



## REVIEW ARTICLE

# Fusarium Wilt of Banana: The Global Enigma and New Vistas in Management through Microbial Allies

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**ABSTRACT:** Fusarium wilt of banana, incited by a soil borne fungus *Fusarium oxysporum* f.sp. *cubense* (*Foc*) considered as a global enigma to the banana cultivation has garnered significant importance in recent times. The symptomatology of Fusarium wilt in banana illustrates a sophisticated and persistent pathology, one that operates below the surface long before visible signs appear. Understanding the full range of symptom expressions, both external and internal symptoms are essential for early detection. The genetic plasticity, and long-term soil persistence of *Foc* makes the management approaches a daunting task and necessitate an integrated approach to surveillance, quarantine enforcement, molecular diagnostics, and resistant cultivar development and most importantly its management through ecologically benign approaches. Use of rhizospheric and endophytic bioagents could be introduced as a new normal strategy in management frontiers. This review aims to provide a comprehensive overview of the current knowledge on *Foc*, covering its biology, pathogenic variability, survival strategies, and the evolving landscape of biological control options. Accordingly, we identify critical knowledge gaps, particularly in the Indian context, and outline strategic directions for future research to inform bio-based green management approaches against this resurgent phytopathogen.

**Keywords:** Biocontrol, Fusarium wilt, host defence, pathogenic variability

## INTRODUCTION

Banana (*Musa* spp.) is one of the most important and traded staple fruit crops cultivated across tropical and subtropical regions, with an annual production of 155 million metric tons globally combining both the banana and plantains (Kema *et al.*, 2021). Despite its prominence, banana production faces a grave threat from Fusarium wilt (FW), caused by *Fusarium oxysporum* f. sp. *cubense* (*Foc*), a soil-borne vascular pathogen that has become one of the most devastating diseases in the history of banana cultivation. First described in Australia (Ploetz and Pegg, 1997), *Foc* has progressively disseminated through informal exchanges of infected planting materials and the transboundary movement of contaminated soil. Ever since its first report from Australia in 1876 (Bancroft, 1876), the fungal pathogen made its global presence and by the mid-1900s, the fungal disease almost wiped out the Gros Michel (AAA), the dominant cultivar in global trade. Following this epidemic, Gros Michel (AAA) banana was replaced by Cavendish cultivars, known to be resistant to *Foc* (Stover, 1962; Ploetz, 2005). However, the recent emergence of Tropical Race 4 (TR4), a highly virulent strain has once again imperilled banana

cultivation globally by severely infecting the Cavendish cultivars too (Damodaran *et al.*, 2023).

Fusarium wilt, popularly known as Panama disease, invades banana roots, colonizes the xylem, disrupts water and nutrient flow, and eventually leads to plant death (Stover, 1962). Unlike bacterial wilt diseases, fungal wilt pathogens exhibit a unique ecological and pathological adaptation: colonization and systemic invasion of the xylem tissues, which serve as the plant's water-conducting highway. Once established within the vascular system, *Foc* initiates a complex cascade of pathological events including mechanical vessel plugging, toxin production, and enzymatic degradation of plant tissues, ultimately resulting in systemic wilt and death (Baruah *et al.*, 2025). As a soil-borne saprophyte, *Foc* is capable of infecting banana plants at all growth stages, including through asymptomatic colonization during early vegetative development. The more common manifestation of external symptom is yellow leaf syndrome, which begins with chlorosis at the margins of older leaves. As senescence progresses toward the younger canopy, leaves collapse downward from the petiole or midrib base, ultimately forming a characteristic "skirt" of dead foliage around the pseudostem. In some cases,

infected plants display the less conspicuous green leaf syndrome, where the overall canopy remains green and as the infection intensifies, longitudinal fissures appear along the pseudostem base, a hallmark of advanced vascular collapse (Stover, 1962; Baruah *et al.*, 2025). Internal symptoms provide more definitive diagnostic clues, ruling out the nutrient deficiency. Early stages show subtle yellowing of the root and rhizome vascular tissues, progressing to brown or black discoloration as the disease advances. The characteristic symptom is vascular browning in concentric patterns, particularly evident when cross-sections of the pseudostem or rhizome are examined. Eventually, the entire vascular system becomes clogged, obstructing the transport of water and nutrients, leading to wilting, plant death, and failure of fruit development. Infected suckers rarely bear fruit, and if they do, the yield and quality are significantly compromised (Perez-Vincente *et al.*, 2014).

