\text{disease measure (control)}}$$

The measurement unit used to quantify the disease caused by *Foc* was also recorded. In seedling and experimental-plot studies, this referred to the metric applied in the article, while for dual-culture trials, it corresponded to the percentage inhibition of the *Foc* colony.

The mechanism of pathogen control by MBCA was documented as described in the article. Finally, for seedling and experimental-plot trials, the banana variety used in the study was also taken into account.

2.4. Graphical Summary

The matrix data were analyzed quantitatively to identify patterns in the publication of MBCA studies over time and their correlation with the spread of *Foc* TR4 into new regions. Trends in the production of articles by country and their focus on specific MBCAs were also examined, along with the control efficacy of each genus of microorganism, whether used as pure cultures or in consortia. Data visualization was performed using the ggplot2 package (v3.3.5) and the circlize package (v0.4.16) in R (v4.1.2), implemented via the RStudio (v2021.09.02+382) platform. Additionally, studies presenting exceptional or novel findings in *Foc* control and the diversity of biocontrol mechanisms employed by the MBCAs were critically discussed.

3. Results and Discussion

In total, 118 articles on the use of MBCAs for *Foc* control were consolidated. These studies involved contributions from 17 countries and examined 26 MBCA genera. The research findings are organized into three tables: studies addressing *Foc* Race 1 (R1) and Race 2 (R2) are presented in Table 1, and studies focusing on *Foc* Race 4 (R4) presented in Table 2 or those where the pathogen's race is not explicitly mentioned are summarized in Table 3.

Table 1. Efficacy of microorganisms tested with antagonistic activity against *Foc* R1 and R2.

MCBA	Origin of MCBAs	Level	Doses	Efficacy (%)	Measure	Mechanism	Variety	Reference
Pseudomonas fluorescens *Bacillus* spp.	*Pseudomonas fluorescens:* ND *Bacillus* spp.: banana stems	Seedling trial	3 mL/plant ($3{\cdot}10^8$ CFU/mL)	74.05	Control	Resistance induction	Red Banana (AAA)	[25]
Achromobacter *Bacillus cereus*	Rhizosphere and banana plants	Experimental-plot trial	50 g/plant (10^8 cells/g)	4.2	Incidence	Antibiosis	*Musa acuminata* AAA cv. Grand Naine	[26]

Table 1. *Cont.*

MCBA	Origin of MCBAs	Level	Doses	Efficacy (%)	Measure	Mechanism	Variety	Reference
Trichoderma sp. *Trichoderma asperellum*	Banana rhizosphere	Experimental-plot trial	50 g/plant (10^6 spores/mL)	47.63	Incidence	Antibiosis	*Musa acuminata* AAA cv. Grand Naine	[27]
Glomus mossae Pseudomonas spp.	Banana rhizosphere	Seedling trial	*Glomus*: 250 g/plant (80 spores/100 g of soil); *Pseudomonas*: 15 mL/plant (10^8 cells/mL)	100	Severity	Competitive inhiitibon	*Musa acuminata* AAA cv. Grand Naine	[28]
Trichoderma asperellum	Banana plant	Seedling trial	ND (10^6 CFU/mL)	50	Control	Antibiosis, mycoparasitism	Gros Michel (AAA)	[29]
Bacillus subtilis Pseudomonas fluorescens	*Pseudomonas fluorescens:* Rice plants *Bacillus subtilis:* Banana plants	Experimental-plot trial	ND ($3{\cdot}10^{10}$ CFU/mL)	78	Control	Resistance induction	Red Banana (AAA)	[30]
Bacillus spp.	Bank	Seedling trial	ND	100	Severity	Antibiosis	Prata-Anã	[31]
Pseudomonas fluorescens	*Bacillus siamensis*: Banana plant *Pseudomonas fluorescens*: Bank	Seedling trial	200 mL/plant (10^8 CFU/mL)	30	Incidence	Antibiosis, systemic resistance induction	Pisang Awak (Namwa) banana (*Musa* spp. ABB)	[32]
Bacillus amyloliquefaciens	Banana plant	Seedling trial	ND	25	Inhibition	Antibiosis and Enzyme production	Gros Michel (AAA)	[33]
Trichoderma sp.	Maize rhizosphere	Dual-culture trial	NA	52.2	inhibition	Enzyme production	NA	[34]
Bacillus sp.	Banana plant	Dual-culture trial	NA	96	Inhibition	Antibiosis, enzyme production, systemic resistance induction	NA	[35]
Trichoderma sp. *Pseudomonas fluorescens*	Banana rhizosphere	Seedling trial	15 g/pot	*Trichoderma* sp. + *P. fluorescens* 63.43 *T. asperellum* + *P. fluorescens*: 63.43	Control	Mycoparasitism, antibiosis, resistance induction	Rasthali (Silk-AAB)	[36]
Trichoderma harzianum Trichoderma tomentosum	Maize roots and rhizosphere	Dual-culture trial	NA	54	Inhibition	Mycoparasitism, enzyme production, antibiosis	NA	[37]
Streptomyces spp.	Rhizosphere of tomato plants	Seedling trial	10 mL/plant	78.1	Control	Enzyme production	*Musa* (ABB Group) 'Pakchong 50'	[38]
Bacillus spp. *Trichoderma* spp.	Commercial products in Colombia	Seedling trial	100 mL/plant (10^6 conidia of *Trichoderma*/10^7 CFU of *Bacillus*)	73.9	Incidence	Antibiosis, enzyme production, systemic resistance induction	Gros Michel (AAA) and Cavendish cv. Williams (as a control)	[39]

NA: not applicable. ND: could not be inferred.

Table 2. Efficacy of microorganisms tested with antagonistic activity against *Foc* R4.

MCBA	Origin of MCBAs	Level	Doses	Efficacy (%)	Measure	Mechanism	Variety	Reference
Penicillium citrinum	Wild banana plant	Seedling trial	50 mL/plant (10^6 CFU/mL)	27.05	Incidence	Systemic resistance induction	Berangan	[40]
Streptomyces griseus	Soil	Plate assay	5 mL/200 g of soil (10^8 CFU/mL)	66	Abundance	Mycoparasitism	NA	[41]
Bacillus amyloliquefaciens	Banana rhizosphere	Seedling trial	1.5% soil weight (10^9 CFU/g)	28	Incidence	Antibiosis	*Musa AAA* Cavendish cv. Brazil	[42]

Table 2. *Cont.*

MCBA	Origin of MCBAs	Level	Doses	Efficacy (%)	Measure	Mechanism	Variety	Reference
Bacillus pumilus	Banana rhizosphere	Dual-culture trial	NA	42.47	Inhibition	Antibiosis, enzyme production	NA	[43]
Bacillus amyloliquefaciens	Banana plant	Dual-culture trial	NA	30	Inhibition	ND	NA	[44]
Bacillus amyloliquefaciens	ND	Seedling trial	450 g/pot (10^9 CFU/g)	75	Incidence	Antibiosis	*Musa acuminata* AAA Cavendish cv. Brazil.	[45]
Burkholderia cenocepacia	Roots of *Chrysopogon zizanioides*	Experimental-plot trial	10 mL/plant (6–7 OD 60 nm of cells)	86.32	Incidence	Antibiosis	*Musa acuminata* AAA Cavendish cv. Pei-Chiao	[46]
Bacillus amyloliquefaciens	Banana rhizosphere	Experimental-plot trial	In seedlings: 4% *w*/*w* in pots. After transplanting: 500 units/plant	68.5	Incidence	Antibiosis	Musa AAA Cavendish cv. Brazil	[47]
Bacillus amyloliquefaciens	Banana rhizosphere	Seedling trial	2% *w*/*w* (10^9 CFU/g)	64.97	Incidence	Antibiosis	*Musa* AAA Cavendish cv. Brazil	[48]
Serratia marcescens	Rubber tree rhizosphere	Experimental-plot trial	100 mL/plant (10^8 CFU/mL)	70	Severity	Enzyme production	Williams (Cavendish subgroup)	[49]
Bacillus amyloliquefaciens	Banana rhizosphere	Experimental-plot trial	8 a 12 tn/ha per year (10^8 CFU/g)	70	Incidence	ND	*Musa acuminata* AAA Cavendish cv. Brazil	[50]
Streptomyces lunalinharesii	Soil of the banana crop	Seedling trial	100 mL/plant (of the diluted ferment 1/50)	72.72	Control	ND	"Nantian Huang" and "Brazilian bananas"	[51]
Bacillus velezensis	Tomato rhizosphere	Seedling trial	50 mL/seedling (~10^6 cells per gram of soil)	44	Incidence	Antibiosis	Cavendish banana seedling 'Brazilian'	[52]
Streptomyces sp.	Rhizosphere of *Opuntia stricta*	Dual-culture trial	Crude ethanolic extract of *Streptomyces* at 100 µg/mL	67.59	Inhibition	Antibiosis	NA	[53]
Bacillus velezensis	Banana rhizosphere	Seedling trial	0.5% *w*/*w* (10^8 CFU/g)	66.7	Control	Competition	*Musa* AAA Cavendish cv. Brazil	[54]
Bacillus amyloliquefaciens	Banana rhizosphere	Seedling trial	180 g/seedling 10^9 CFU/g)	55	Control	Antibiosis, competition	*Musa acuminata* Cavendish cv. Brazil.	[55]
Schizophyllum	Plant ND	Seedling trial	20 mL suspension ($5{\cdot}10^4$ spores/plant)	78.57	Incidence	Antibiosis, mycoparasitism, competition	*Musa acuminata* AAA Cavendish cv. Gran Naine and GCTCV 219	[56]
Pseudomonas aeruginosa Trichoderma harzianum	Bank	Seedling trial	50 g/plant	66.67	Severity	ND	*Musa acuminata* AAA Berangan	[57]
Trichoderma harzianum, *Glomus* spp.	*Trichoderma harzianum*: Commercial inoculant; *Glomus* spp.: commercial mycorrhiza	Seedling trial	*Trichoderma harzianum*: $3{\cdot}10^5$ conidia/g; *Glomus* spp.: 5 g/plant (does not specify cubic centimeters (cc)	100	Control	ND	Lakatan banana seedlings	[58]
Serendipita indica	ND	Seedling trial	100 mL/kg of soil (10^5 chlamydospores/mL)	ND	Severity	Systemic resistance induction	*Musa acuminata* cv. Tianbaojiao	[59]
Streptomyces manipurensis	Banana rhizosphere	Seedling trial	50 mL/plant	78.95	Incidence	Antibiosis	NA	[60]