The historical spread and persistent re-emergence of Fusarium wilt, despite decades of research and intervention, emphasize the need for integrated, genomically informed, and region-specific management strategies. In recent years, biological control has emerged as a sustainable and environmentally sound strategy to manage the dreaded soil-borne pathogens including *Foc* without compromising the soil health. Plant beneficial microbes of different fungal and bacterial genera such as *Trichoderma*, *Aspergillus*, *Beauveria*, *Metarhizium*, *Bacillus*, *Pseudomonas* etc. have long been used in crop production as growth promoter, biofertilizer and biopesticides in different crops including banana (Bora and Bora, 2020). Of late, owing to rising concern about ecosystem and human health, biocontrol approaches have garnered global attention. Microbial bioagents, including rhizobacteria, endophytes, and fungal antagonists, have demonstrated multifaceted benefits, not only in disease suppression but also in promoting plant growth through the production of phytohormones (e.g., indole-3-acetic acid), siderophores, and nutrient solubilization mechanisms (e.g., phosphorus, zinc) (Bora and Rahman, 2022; Saikia *et al.*, 2020). Many of the bioagents of rhizospheric and endophytic origin such as *Trichoderma* spp., *Bacillus* spp., have shown potential inhibition of *Foc* under *in vitro* and *in planta* condition. However, large-scale field validations remain limited, and mechanisms underlying their interaction with both host and pathogen require deeper exploration.

## HISTORICAL TRAJECTORY OF FUSARIUM WILT FROM REGIONAL OUTBREAK TO GLOBAL CRISIS

A noteworthy aspect of *Foc* biology is its shared biogeographical origin with banana; both the pathogen and its host are believed to have co-evolved in Southeast Asia (Li *et al.*, 2013). This includes the recently emerged and highly virulent Tropical Race 4 (TR4) strain. The epicenter of genetic diversity for *Foc* lies in areas such as Java, Sumatra, Malaysia, and the Borneo islands, where wild and cultivated *Musa* species provide an ideal ecological niche for pathogen evolution (Bentley *et al.*, 1995). It is widely accepted that human-mediated dispersal, including the trade of infected planting material and poor quarantine measures, facilitated the inadvertent spread of *Foc* to other continents (Butler, 2013).

The early 20<sup>th</sup> century witnessed one of the most catastrophic agricultural epidemics in history. The proliferation of Race 1 devastated Gros Michel monocultures across Central America, causing the collapse of the banana export industry and necessitating a shift to the Cavendish group, which was then considered resistant. The term “Panama disease” originates from the heavy toll the disease took in Panama and surrounding regions during this period. However, the reprieve offered by the Cavendish cultivars was short-lived. Since the 1960s, new outbreaks, especially involving TR4, have been recorded across Asia. Taiwan, once a major banana exporter to Japan, witnessed a severe decline in production due to *Foc*, with banana-cultivated land shrinking from approximately 50,000 hectares in the 1960s to just 6,000 hectares by the 2000s. Similar devastation occurred in Indonesia and Malaysia during the early 1990s (Molina *et al.*, 2009). Although *Foc* was reported in the Philippines as early as the 1970s, the arrival of TR4 in 2006 marked a tipping point. The disease triggered massive plantation abandonment, annual losses estimated at \$3 billion, and the displacement of approximately 66,000 farming families (Molina *et al.*, 2009). In response, the Federation of Cooperatives in Mindanao (FEDCO) in 2014 recommended shifting from banana to oil palm cultivation, highlighting both the severity of TR4 and the urgent need for sustainable alternatives (Carillo, 2014). In China, the situation was equally alarming. A 2006 survey in Guangdong Province revealed approximately 6,700 hectares of infected plantations, followed by severe outbreaks in Guangxi Province and Hainan Island by 2012 (Farquhar, 2012). These incidents further