Table 2. *Cont.*

MCBA	Origin of MCBAs	Level	Doses	Efficacy (%)	Measure	Mechanism	Variety	Reference
B. amyloliquefaciens Pseudomonas spp.	Banana rhizosphere	Seedling trial	10^8 CFU/g of substrate per plant	91.66	Abundance	Antibiosis	Cavendish cv. Brazil	[61]
Trichoderma reesei, *Trichoderma asperellum*, *Trichoderma koningiopsis*	*Trichoderma reesei:* banana rhizosphere. *Trichoderma asperellum:* banana rhizosphere. *Trichoderma koningiopsis:* rhizosphere of *Saccharam spontaneum*	Experimental-plot trial	500 mL of a 3% formulation (10^8 spores/mL)	85.19	Inhibition	Mycoparasitism, resistance induction	*Musa acuminata* AAA Cavendish cv. Grand Naine (G-9)	[62]
Streptomyces violaceusniger	Soil of the banana crop	Seedling trial	100 mL/plant (ND concentration)	64.94	Control	Enzyme production	*Musa acuminata* AAA Cavendish cv. Brazilian	[63]
Bacillus velezensis	Banana rhizosphere	Seedling trial	500 mL (50 times diluted from 10^8 CFU/mL of *Bacillus*)	ND	Incidence	Resistance induction, microbial community modification	*Musa acuminata* cv Cavendish	[64]
Consorcio: *Bacillus subtilis*, *Bacillus velezensis*, *Penicillium* sp.	Banana rhizosphere	Seedling trial	*Bacillus*: 5 mL per $1.5{\cdot}10^8$ CFU/mL *Penicillium*: $1.8{\cdot}10^3$ spore/mL	60.4	Control	Enzyme production, mycoparasitism, antibiosis	*Musa acuminata* William B6	[65]
Trichoderma asperellum	Banana rhizosphere	Seedling trial	5 mL; $2.4{\cdot}10^3$ spore/mL per planta	32.38	Severity	Antibiosis, mycoparasitism	Williams B6	[66]
Streptomyces sp.	Soil of the banana crop	Seedling trial	100 mL/700 g of soil (of the filtered and diluted ferment 1/50)	83.12	Control	Antibiosis	Not mentioned (the paper does not specify the variety of banana used in the experiments)	[67]
Streptomyces huiliensis	Rhizosphere of *Opuntia stricta*	Dual-culture trial	NA	62.55% (*Foc* R4) 44.51% (*Foc* R1)	Inhibition	Antibiosis	NA	[68]
Streptomyces hygroscopicus	Roots of *Piper austrosinense*	Seedling trial	ND (10^6 CFU/mL)	71.36	Control	Enzyme production, systemic resistance induction	*Musa* AAA Cavendish 'Brazil'	[69]
Pseudomonas aeruginosa	Compost	Dual-culture trial	ND	75	Inhibition	Systemic resistance induction, enzyme production	NA	[70]
Bacillus amyloliquefaciens	Banana plant	Dual-culture trial	NA	85.72	Inhibition	Antibiosis	NA	[71]
Talaromyces pinophilus, *Clonostachys rossmaniae*	Soil	Seedling trial	1.5 kg of soil (10^5 CFU/g)	ND	ND	Antibiosis and competition for resources	*Musa acuminata* AAA Cavendish cv. Brazilian	[72]
Streptomyces aureoverticillatus	ND	Seedling trial	200 mL/plant (10^5 CFU/mL)	86.09	Control	Antibiosis	Cavendish banana subgroup cv. Brazil	[73]
Streptomyces sp.	Banana rhizosphere	Seedling trial	100 mL/plant (10^7 CFU/mL)	89.4	Control	Antibiosis	Cavendish banana	[74]
Streptomyces morookaensis	Bank	Seedling trial	100 mL/plant (10^6 spores/mL)	78.12	Incidence	Antibiosis	Banana variety Brazilian (*Musa* sp., AAA, Cavendish subgroup)	[75]

Table 2. *Cont.*

MCBA	Origin of MCBAs	Level	Doses	Efficacy (%)	Measure	Mechanism	Variety	Reference
Streptomyces sp. nov.	Rhizosphere of *Machilus pingii*	Dual-culture trial	NA	80.48	Inhibition	Antibiosis	NA	[76]
Bacillus mycoies	Bank	Dual-culture trial	NA	61.1	Inhibition	Antibiosis, systemic resistance induction	NA	[77]
Ceratobasidium sp.	Banana crop weeds	Seedling trial	50 mL/plant	28.94	Severity	Mycoparasitism, antibiosis, competition for nutrients	Grand Nine GCTCV 218	[78]
Bacillus	Banana cultivation in vitro tissue seedlings	Dual-culture trial	NA	79.63	Inhibition	Antibiosis	NA	[79]
B. amyloliquefascens	Infected banana plants	Seedling trial	40 mL/plant	85.61	Control	Mycoparasitism, antibiosis, systemic resistance induction	Cavendish	[80]
Bacillus velezencis	Banana plant	Seedling trial	1% (10^8 CFU/mL)	100	Incidence	Antibiosis, resistance induction, hyperparasitism	Karpooravalli	[81]
Streptomyces sp.	Coral *Dichotella gemmacea*	Seedling trial	1 kg of soil (10^6 CFU/g of soil)	ND	Incidence	Antibiosis	Banana (Baxi Jiao, *Musa acuminata* AAA genotype cv. Cavendish)	[82]
Trichoderma harzianum and *Trichoderma viride*	Banana cultivation	Seedling trial	ND	ND	ND	Antibiosis and enzyme production	*Musa paradisiaca* cv. Malnad Rasbale	[83]
Streptomyces sichuanensis	Rhizosphere of *Opuntia stricta*	Seedling trial	100 mL/plant	51.01	Control	Antibiosis	Cavendish cultivar 'Brazilian' (AAA)	[84]
Streptomyces yongxingensis	Coral	Dual-culture trial	NA	75.42	Inhibition	Antibiosis	NA	[85]
Streptomyces sp.	Coral	Seedling trial	10^6 CFU/g of soil	80	Inhibition	Antibiosis	Not specified variety	[86]
Streptomyces sp.	Plant of *Curculigo capitulata*	Dual-culture trial	NA	73.18	Inhibition	Antibiosis	NA	[87]
Bacillus siamensis	Banana rhizosphere	Seedling trial	25 mL/plant (10^7 CFU/mL)	88.26	Control	Antibiosis and hyperparasitism	Brazilian bananas (*Musa acuminata* AAA genotype cv. Cavendish)	[88]
Trichoderma harzianum, *Burkholderia cepacia*, *Paenibacillus terrae*, *Bacillus amyloliquefaciens*	Banana rhizosphere	Experimental-plot trial	62.5 L/ha (10^9 CFU/mL)	57.14	Control	ND	Banana Cavendish subgroup cv. Williams	[89]
Pseudomonas chlororaphis, *Bacillus velezensis*, *Trichoderma virens*	Banana rhizosphere	Seedling trial	50 mL/plant (10^7 cells or conidia/mL)	62	Incidence	Antibiosis and systemic resistance induction	Gran Enana	[90]
Streptomyces malaysiensis	Roots of *Curculigo capitulata*	Dual-culture trial	NA	42.88	Inhibition	Systemic resistance induction and antibiosis	Banana Cavendish subgroup cv. Brazil	[91]

Table 2. *Cont.*

MCBA	Origin of MCBAs	Level	Doses	Efficacy (%)	Measure	Mechanism	Variety	Reference
Pseudomonas spp.	Banana cultivation	Seedling trial	50 mL/plant (ND concentration)	39.4	Incidence	Antibiosis, biofilm formation, quorum sensing, and competition for resources	*Musa acuminata* Cavendish cv. Brazil	[92]
Pseudomonas aeruginosa	Soil in banana cultivation	Dual-culture trial	NA	50.38	Inhibition	Antibiosis	NA	[93]
Bacillus amyloliquefaciens + *Burkholderia cepacia*	Rhizosphere of various crops	Seedling trial	100 mL/plant (10^8 CFU/mL)	68.89	Severity	Antibiosis, Parasitism	Williams B6	[94]
Bacillus licheniformis	Banana rhizosphere	Seedling trial	500 mL (10^8 cells/mL)	77.59	Inhibition	Antibiosis and systemic resistance induction	*Musa acuminata* AAA Cavendish cv. Grand Naine	[95]
Trichoderma parareesei	Banana rhizosphere	Seedling trial	100 mL/plant (10^7 CFU/mL)	72	Control	Antibiosis, enzyme production, hyperparasitism	*Musa acuminata* L. AAA genotype cv. Cavendish	[96]
Macrophomina phaseolina and *Xylaria feejeensis.*	Banana plant	Dual-culture rial	NA	96.56	Inhibition	Antibiosis, mycoparasitism	NA	[97]
Bacillus siamensis	Stem of *Vicia villosa*	Seedling trial	100 mL/plant (10^8 CFU/mL)	79.25	Control	Antibiosis	Baxi (*Musa* spp. AAA)	[98]
Piriformospore indica Streptomyces morookaensis	*Piriformospora indica*: Commercial *Streptomyces malaysiensis*: Native	Experimental-plot trial	50 mL (10^6 chlamydospore /mL)	90	Incidence	Antibiosis and mycoparasitism	*Musa acuminate* AAA Cavendish cv. Brazilian	[99]
Pseudomonas spp.	Rhizosphere and banana plants	Seedling trial	20 mL of broth 5.0·10^7 CFU/g per plant	ND	ND	Antibiosis and systemic resistance induction	*Musa*, AAA Cavendish cv. Brazil	[100]
Bacillus velezensis	Banana plant	Seedling trial	0.1 mL/plant (10^6 CFU/mL)	80	Severity	Antibiosis and systemic resistance induction	*Musa acuminata* AAA Cavendish cv. Brazilian	[101]
Streptomyces hygroscopicus	Roots of *Piper austrosinense*	Dual-culture trial	50 µL (500 µg/mL)	82.09	Inhibition	Antibiosis	NA	[102]
Streptomyces sp.	Leaves of a tea plant	Seedling trial	15 mL/plant (10^6 CFU/mL)	87.7	Control	Antibiosis	*Musa acuminata* AAA Cavendish	[18]
Bacillus velezensis	Isolated from banana suppressive bulk-soils	Seedling trial	40 mL/plant (10^8 CFU/mL)	81.67	Control	Antibiosis and systemic resistance induction	*Musa acuminata* AAA Cavendish cv. Brazilian	[103]
Bacillus amyloliquefaciens	Banana rhizosphere, medicinal plants, commercial product	Seedling trial	5 mL/plant	1.86	Severity	Systemic resistance induction	*Musa acuminata* AAA Cavendish cv. Brazilian, Yunjiao No. 1 (AAA)	[15]
Trichoderma koningiopsis	Roots of *Dendrobium* plants	Seedling trial	10 g/plant	52.92	Control	Systemic resistance induction	*Musa* spp. AAA group Cavendish	[104]
Bacillus subtilis	Banana rhizosphere	Seedling trial	10^7 CFU/g of soil	48.3	Control	Antibiosis	ND	[105]
Pseudomonas aeruginosa	Banana rhizosphere	Dual-culture trial	100 µL per plate	69	Inhibition	Enzyme production	NA	[106]
Neofusicoccum parvum	Plant of *Moringa oleifera*, *Azadirachta indica*, and *Lavandula angustifolia*	Seedling trial	25 mL/plant (10^6 spores/mL)	100	Inhibition	Antibiosis and systemic resistance induction	Grand Naine	[107]

Table 2. *Cont.*

MCBA	Origin of MCBAs	Level	Doses	Efficacy (%)	Measure	Mechanism	Variety	Reference
Bacillus subtilis	Plant tissues of Moringa	Seedling trial	25 mL/plant (10^8 CFU/mL)	56.25	Inhibition	Antibiosis and systemic resistance induction	Berangan	[108]
Bacillus velezensis	Bank	Seedling trial	100 mL/plant ($5{\cdot}10^7$ CFU/mL)	64.48	Control	Antibiosis	*Musa acuminata* Cavendish cv. Brazilian	[109]
Bacillus subtilis	ND	Experimental-plot trial	30 mL/plant (10^8 CFU/mL)	63.05	Control	Systemic resistance induction	Berangan	[110]
Trichoderma harzianum	Natives: Rhizosphere of *Musa Paradisiaca* cv. Malnad Rasbale Bank: *Trichoderma harzianum* and *Trichoderma viride* of the NFCCI-Agarkar Research Institute	Dual-culture trial	NA	ND	ND	Antibiosis and mycoparasitism	NA	[111]
Streptomyces solisilvae	Soft coral *Menella woodin*	Seedling trial	10^6 CFU/g of soil	73.46	Severity	Antibiosis	Not mentioned (the paper does not specify the variety of banana)	[112]
Trichoderma brevicompactum	Rhizosphere of broad beans and coriander	Seedling trial	50 mL/plant	52.6	Severity	Antibiosis, competition, mycoparasitism, systemic resistance induction	Cavendish (AAA)	[113]
Pochonia chlamydosporia	Root nodules of *Dolichos lablab* in banana fields	Seedling trial	ND (10^6 CFU/mL)	96.87	Control	Competition for nutrients, antibiosis, enzyme production	*Musa* spp. AAA Brazilian cultivar	[114]
Streptomyces luomodiensis	Soil from a hot–arid valley	Dual-culture trial	NA	74.22	Inhibition	Enzyme production	NA	[115]

NA, not applicable. ND, could not be inferred.

Table 3. Efficacy of microorganisms tested with antagonistic activity against unspecified (ND) *Foc*.

MCBA	Origin of MCBAs	Level	Doses	Efficacy (%)	Measure	Mechanism	Variety	*Foc* race *	Reference
Bacillus amyloliquefaciens	Banana plant	Seedling trial	1.5% soil weight (10^9 CFU/g)	77	Control	Antibiosis	*Musa* AAA Cavendish cv. Brazil	R4 **	[116]
Pseudomonas fluorescens	ND	Experimental-plot trial	4 L/ha ($9{\cdot}10^8$ CFU/mL)	60	Incidence	Antibiosis	ND	ND	[117]
Bacillus amyloliquefaciens	Banana cultivation soil	Seedling trial	5 g of biofertilizer/kg of soil	84.94	Incidence	Resistance induction, niche competition	ND	ND	[118]
Bacillus amyloliquefaciens	Banana rhizosphere	Seedling trial	2% *w*/*w* soil ($3{\cdot}10^8$ CFU/g)	24.3	Incidence	Antibiosis	*Musa* AAA Cavendish subgroup cv. Brazil	R4 **	[119]
Bacillus amyloliquefaciens	Bank	Experimental-plot trial	6 kg/plant (10^9 CFU/g)	88	Incidence	Antibiosis	*Musa* AAA Cavendish cv. Brazil	R4 **	[120]
Trichoderma harzianum	Bank	Seedling trial	20% of the culture filtrate of *T. harzianum*	16.66	Incidence	Antibiosis, enzyme production	Dwarf Cavendish	R4 **	[121]