underline the transboundary nature of the disease and its capacity to disrupt banana production systems at scale. India, currently the largest producer of bananas globally, have 70% Cavendish cultivar ‘Grand Naine’. This heavy reliance on a single genotype places the country at high risk of TR4 infection. The AAB genomic group of banana cultivars *viz.*, Rasthali, Malbhog and Silk is reported to be susceptible to Race 1 (Kumari *et al.*, 2022). India witnessed the first TR4 record in Bihar and later on, it was reported from Uttar Pradesh with 40% disease incidence (Thangavelu *et al.*, 2019; Damodaran *et al.*, 2019). Beyond India, TR4 has rapidly spread to countries including Jordan, Lebanon, Pakistan, Laos, Vietnam, Myanmar, and Israel (Zheng *et al.*, 2018), highlighting its capacity for global invasion.

### GENETIC AND PATHOGENIC DIVERSITY OF *Fusarium oxysporum* f. sp. *cubense*

*Fusarium oxysporum* f. sp. *cubense* exhibits extensive genetic and pathogenic diversity, structured into at least 24 vegetative compatibility groups (VCGs) and multiple evolutionary lineages. These VCGs differ in their host range and aggressiveness. Several traditional cultivars of India, including ‘Silk’ (AAB), ‘Ney Poovan’ (AB), ‘Pisang Awak’ (ABB), ‘Pome’ (AAB), ‘Bluggoe’ (ABB), ‘Monthan’ (ABB), and ‘Mysore’ (AAB), have exhibited severe disease incidence, with crop losses reaching up to 80-90% (Mustaffa and Thangavelu, 2011). Based on host specificity and symptom expression, *Foc* strains have been categorized into four physiological races. Beyond banana, *Foc* can also infect related members of the Musaceae and Heliconiaceae families. Moreover, more than 100 formae speciales have been described within *F. oxysporum* each specialized to specific host plants (Pastrana *et al.*, 2017). These special forms are morphologically indistinguishable but exhibit stark differences in pathogenicity and host specificity (Ploetz, 2005).

Various phenotypic and molecular methods have been deployed to differentiate *Foc* races and assess pathogen variability, including VCG assays, volatile aldehyde profiling, and molecular markers such as restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), and amplified fragment length polymorphism (AFLP) (Bentley *et al.*, 1996). The *Foc* isolates are known for their high genomic plasticity, a trait that facilitates rapid adaptation and pathogenic evolution. At least 24 vegetative compatibility groups (VCGs) have been identified to date (Mostert *et al.*, 2017; Kumari *et al.*,

2022), and these VCGs correlate with diverse pathogenic lineages, each adapted to specific banana cultivars.

Since the 1950s, classification of *Foc* has been primarily based on host range and virulence, leading to the identification of distinct physiological races (Waite and Stover, 1960; Stover, 1962). Although molecular diagnostics have since refined our understanding, race classification remains a practical framework for disease monitoring and breeding programs. The *Foc* isolates are traditionally grouped into four main physiological races, *viz.*, Race 1, Race 2, Race 3 and Race 4 each showing unique pathogenicity profiles toward different banana genotypes. However, Race 3 is no longer considered as a part of *Foc* complex.

**Race 1:** Race 1 was the original culprit behind the infamous collapse of the global banana export industry in the early 20th century, particularly targeting the cultivar ‘Gros Michel’ (AAA). This monoculture dominated tropical America until the 1960s, when catastrophic losses due to Race 1 forced a shift to the ‘Cavendish’ group. Although Cavendish cultivars were initially resistant, subsequent reports have suggested occasional susceptibility under certain conditions (Thangavelu and Mustaffa, 2010). Race 1 also affects several AAB group cultivars such as ‘Manzano’, ‘Apple’, and ‘Latundan’ (Silk), making it a persistent threat even today. Recently Baruah *et al.* (2025) reported existence of 5 five major clusters of *Foc* infecting Malbhog banana (AAB), a premium banana cultivar from North Eastern region of India.