Table 3. *Cont.*

MCBA	Origin of MCBAs	Level	Doses	Efficacy (%)	Measure	Mechanism	Variety	*Foc race* *	Reference
Trichoderma viridae	Chili pepper roots	Seedling trial	Seedlings:10 g of rice (1.73·10^8 spores/g) Soil: 10 g of rice (1.69·10^8 spores/g)	65	Control	ND	Cavendish	R4 **	[122]
Bacillus subtilis	Bank	Seedling trial	60 mL (10^8 CFU/mL)	45.08	Incidence	Oxidative stress reduction	*Musa acuminata* cv. Berangan	R4 **	[123]
Azotobacter and *Bacillus* sp.	*Azotobacter* sp.: reed rhizosphere; *Bacillus* sp.: sugar cane and banana rhizosphere	Seedling trial	10^8 CFU/mL per plant	60	Inhibition	Antibiosis, resistance induction	ND	ND	[124]
Trichoderma asperellum	Soil	Seedling trial	500 mL/plant (10^7 conidia/mL)	94.44	Severity	Mycoparasitism, enzyme production	Cavendish banana cultivar	R4 **	[125]
Trichoderma spp., *Bacillus subtilis*	*Trichoderma* sp.: commercial *Bacillus subtilis*: commercial	Experimental-plot trial	8 L (*Trichoderma*) + 250 g (*Bacillus subtilis*)/ha	93.79	Severity	Competitive exclusion	*Musa balbisiana* ABB	R2 *	[17]
Trichoderma guizhouense Humicola spp.	Banana cultivation soil	Seedling trial	300 mL/plant	72	Incidence	Competition for nutrients and systemic resistance induction	*Musa* AAA Cavendish cv Brazil	R4 **	[126]
Trichoderma reesei	Bank	Dual culture	NA	36	Inhibition	Mycoparasitism	NA		[127]
Bacillus siamensis	*Volvariella volvacea* culture media	Dual culture	ND	ND		Antibiosis	NA		[128]
Bacillus vallismortis	Soil	Dual culture	NA	26.17	Inhibition	Antibiosis, systemic resistance induction	NA		[129]
Brachybacterium paraconglomeratum	Banana plant	Dual culture	NA	65.5	Control	Antibiosis	NA		[130]
Sarocladium brachiariae	*Brachiaria brizantha* leaves	Dual culture	ND	ND	ND	Antibiosis	ND	ND	[131]
Bacillus amyloliquefaciens	Costa marina	Dual culture	NA	78	Inhibition	Antibiosis	ND	ND	[132]
Beauveria caledonica	Banana weevils	Dual culture	NA	47.68	ET50	Antibiosis	ND	ND	[133]
Bacillus subtilis	Banana rhizosphere	Dual culture	NA	11.5	Inhibition	Antibiosis	ND	ND	[134]
Trichoderma harzianum	Soils of Agricultural Fields, cocoa bark and *Pleurotus* spp. substrate	Dual culture	NA	74.1	Inhibition	Mycoparasitism	ND	ND	[135]
Streptomyces albosporus	Banco	Dual culture	NA	76.33	Inhibition	Antibiosis	ND	ND	[136]
Bacillus spp.	Rizósfera de banano	Dual culture	NA	80.47	Inhibition	Antibiosis, enzyme production	ND	ND	[137]
Bacillus sp.	NA	Dual culture	NA	87.71	Inhibition	Competition for nutrients	ND	ND	[138]
Paenibacillus sp.	Banco	Dual culture	NA	46.6	Inhibition	Antagonism	NA	ND	[139]

Fusarium races are not indicated in the article, but they are inferred as follows: R2 * affects bananas of the Bluggoe subgroup (ABB), which includes *Musa balbisiana* ABB. R4 **: R1 and R2 are not pathogenic for the Cavendish group (AAA). NA: not applicable. ND: could not be inferred.

3.1. Asian Leadership in Antagonistic Microorganism Research and the Approach on Foc TR4

Most studies were published between 2014 and 2024, reflecting a growing interest in applying biocontrol methods in banana cultivation. The referenced studies span various authors and years, highlighting a diverse and evolving body of research on biocontrol strategies. Notably, research on microorganisms antagonistic to *Foc* is predominantly focused on the control of TR4, with 84.05% of the articles in this review addressing the use of this race.

Overall, the scientific community's response to the spread of *Foc* TR4 in various regions reflects the growing effort of countries to investigate the potential of different microorganisms for biological control as an alternative management strategy for this disease (Figure 2). However, the incursion of *Foc* TR4 into Africa in 2013 did not result in a sustained increase in biocontrol studies targeting this pathogen. One possible explanation is that the initial reports of *Foc* TR4 in Africa lacked scientific validation until 2020 and 2021, as noted in previous studies [7,140]. Additionally, historical reports as early as the 1940s documented cases of Cavendish banana plantations affected by *Foc* ST4 [141].

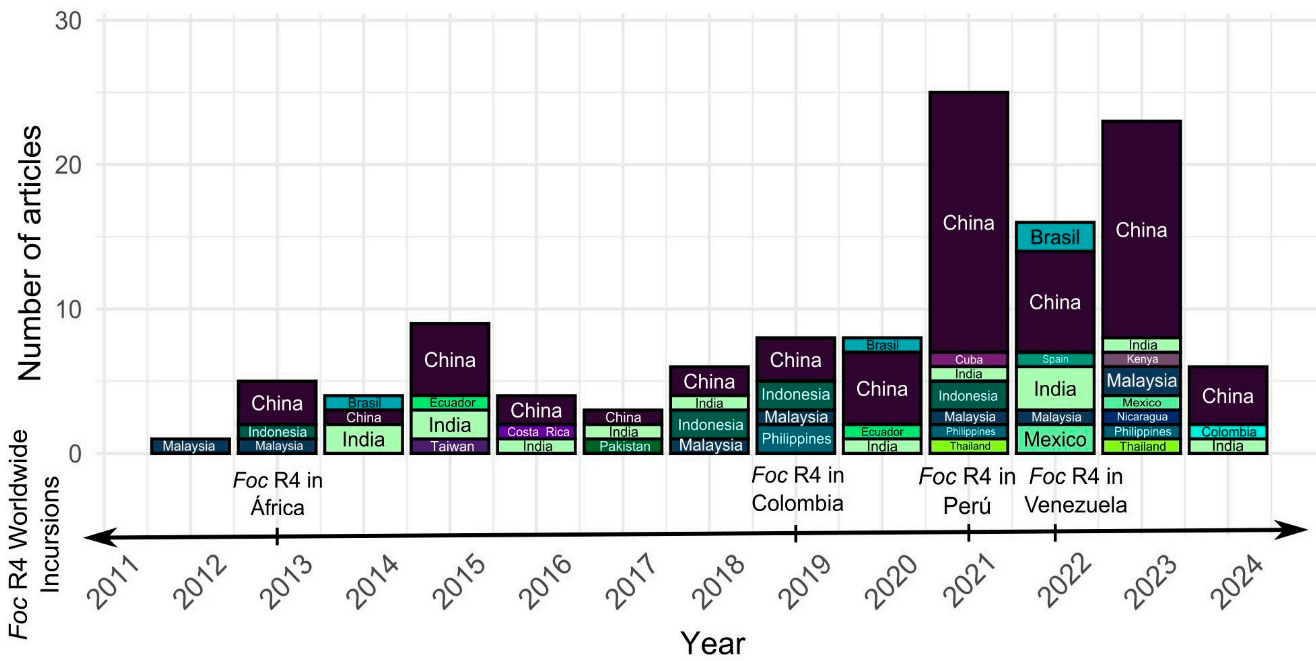

Figure 2. Number of studies included by country and year in the context of the emergence of *Fusarium oxysporum* f. sp. *cubense* races.

Since 2020, there has been a sustained increase in the publication of scientific articles, with peak outputs recorded in 2021 (25 articles) and 2023 (23 articles). This trend is likely associated with the emergence of *Foc* TR4 in South America, first reported in Colombia in 2019 [20], followed by its subsequent detection in additional countries in the region, such as Peru in 2021 [21] and Venezuela in 2023 [22], as well as with its prompt reporting [23].

Most studies on antagonistic microorganisms against *Foc* are predominantly conducted by Asian countries, accounting for 87.29% of the 118 analyzed studies in this publication. Research originating from China (55.9%) and India (11.86%)—countries with a long-standing history of this disease [93,142]—as well as Malaysia [143] and the Philippines [58], is particularly prominent. *Foc* TR4 is the predominant strain in these countries and is the focus of their publications. This trend in research output persists even after the incursion of *Foc* into South America, with Asian studies comprising 84.72% of publications between 2020 and 2024. It is worth noting that China and India remain the world's largest banana producers, although India's recorded production in 2022 (34.5 Mtn) significantly exceeds that of China (12.11 Mtn) [144].

Malaysia represents a noteworthy case, being the third-largest contributor to the analyzed studies in this review, despite ranking significantly lower in global banana production in recent years (42nd in 2022), with a production volume of just 329,573 tons [144]. This indicates a particular interest in developing sustainable alternatives for a crop primarily for local consumption. Bananas are the country's most widely cultivated crop, with only 15% of the total production destined for export [145]. Furthermore, Malaysia's research is oriented mainly toward varieties its domestic population prefers, such as Berangan [40,57,107,123].

South America, Brazil, Ecuador, and Colombia have demonstrated a growing research interest, driven by the incursion of *Foc* TR4 in Colombia and the subsequent spread of the pathogen to neighboring countries. However, participation in South American countries is still minimal compared to other regions (5.93%).

Figure 2 also highlights the efforts of Central American and Caribbean countries, including Costa Rica and Nicaragua, which have historically faced challenges with *Fusarium* wilt of bananas [146], and Cuba, which experienced significant issues with the disease in the 20th century [147].

The trend suggests that interest in studying *Foc* R4 is driven by the spread of TR4 into new regions and the urgent need to develop control and prevention strategies in countries vulnerable to its economic impact. This underscores that *Foc* is a global concern, affecting Asia and Central and South America. China leads in the number of studies on this phytopathogen, followed by India, highlighting the critical role of scientific collaboration and international surveillance in addressing its potential impact on global food security and banana industry production.

The predominance of Asian studies in the literature on the biocontrol of *Fusarium* in bananas may influence the global applicability of the findings due to agroecological, genetic, and crop management differences in other banana-producing regions. Asia is a key epicenter for banana production and the impact of *Foc* TR4, which has driven increased research efforts in this region. However, the limited representation of studies from Latin America and Africa—also major banana-producing areas—could hinder the extrapolation of biocontrol strategies to other soil and climate conditions, production systems, and locally cultivated banana varieties.

It would be relevant to assess how this geographical bias affects the generalization of results and whether the approaches developed in Asia are equally effective on other continents. Therefore, there is a clear need to expand research across different contexts to strengthen the scientific foundation of biocontrol and its global application.

3.2. Preference for Antagonistic Microorganisms Studied in the Scientific Community

Some countries demonstrate strong trends in studying certain microorganisms, as shown in Figure 3. China, the country with the highest number of research studies, strongly focused on the genera *Bacillus* and *Streptomyces*. Specifically, 39.39% of the studies conducted in China focus on *Bacillus*, while 33.33% focus on *Streptomyces*. In terms of global research output, China contributed 88% of all publications on the genus *Streptomyces* and 58.5% of those on the genus *Bacillus*.

India ranked as the second-largest contributor to research on biocontrol agents for *Foc*. Studies in this country primarily focus on three genera of microorganisms: *Trichoderma*, *Bacillus*, and *Pseudomonas*.

Regarding the genus *Trichoderma*, 50% of the studies are concentrated in China and India. Notably, Latin American countries contributed 25% of the research on this genus, making it the most predominant microorganism in studies from this region.

The research production from the Philippines is noteworthy for its focus on novel microorganisms for *Foc* control, including *Schizophyllum*, *Ceratobasidium*, *Glomus*, *Macrophomina*, and *Xylaria*.

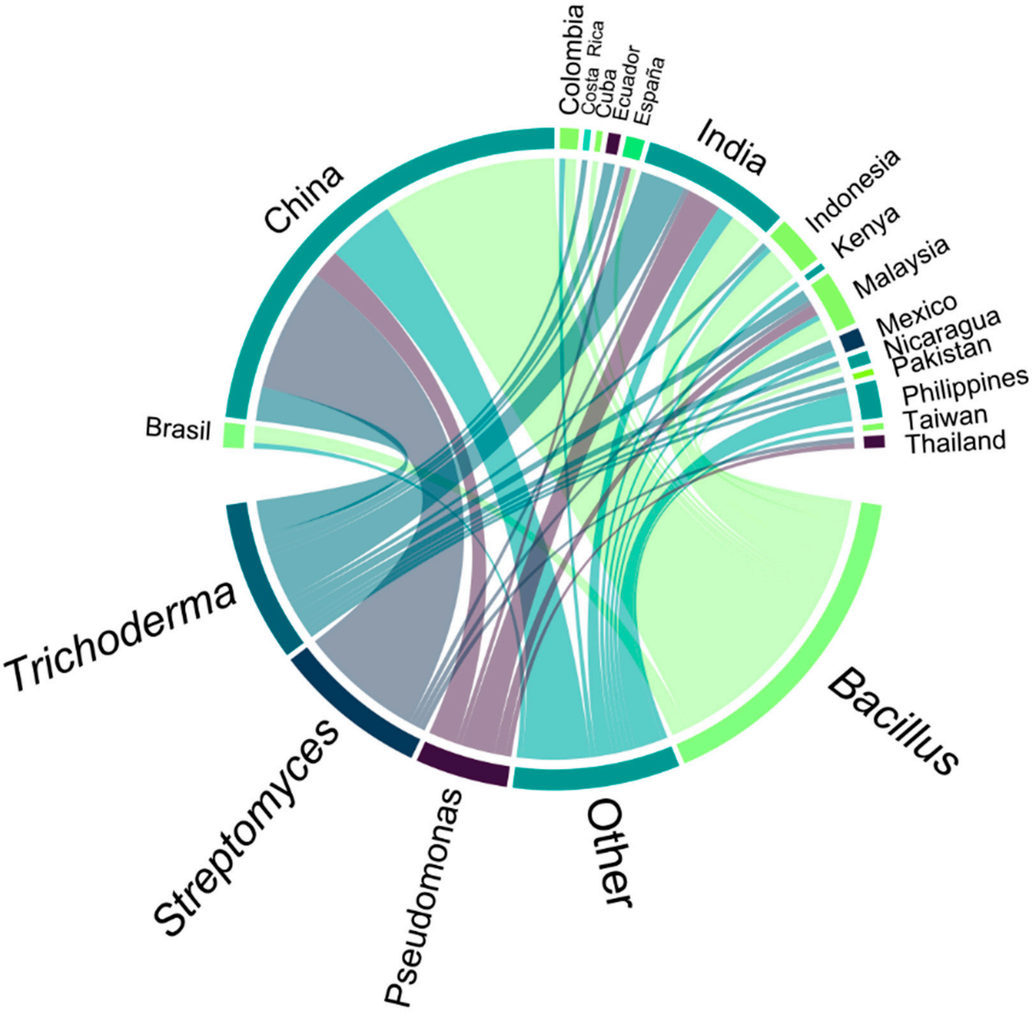

Figure 3. Chord chart showing the relationship between biocontrollers' genera and countries. Line thickness is proportional to the number of articles in each group.

3.3. General Efficacy and Action Mechanisms of Microbial Biological-Control Agents (MBCAs)

The studies measured control efficacy by different metrics, such as disease incidence, severity, and the number of operational taxonomic units (OUTs) of *Foc*, in seedling trials and experimental plots. These metrics help us to understand not only the reduction in the presence of the pathogen but also the reduction of its impact on plants. Additionally, a broad overview of the different mechanisms of action and application doses for each of the different biological-control microorganisms (MBCAs) that can be used to manage diseases in bananas, particularly in relation to the control of fungal or bacterial pathogens, is shown in Tables 1–3. It also details the source of the microorganism, the trial type, the control efficacy (in percentage), the variety of bananas on which it was tested, the MCBA mechanism involved in biocontrol, the *Foc* race used in each experiment, and the references of the studies.

In summary, four microbial genera were identified as predominant in the reviewed articles: *Bacillus*, *Pseudomonas*, *Trichoderma*, and *Streptomyces*, accounting for 88.14% of the studies. These MBCAs have been used individually and in a consortium and have proven effective as potential biocontrol antagonists of *Foc* in bananas, significantly reducing the incidence and severity of the disease [15,16,27,31,39,45–47,56,60,66,75,78,82,94,99,112,117,118,123,125,148–153]. The efficacy of these microorganisms against phytopathogens such as *Foc* TR4 is attributed to their modes of action, which include direct antagonism through antibiosis (production of substances that inhibit the pathogen), mycoparasitism, and indirect competition, such as altering plant metabolism by inducing systemic resistance and protective effects [15,25,36,40,59,62,64,69,70,77,80,90,91,100,101,103,124,126] or competing for nutrients or space [72,78,92,114,126,154].

3.3.1. Mechanisms of Microbial Action in the Biocontrol of *Foc*

Antibiosis is the production of antifungal metabolites, mainly antibiotics, that contribute to the biological control of fungi and bacteria and target a broad variety of phytopathogens [155,156]. The genera *Pseudomonas* and *Bacillus* spp. have received particular attention because of the potential to exploit the antifungal properties of strains for biological-control applications in agriculture. Some of these metabolites have a broad spectrum of activities against many plant pathogenic fungi, including *Fusarium* as cyclic lipopeptides, which are also produced by *Pseudomonas* spp.; similar target areas seen with iturin A; surfactin produced by *B. subtilis*; and other metabolites produced by *Bacillus* spp., such as zwittermicin A. Species of *Streptomyces* are well-known for their production of antifungals, including amphotericin B and nystatin, both belonging to the group of polyene antibiotics that target the fungal membrane [157]. The secondary metabolites produced by *Trichoderma* spp. play an important role in its antifungal activity. Antibiotic compounds produced by species of *Trichoderma* include viridans (produced by *T. virens*), kininogenins (produced by *T. koningii*), cytosporone, trichodermol, mannitol, and 2-hydroximalonate acid [156]. This mechanism is the most described among authors as being associated with *Foc* biocontrol, with an efficacy between 48% and more than 90% in the different investigations at the seedling-trial and experimental plot-trial levels.

Induced systemic resistance (ISR) is a mechanism by which certain plant-beneficial rhizobacteria and fungi produce immunity, which can stimulate crop growth and resilience against various phytopathogens, insects, and parasites [158,159]. These beneficial rhizobacteria and fungi improve plant performance by regulating hormone signaling, including salicylic acid (SA), jasmonic acid (JA), prosystemin, pathogenesis-related gene 1, and ethylene (ET) pathways, which activate the gene expression of ISR, the synthesis of secondary metabolites, various enzymes, and volatile compounds that ultimately induce defense mechanisms in plant [158–160]. Whitin the genus *Pseudomonas*, strains of *Pseudomonas fluorescens* can induce ISR in plants, enhancing resistance against *Fusarium oxysporum* mediated by the activity of defense enzymes such as polyphenoloxidase (PPO) or activating JA and ET pathways [25,159,160]. *Bacillus* strains such as *Bacillus tequilensis* and *Bacillus licheniformis* can induce systemic resistance in tomatoes against *Fusarium* wilt by increasing defense enzymes like β-1,3 glucanase and peroxidase [161]. *Trichoderma* spp. have been shown to activate plant systemic resistance, in addition to having biocontrol attributes [104]. *Trichoderma* strains demonstrated a significant increase in the activity of antioxidant enzymes, such as catalase (CAT), phenylalanine ammonia-lyase (PAL), polyphenoloxidase (PPO), and peroxidase (POD), suggesting that *Trichoderma* strains can enhance plant defense systems by activating their antioxidant mechanisms, showing protective effects against FOC TR4 infection [104,162]. This mechanism, associated with plant defense against *Foc* infection, has an efficacy between 27% and 100% in the different investigations at the seedling-trial and experimental plot-trial levels.