**Race 2:** Predominantly pathogenic to cooking bananas and plantains in the ABB and AAB genomic groups, Race 2 is widely distributed in banana-growing regions. It targets cultivars such as ‘Bluggoe’ (ABB), ‘Monthan’ (ABB), and the bred tetraploid ‘Bodles Altafort’ (Pillay *et al.*, 2012). Interestingly, Race 2 is also capable of infecting *Ensete ventricosum* (enset), a close relative of banana, expanding its host range beyond *Musa* species.

**Race 3:** Initially identified in *Heliconia* spp. in Central and South America (Waite, 1963), Race 3 was once considered part of the *Foc* complex. However, it is now regarded as a misclassified forma specialis, as it exhibits weak or no pathogenicity to banana cultivars (Ploetz, 2005). As such, Race 3 is no longer included in the standard classification of *Foc* races.

**Race 4:** Race 4 represents the most advanced and dangerous iteration of the pathogen. It is virulent against Cavendish cultivars (AAA group), even in the

absence of predisposing environmental factors. It is further subdivided into Tropical Race 4 and Subtropical Race 4. The Subtropical Race 4 (SR4) causes disease in Cavendish bananas predominantly under stress conditions such as low temperatures, common in subtropical regions. On the other hand, the Tropical Race 4 (TR4) is highly aggressive and invasive strain that can infect Cavendish bananas and many other clones previously considered resistant, including those susceptible to Races 1 and 2 (Ploetz, 2005). It can cause severe epidemics without any environmental predisposition, thriving in the tropics with devastating consequences (Thangavelu *et al.*, 2001).

The global distribution of TR4 is associated with specific VCGs, primarily VCG 01213/16 for TR4, while several others (e.g., VCGs 0120, 01201, 01202, 01209, 01210, 01211, 01215, and their combinations) are linked to SR4 variants. These VCGs serve as useful molecular markers in the epidemiological tracing and regional monitoring of *Foc* lineages.

This dynamic pathogen continuously evolves, often rendering conventional management strategies obsolete. The complexity of *Foc* diversity underscores a central challenge: resistance in one cultivar or region does not guarantee protection elsewhere. Understanding the molecular and physiological diversity of *Foc* is not just a scientific imperative, it is a prerequisite for safeguarding global banana production against one of its most formidable foes.

### **SURVIVAL ARSENAL OF *Fusarium oxysporum* f. sp. *cubense***

The remarkable persistence of *Fusarium oxysporum* f. sp. *cubense* (*Foc*) in the environment is a testament to its sophisticated survival strategies. Like other members of the *F. oxysporum* species complex, *Foc* is equipped to endure prolonged periods without its primary host by producing thick-walled, long-lived spores known as chlamydospores. These durable structures can withstand desiccation and other adverse environmental conditions, remaining viable in the soil for more than two decades (Stover, 1962; Buddenhagen, 2009). Contrary to earlier assumptions that chlamydospores form only after the host plant dies, recent evidence suggests that *Foc* begins producing these spores soon after colonization begins, often before any external symptoms of Fusarium wilt are visible. This early production significantly enhances the pathogen's chances of persisting unnoticed

in the soil, especially as it thrives in dead plant debris and litter, where saprophytic growth triggers further sporulation (Stover, 1962). Latent infections are often introduced into new fields through vegetative propagation, especially via infected suckers or ratoon crops. Thangavelu *et al.* (2010) reported that ratoon crops are particularly susceptible, with greater losses observed in subsequent cycles compared to the main crop.