Mycoparasitism is a mechanism of interaction where a fungus (mycoparasite) parasitizes another fungus (host), using it as a source of nutrients. This process can be biotrophic, where the mycoparasite obtains nutrients from living cells of the host, or necrotrophic, where the mycoparasite kills the host and then feeds on its remains [163]. Mycoparasites, such as *Trichoderma* species, are widely studied and used in the biological control of plant diseases due to their ability to invade and destroy plant pathogenic fungi through the production of lytic enzymes and toxic metabolites [163,164]. Mycoparasitic fungi of the Trichoderma genus are known for their ability to coil around pathogen hyphae, penetrate their cell walls, and secrete enzymes such as chitinases and glucanases that degrade the cell structure of the host fungus [165,166]. This mycoparasitism process is crucial for the control of *Fusarium oxysporum* f. sp. *cubense* (*Foc*) TR4. The efficacy of mycoparasitism is associated with other mechanisms of action, such as antibiosis and enzyme production [37,111].

Hyperparasitism refers to a biological-control strategy where one parasite (hyperparasite) attacks another parasite (the primary pathogen). This mechanism can significantly influence host–parasite interactions, reducing the virulence and transmission rate of pathogens [165]. Hyperparasitic fungi, such as certain strains of *Trichoderma harzianum* and *Trichoderma asperellum*, can directly attack and parasitize *Fusarium oxysporum* hyphae. This interaction often involves mechanisms such as the coiling of the hyperparasite around the hyphae of the pathogen and the production of antimycotic metabolites, leading to its destruction [166]. Several studies highlight the efficacy of *Trichoderma* species in the control of *Fusarium*. *Trichoderma* isolates have shown significant suppression of *Fusarium* growth through mechanisms such as space occupation, competition for nutrients, and direct mycelial growth on the pathogen, indicating hyperparasitism [167]. The effectiveness of hyperparasitism as a biological-control method depends on the ecological fitness of the hyperparasite and its ability to establish itself in the soil and interact effectively with the pathogen.

Competition for space and nutrients is a mechanism of interaction, while competitive exclusion is a possible outcome in which one microorganism outcompetes another to occupy physical space and access essential nutrients in their environment. This competition is a fundamental aspect of microbial ecology and plays an important role in determining the structure and dynamics of fungal communities. Fungi compete for limited resources, such as nutrients and space. This competition can lead to the inhibition or suppression of one species by another, affecting its growth and survival [167]. These antagonistic interactions can be direct, as in the case of *Trichoderma* spp., where species effectively compete against *Foc* TR4 for space and nutrients in the soil by producing antifungal compounds limiting the ability of the pathogen to establish and proliferate [168,169] or indirectly by altering the nutrient composition of the environment to favor a particular species [167,170]. This mechanism in the plant defense against *Foc* infection has an efficacy between 66% and 100% for some studies carried out with *Bacillus velezensis* [54], *Trichoderma* spp. [17], *Glomus mossae* [28], *Pseudomonas* spp. [92], and *Pochonia chlamydosporia* [114], thus demonstrating the high potential of efficacy for these mechanisms in their application for biological control.

3.3.2. General Efficacy of Microbial Biological-Control Agents (MBCAs)

As illustrated in Figure 4, the *Bacillus* genus exhibits a high and quite variable control efficacy, with values ranging from 50% to 100%. Notably, the results from studies involving *Bacillus velezensis* [101,103,149], *Bacillus siamensis* [32,98], and *B. amyloliquefaciens* [71,80,171] demonstrate pathogen-inhibition efficacy ranging from 70% to 100%. Strains of the *Bacillus* genus isolated from rhizospheric soil or native endophytes generally show significantly higher efficacy than studies utilizing strains from microorganism banks of research institutes or universities.

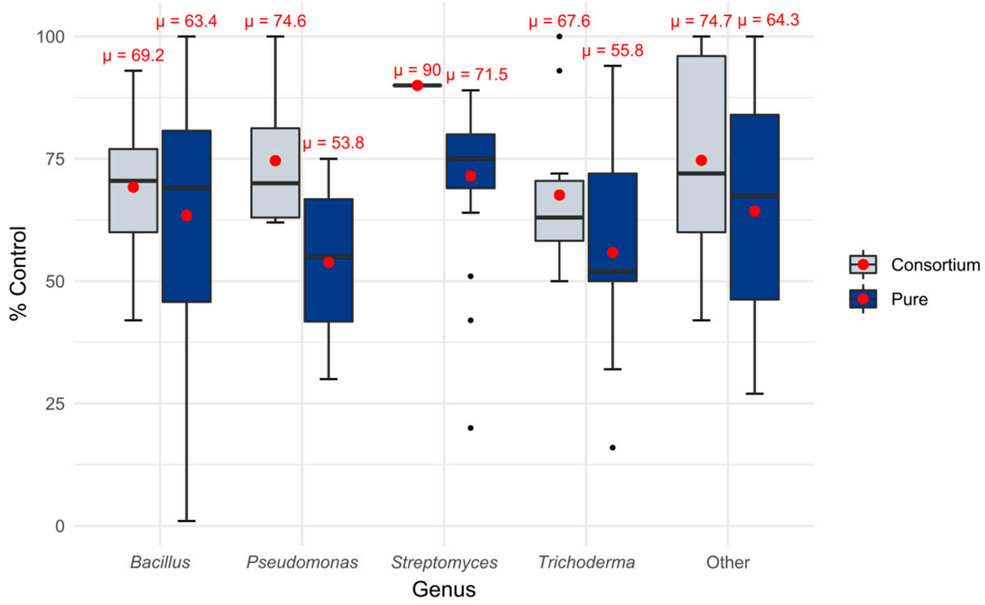

Figure 4. Efficacy of MBCAs genera according to their mode of application: single (pure) or in consortium. The category "Other" includes microorganisms reported in less than four studies. μ: arithmetic mean.

Bacillus spp. has demonstrated effectiveness as a biocontrol agent against various plant pathogens, including *Foc*, through direct antibiosis, plant growth promotion, and systemic resistance induction in host plants. Species such as *Bacillus subtilis*, *B. velezensis*, and *B. amyloliquefaciens* have exhibited high efficacy in colonizing banana plants [80] and inhibiting *Foc* TR4 [120], with plasmid retention exceeding 98% and chemotaxis toward *Foc* hyphae [80], highlighting their potential for biocontrol applications [15].

Specific antibiosis mechanisms employed by *Bacillus* against *Fusarium* (*Foc*) include the production of lipopeptides, such as bacillomycin D, iturin A, and phengicin homologous compounds, which inhibit *Fusarium* fungi growth by inducing morphological changes in the plasma membranes and cell walls of the fungi [172,173]. Lipopeptides, including iturin A, phengicin, and surfactin, have been emphasized in inhibiting *Fusarium* growth, suggesting that these metabolites are key components of the antibiosis mechanisms [174]. Additionally, *Bacillus* employs other antagonistic strategies against *Foc*, such as the production of lytic enzymes like chitinases A and B, chitosanase, and glycoside hydrolase, which are induced and contribute to the *Fusarium* growth control [175].

In contrast, the biocontrol efficacy of *Pseudomonas* is moderate, with values ranging from 50% to just over 70%. Most of the available data pertain to native microorganisms. *Pseudomonas fluorescens* has been shown to inhibit *Foc* TR4 under in vitro conditions [176]. Additionally, studies have identified *Pseudomonas aeruginosa* strains as potential biocontrol agents, demonstrating high antifungal activity against *Foc* through a multifaceted antagonistic approach. This includes the production of bioactive compounds and the secretion of cell wall hydrolytic enzymes, positioning *Pseudomonas* as a promising candidate for controlling *Fusarium* wilt in bananas [106].

Secondary metabolites produced, such as DAPG (2,4-diacetyl phloroglucinol) by *Pseudomonas fluorescens* strains, are well-documented for their antifungal properties, particularly by affecting mitochondrial function [177]. This disruption is critical for plant pathogenic fungi's energy production and cellular metabolism. Additionally, pyoluteorin, which exhibits broad-spectrum antifungal activity, including against *Foc*, has been reported [178]. Pyrrolnitrin, another antifungal compound produced by *Pseudomonas fluorescens*, has shown inhibitory effects on *Foc* growth, as well as phenazines, which possess broad-spectrum antimicrobial properties [178,179]. These compounds can inhibit fungal growth by generating reactive oxygen species (ROS) that damage cellular components [178].

The control efficacy of Streptomyces is moderate to low, ranging from 20% to 60%. Some outliers (black dots, Figure 4) correspond to trials with significantly lower efficacy. Strains of different *Streptomyces* species have been identified as potential biocontrol agents for managing banana wilt caused by *Foc* TR4. Characteristic strains of the *Streptomyces* genus exhibit intense antifungal activity against *Foc* TR4 by producing indoleacetic acid (IAA), siderophores, and various hydrolytic enzymes. The presence of PKS-I and PKS-II genes in the genome of *Streptomyces* sp. suggests potential for the biosynthesis of bioactive substances [180]. Additionally, *Streptomyces* genus is known to produce secondary compounds such as lipoproteins A and B, which alter fungal cell membranes, inhibiting mycelial growth and conidial sporulation [181]; xerucitrin A and 6-pentyl-α-pyrone, which exhibit inhibitory activity against *Foc* TR4; chitinase and β-1,3-glucanase, which degrade fungal cell walls [69]; hygromycin B, which disrupts the integrity of the *Foc* TR4 cell membrane, inhibiting mycelial growth [102]; and salvianolic acid B, which has broad-spectrum antifungal activity. Salvianolic acid B is photostable, thermostable, and non-mutagenic, making it a promising biofungicide [182].

The biocontrol efficacy of *Trichoderma* species against *Foc* shows variability, with values typically ranging from 35% to 90%, depending on the species and trial type (double cropping, seedling trial, or experimental plot contaminated with *Foc*). The *Trichoderma* genus is well-known for its biocontrol capacity against various pathogens, including *Foc*. The species that have shown the best results in trials against *Foc* are *Trichoderma asperellum* [125,137], *Trichoderma harzianum* [121,135], and *Trichoderma viridae* [122], which have been demonstrated to significantly inhibit the mycelial growth of *Foc* and enhance plant growth parameters [183,184]. As with other microbial groups, indigenous microorganisms exhibit slightly greater efficacy than strains from culture collections, although this is not always consistent.

Trichoderma species employ multiple mechanisms to antagonize and inhibit *Foc*, as outlined below: mycoparasitism, in which *Trichoderma* directly parasitizes *Foc* by enveloping its hyphae and penetrating its cell walls, leading to the destruction of the pathogen [184,185]; hydrolytic enzyme production, such as chitinases, β-1,3-glucanases, and proteases, which degrade the cell walls of *Foc*, thereby inhibiting its growth [185]; and antibiosis through the production of secondary metabolites and antibiotics that suppress the *Foc* growth. These metabolites include volatile organic compounds (VOCs) and non-volatile compounds with antifungal properties [156–159,185–188]. The induction of plant defense mechanisms, such as systemic resistance, enhances the plant's ability to resist *Foc* infections by activating plant defense pathways and stimulating the production of defensive compounds [189,190].

Trichoderma asperellum was generally noted for its high efficacy (94.44%) under seedling test conditions. On the other hand, *Bacillus amyloliquefaciens* also demonstrated high efficacy (88%) in experimental plots, which is promising for large-scale applications. Most of the trials involving *Bacillus* spp. and *Trichoderma* spp. exhibited efficacy through mechanisms such as antibiosis, mycoparasitism, and enzyme production, with some variability in results depending on the dose and type of trial.

Other microorganisms, such as *Pseudomonas fluorescens* and *Streptomyces albosporus*, demonstrated potential, although their efficacy was generally lower compared to *Bacillus* and *Trichoderma*.

3.4. Efficacy of MBCAs in Consortia

The combined use of different genera of biocontrol microorganisms can enhance the efficacy of *Foc* control, as illustrated in Figure 4. These consortia reduce disease incidence and severity, promote plant growth, and improve soil properties. The combination of *Trichoderma* spp. and *Bacillus* spp. has shown promising results in reducing disease severity and incidence, with control efficacy ranging from 57.14% to 93.79% [17,39,89]. In contrast, combinations of different *Trichoderma* species exhibited lower efficacy, ranging from 47.63% to 77.24% for disease control [27,62]. Studies indicate that combining different strains of *Bacillus* and *Pseudomonas* results in increased efficacy in controlling *Foc*, with values ranging from 74.05% to 91.66% [25,61], surpassing those reported in studies combining strains of *Trichoderma* and *Pseudomonas*, which showed efficacy between 62% and 66.67% [36,57,90,153]. The best results were achieved in studies combining strains of the *Glomus* genus with *Trichoderma* and *Glomus* with *Pseudomonas*, achieving 100% control efficacy in both cases [28,58]. Similar outcomes were obtained when combining rhizospheric bacteria (such as *Achromobacter* sp. and *Rhizobium* sp.) as a consortium for *Bacillus* and *Pseudomonas*, yielding control efficacy (incidence) against *Foc* ranging from 57.8% to 72% in field studies. In comparison, potted-seedling trials demonstrated total suppression (100%) of *Fusarium* wilt [27]. Microbial consortia as a strategy for *Foc* control showed synergistic activity, with different microbial strains combined in a single formulation improving biocontrol efficacy compared to single-strain applications [89,90]. These consortia enhance disease control through multiple mechanisms, including direct antagonism [26,61,89,90,94], induction of plant resistance [25,30,36,39,62], and enhanced nutrient uptake. Further research and field trials are required to optimize formulations and application protocols for consistent and effective disease control.

3.5. Efficacy of MBCAs Associated with Their Origin

Regarding the origin of the microorganisms, it cannot be conclusively stated that native microorganisms generally exhibit higher efficacy compared to those sourced from collections or research facility banks. For the *Bacillus* genus, microorganisms from collections tend to display more consistent efficacy, though their performance is typically lower or comparable to that of native microorganisms from other genera. Given the diverse environments and isolation sites of the strains used across various studies targeting *Foc*, environmental variability appears to be a significant factor influencing their efficacy.

In terms of control, native microorganisms generally appear to be more effective, particularly in genera such as *Bacillus*, *Trichoderma*, *Pseudomonas*, and *Streptomyces*, and their consortia. This suggests that native microorganisms may be better adapted to the specific environmental conditions where control is implemented, thereby enhancing their efficacy [108,137,149]. However, microorganisms from collections or banks, while generally less variable in their performance, have occasionally demonstrated considerably higher efficacy than native strains, as observed with *Streptomyces* or *Bacillus* sourced from research institute banks in various studies [28,123,136]. Most studies utilized dual culture or seedling trials, which are common methods for assessing efficacy under controlled conditions and during early stages [35,56–58,71,77,123,124,134,137]. While trends can be observed, the results are not conclusive due to variations in experimental conditions and strain provenance across the trials.

Regarding the substrate from which MBCAs were isolated, the majority originated from soil [43,52,59,62,63,116,118,137], the rhizosphere [43,52,72,90,117,137], or parts of banana plants [25,32,71,97,118,134]. Other sources included marine environments [85] and different crops, such as rice [135,137], maize [37], and sugarcane [124], with the isolation processes detailed in the respective studies. Additionally, some MBCAs were obtained from research-institute culture banks [25,32,57,118,153,191,192] or commercial products [32,50,58].

3.6. Efficacy of MBCAs at Different Trial Levels: Dual Culture, Pots, and Plots

3.6.1. Dual Culture in the Laboratory

This preliminary method assesses the antagonistic potential of MBCAs against *Foc* directly in culture medium. Under these conditions, microorganisms demonstrate their activity through mechanisms such as competition, production of antifungal metabolites [104,108], enzyme production [43], or mycoparasitism [135]. While this assay provides valuable insights into the intrinsic capabilities of MBCAs, it does not account for complex factors such as soil interactions, climatic variability, or interaction with the plant. Overall, these studies represent a first approach to select promising MBCAs from a group of isolated microorganisms [34,76].

3.6.2. Seedling Trials

Seedling trials provide a more realistic environment to evaluate the effects of MBCAs, taking into account factors such as soil microbiota, application doses, and, most critically, interaction with the host plant. At this experimental level, additional control mechanisms can be assessed, including resistance induction [25,40,79] and modifications to the microbial community [45,57]. Moreover, many of the MBCAs studied have demonstrated the ability to promote banana plant growth [48,52] and enhance soil chemical properties [45]. An important factor in these trials is the application doses of MBCAs, which vary significantly among studies. For instance, some studies report the application of small volumes, from 3 mL per plant of a microbial suspension at a concentration of 3×10^8 CFU/mL [45], while others use larger volumes, up to 500 mL per plant, with a *Bacillus* suspension at a 1×10^6 CFU/mL per plant [64], or even up to 4 L of *Pseudomonas fluorescens* per hectare at a 9×10^8 CFU/mL, depending on the experimental conditions. The concentrations of microorganisms in these applications vary, generally between 10^6 and 10^8 colony-forming units (CFU) or conidia per milliliter. The application rate is a critical factor influencing the efficacy of MBCAs against *Foc* control [78]. Disease-control efficacy in seedling trials also varies widely, ranging from 25% to 100% under optimal conditions.