The survival of *Foc* is further enhanced by its ability to colonize weed species and alternate hosts without inducing visible symptoms, thereby functioning as a stealthy endophyte. Studies have detected *Foc* Race 1 in weed species such as *Paspalum fasciculatum*, *Panicum purpurescens*, *Ixophorus unisetus* (Poaceae), and *Commelina diffusa* (Commelinaceae) in Central America. Likewise, Subtropical Race 4 (SR4) has been identified in *Paspalum* and *Amaranthus* spp. in Australia, while Tropical Race 4 (TR4) has been detected in the roots of *Chloris inflata*, *Euphorbia heterophylla*, *Cyanthillium cinereum*, and *Tridax procumbens* (Hennessy *et al.*, 2005). None of these alternate hosts exhibited symptoms resembling Fusarium wilt, revealing *Foc*'s insidious capacity to establish cryptic reservoirs of inoculum that reactivate infection once susceptible banana cultivars are replanted. Such sophisticated ecological adaptations make *Foc* not just a pathogen but a masterful survivor, hiding in plain sight and waiting for favourable conditions to strike again.

### **SUSTAINABLE STRATEGIES FOR FUSARIUM WILT SUPPRESSION**

Fusarium wilt of banana is a polycyclic disease, meaning it can complete several disease cycles within a growing season (Dita *et al.*, 2018). Given that banana is a perennial monoculture, controlling Fusarium wilt poses a uniquely intractable challenge. While tissue-cultured, disease-free plantlets and resistant cultivars remain frontline defense tools, these solutions are neither universally effective nor economically viable across all cultivars and regions (Moore *et al.*, 1999). Early attempts at disease control, such as soil fumigation, crop rotation, fungicide applications, and flood-fallowing yielded limited success (Hwang, 1985; Herbert and Maarx, 1990). In practice, resistant cultivars often fail to meet commercial standards for yield, taste, or shelf life and are susceptible to emerging races of *Foc* over time (Viljoen, 2002).

The emergence and spread of Tropical Race 4 (TR4) represent the most significant global threat,

jeopardizing over 80% of global banana production and trade (Ploetz, 2015). This hypervirulent strain is difficult to contain, especially in tropical environments where predisposing stress factors are minimal. Preventative strategies such as quarantine, exclusion, and awareness campaigns are essential for minimizing spread (Dita *et al.*, 2018). Moreover, precise and early diagnostic tools are key to preventing outbreaks before fields become irreversibly infested.

Recent findings suggest that bio-organic amendments can reduce TR4 infection by reshaping the soil microbiome to create a suppressive environment (Shen *et al.*, 2015). Although chemical fumigants remain available, they are often cost-prohibitive and environmentally detrimental (Siamak and Zheng, 2018). As the global community increasingly shifts away from recalcitrant agrochemicals and embraces eco-friendly, microbial-based solutions, there is a pressing need to explore the full potential of plant growth-promoting bacteria (PGPB) and their bioactive metabolites (Srivastava *et al.*, 2022). Biological agents offer dual benefits, enhancing plant growth while simultaneously suppressing pathogen establishment, a vital step toward integrated, sustainable disease management.

## PLANT BENEFICIAL MICROBES IN THE BIOLOGICAL WAR AGAINST FUSARIUM WILT

Biological management offers a sustainable and eco-conscious countermeasure to combat soil-borne diseases, especially those as persistent and devastating as Fusarium wilt of banana caused by *F. oxysporum* f. sp. *cubense*. The term “biological control” was first introduced in 1914 by C.F. Von, and since then, science has significantly advanced in understanding and applying this method. The core principle underlying biological control lies in the disease triangle, which encapsulates the dynamic interplay between the host, pathogen, and environment. By manipulating these interactions, specifically tipping the balance through beneficial microorganisms, we can naturally suppress the pathogen and bolster plant health (Sharma *et al.*, 2020). Natural disease suppression lies on the principle of soil suppressiveness, characterized by predominance of beneficial microbes and higher diversity richness of microbial community compositions (Handique *et al.*, 2023). In augmented biocontrol, manipulation of rhizospheric microbes by the introducing well tested biocontrol agents (BCAs) has been achieved against *Foc* including *Foc* TR4 (Xue *et al.*, 2015).