3.6.3. Experimental-Plot Trials

These tests are conducted directly in the field, offering the most realistic conditions for evaluating the efficacy of MBCAs. At this level, factors such as the spatiotemporal variability of the pathogen, environmental conditions, edaphic conditions, and agricultural practices significantly influence the outcomes. Although field trials often report more conservative control values compared to laboratory experiments, they are essential for validating the practicality and feasibility of MBCAs in agricultural production systems. The field studies reviewed here were conducted in fields with a long history of the disease to ensure uniform infection levels and optimal experimental conditions. Notably, only one study extended over at least three years and three growing seasons [50], and few studies included yield as a variable [47,50,110]. Disease assessment at this level is typically reported in terms of incidence and severity, using percentages or scoring systems. It is important to consider the unique spatial distribution of the disease in the field, which can contribute to variability in results. Additionally, the temporal progression of the disease and its infection rate are critical factors to account for [193]. These parameters provide valuable insights into the efficacy and longevity of control measures across growing seasons. Only one study evaluated the area under the disease progress curve (AUDPC), but this was conducted at the potted-seedling level [98].

In general, the efficacy of MBCAs varies depending on factors such as the species of MBCA, its specificity for *Foc*, the applied dose, and the experimental conditions. Nevertheless, under optimal conditions, complete disease inhibition has been achieved, as previously noted. However, the integration of MBCAs with other control methods, such as chemical control, has primarily been explored at in vitro levels [127]. Further research, particularly under field conditions, is essential to develop and validate an integrated disease management strategy.

Disease control efficacy varies widely, with values ranging from 25% to 100%. Some field trials show 100% efficacy, such as the application of *Pseudomonas putida* and other agents on banana cv. Grand Naine [27].

3.7. Banana and Plantain Varieties Tested

In the review of studies on the biological control of wilt caused by *Foc* in bananas, various varieties within the *Musa acuminata* and *Musa balbisiana* groups, belonging to different genomic subgroups, have been evaluated. The reviewed studies primarily include varieties from the Cavendish subgroup (AAA), which is the most commercially cultivated worldwide. Some of the most represented varieties in the studies were Grand Naine (AAA) [26–28,56,62,78,95,107], Williams (AAA) [39,65,66,89,94], Brazilian (AAA Cavendish) [47,48,52,54,61,63,69,75,84,101,103,120,126], and Dwarf Cavendish (AAA Cavendish) [119]. Studies were also found on other important varieties, such as Lakatan (AAA) [58], Red Banana (AAA) [137], Pisang Awak (ABB, Namwa) [32], and Prata-Anã (AAB) [31].

Regarding the efficacy of biocontrol in relation to variety, most studies on Cavendish (AAA) observed variable efficacy of microbial control agents (MCBAs), with control values ranging from 24.3% to 100% (Tables 1–3). Studies on Williams (AAA) and Grand Naine (AAA) reported intermediate-to-high efficacies (>50%), highlighting combinations with *Bacillus* spp., *Trichoderma* spp., and *Pseudomonas* spp. In the case of Berangan (AAA) and Brazilian (AAA), significant efficacies (>70%) were reported with *Bacillus velezensis*, *Pseudomonas* spp., and *Streptomyces* spp. (Figure 4). The combination of biocontrol agents and the formulation of microbial consortia show the best results in commercial varieties such as Grand Naine [26,28,62] and Williams [65,89], with control percentages of up to 100%. This diversity enables an understanding of how different treatments impact specific varieties, which is crucial for the implementation of strategies in commercial plantations.

Concerning the relationship between variety and *Foc* race, studies on varieties such as Cavendish (AAA) have been the most widely used to assess the impact of *Foc* R4, as they are susceptible to this pathogenic race. Additionally, some research included *Musa balbisiana* (ABB) [75] and less commercially relevant varieties, such as Pisang Awak (ABB) [32]. This diversity indicates that the trials have focused on cultivars that are susceptible to a wide range of *Foc* races, making the findings relevant for application across multiple banana-growing regions.

The success of biocontrol varies depending on the variety due to differences in soil microbiome and plant immune responses. This analysis highlights the need to expand research on less-studied varieties and to explore more specific strategies based on microorganism–variety interactions to improve the efficacy of BFW biocontrol.

3.8. Is There an Effective Microorganism for Controlling Foc?

Species of the *Bacillus* genus exhibit highly variable control values against *Foc*, with an average efficacy of 65%. However, some studies have reported complete suppression, achieving a 100% reduction in both the severity index and disease incidence [31,149]. Similarly, the *Trichoderma* genus also shows variable results, with a mean efficacy of 61%. Notably, some species, such as *Trichoderma asperellum*, have demonstrated up to a 94.44% reduction in the disease index during biocontrol against *Foc* [125]. On the other hand, *Streptomyces* genera, with a mean efficacy of 72.3%, exhibit less variability compared to other genera, such as *Bacillus* and *Trichoderma*, with efficacy reaching up to 89.4% in biocontrolling *Foc*. Additionally, *Neofusicoccum parvum* has shown promising results, with 100% inhibition of the disease, although further studies are necessary to fully assess the real potential of this species as a biocontrol agent against *Foc*.

In the case of microbial consortia, it can be concluded that the combined application of two or more genera for the biocontrol of *Foc* yields more favorable results (Figure 4). Notably, the *Glomus* genus in consortium with *Trichoderma* [58] and *Pseudomonas* [28] has demonstrated 100% efficacy in seedling trials. Similarly, the inclusion of rhizospheric bacteria, such as *Achromobacter* sp. [28], in the formulation of *Bacillus* consortia has shown a synergistic effect, achieving enhanced efficacy in disease suppression against *Foc* compared to consortia composed solely of *Bacillus* species. Further investigation into the synergistic mechanisms that enable consortia to achieve superior results in *Foc* control is needed. Studies examining the trophic relationships among microorganisms in soil and their role in *Foc* control provide a comprehensive understanding of the ecological dynamics involved, offering insights into how these relationships can be leveraged to suppress the *Foc* population [61]. However, such studies remain limited.

4. Conclusions

In conclusion, this analysis provides valuable guidance for the selection of microorganisms with biological-control potential, allowing their use to be tailored to the specific banana-growing conditions and agro-ecological characteristics of each region. By considering factors such as environmental compatibility, appropriate formulation, and application protocols, field results can be optimized, maximizing the efficacy of *Foc* control and contributing to a more sustainable management of *Fusarium* wilt.

Despite significant advances in research on the biological control of BFW, important gaps remain that hinder its widespread adoption and effective integration into production systems. One of the primary challenges is the variability in the efficacy of biological-control agents, as such variability heavily depends on specific soil conditions, such as pH, salinity, and structure, as well as the banana variety used. These limitations highlight the need for more comprehensive studies to adapt biocontrol strategies to specific environments and cultivars, ensuring consistent and replicable results across different growing regions.

Another crucial aspect is the development of efficient formulations that maintain the viability of microorganisms during storage and transport, while ensuring their ability to establish and compete with native microbial communities. This encompasses not only the stability of commercial products but also the standardization of application methods to optimize root colonization and enhance their effectiveness in controlling BFW. Moreover, the absence of large-scale testing under field conditions presents a significant gap, as promising results observed in the laboratory and controlled trials do not always translate into commercial or agricultural success.

This review has identified strategies that have demonstrated greater efficacy in improving the establishment of microorganisms in the soil. To strengthen the applicability of these findings, it is recommended to apply, in order of importance, *Trichoderma* spp., *Bacillus* spp., *Streptomyces* spp., and *Pseudomonas* spp. Based on available evidence, adopting specific practices can further optimize their effectiveness.

In the selection of microorganisms, it is recommended to prioritize the use of microbial consortia over pure cultures. Consortia that combine microorganisms from the genera *Trichoderma*, *Bacillus*, and *Pseudomonas* spp. have demonstrated greater stability and consistency in controlling *Foc*. Additionally, the use of arbuscular mycorrhizal fungi from the genus *Glomus* has shown a high level of efficacy. Although studies specifically on *Glomus* in this context are still limited, the available evidence suggests that it holds great potential.

To maximize the effectiveness of microbial applications, it is essential to optimize their timing, soil conditions and dosage. At the time of application perform inoculations on seedlings before transplanting or in early stages of the crop to favor rhizosphere colonization. Regarding soil conditions, we recommend incorporating organic matter along with the microorganisms to improve their persistence and activity in the soil. In terms of monitoring and dose adjustment, given the variability in efficacy due to soil type, climate, and banana variety, it is crucial to conduct preliminary trials under local conditions before large-scale adoption. Dosage should also be carefully adjusted, with recommended concentrations averaging between 1×10^6 and 1×10^8 CFU or conidia, depending on whether the microorganisms are applied in solid form combined with organic matter or as a direct liquid application per plant.

Finally, economic and social factors, such as production costs, lack of technical training, and negative perceptions toward bio-inputs, pose additional barriers to their widespread implementation. The successful integration of biological control into holistic crop management systems requires not only scientific advancements but also supportive policies, technology transfer, and incentives for adoption. Addressing these challenges is crucial to fully harness the potential of microorganisms as biofertilizers and biological-control agents, thereby promoting more sustainable and resilient agricultural systems.

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