Today, a range of microbial BCAs and formulations of *Trichoderma* spp., *Aspergillus* spp., *Pseudomonas* spp., *Bacillus* spp., *Burkholderia* spp. etc. have emerged as promising tools in the suppression of plant diseases of fungal and bacterial origin (Saha *et al.*, 2024; Sharma and Bora, 2025). The rhizosphere microbes are mostly explored as biocontrol agents against plant disease. The rhizospheric BCAs remain as close aide in plant system and can suppress the growth or inhibit soil borne pathogens including *Foc* through direct antagonism via antibiosis, hyper-parasitism, release of volatile toxic metabolites or through indirect mechanism via siderophore production, competition for nutrients and inducing host defense response (Ravi *et al.*, 2022). Several studies have documented the successful control of *Foc* using rhizospheric BCAs, both under in vitro and in vivo conditions (Thangavelu *et al.*, 2004; Thangavelu *et al.*, 2001). Among the most effective are strains of *Trichoderma*, *Bacillus*, and *Pseudomonas*, resilient rhizosphere colonizers capable of targeting a broad spectrum of phytopathogens, including virulent strains of *Foc* (Bora and Bora, 2020; Baruah *et al.*, 2024).

In recent time, endophytes, a subset of rhizospheric organisms have caught researchers’ attention as promising solution against *Foc* in banana. Endophytes are the neutral or beneficial microbes reside inside the plant system without causing any deleterious effect on the host. They contribute in plant health management by promoting plant growth through production growth hormones, nutrient solubilisation or by suppressing plant pathogens invading the host (Compant *et al.*, 2016). Many bacterial endophytes from the genera *Bacillus*, *Brevibacterium*, *Serratia*, *Arthrobacter*, *Enterobacter*, *Corynebacterium*, *Sphingomonas* and *Pseudomonas* have been reported as endophyte in different wild and cultivated banana (Sekhar and Pious, 2015; Baruah *et al.*, 2024).

*Trichoderma* spp. (teleomorph: *Hypocrea*) are among the most studied fungal biocontrol agents. First isolated in 1794 and brought to scientific attention by Weindling in the 1930s, *Trichoderma* has evolved into a cornerstone of bio fungicide formulations, now accounting for over 60% of commercial biocontrol products (Abbey *et al.*, 2019). The biocontrol efficacy of *Trichoderma* arises from its multifaceted arsenal: it exhibits mycoparasitism, antibiotic production, plant growth promotion, induction of systemic resistance (ISR), and root colonization. These fungi are remarkably intelligent organisms, able to sense neighbouring

phytopathogens, migrate toward them, and degrade their cell walls using a suite of hydrolytic enzymes like chitinases and glucanases (Rahman *et al.*, 2023; Bora *et al.*, 2022). Recent studies have highlighted the potential of *T. reesei* isolate CSR-T-3, which showed significantly higher antagonistic activity against the virulent TR4 strain of *Foc*, reducing disease severity while enhancing plant biochemical defense markers like peroxidases, chitinases, polyphenol oxidase, and phenylalanine ammonia lyase (Damodaran *et al.*, 2021). Further, bioimmunization protocol was developed by Damodaran *et al.* (2023) where in, metabolite-based biomolecule was incorporated in tissue culture media as Bio-immunization technology Grand Naine banana against *Foc* TR4 to develop tolerant plants. The bioimmunized plants demonstrated significant root and shoot development under pot trial along with enhanced survival of 97.8% under *Foc* challenged condition. Further, integration of bioimmunization technique coupled with soil application of *T. reesei* in field condition reduced disease severity with enhanced growth parameters in Bihar.

On the bacterial front, *Bacillus* species stand out for their dual role in plant growth promotion and disease suppression. These Gram-positive, spore-forming bacteria are well-suited for field applications due to their resilience, shelf-stability, and metabolic diversity. Many strains produce cyclic lipopeptides, including iturins, fengycins, and surfactins, which exhibit strong antifungal activity and can disrupt *Foc* hyphal membranes (Falardeau *et al.*, 2013; Saikia *et al.*, 2022).

Beyond direct antagonism, *Bacillus* spp. can outcompete pathogens for space, nutrients and form biofilms on root surfaces (Guerra-Cantera *et al.*, 2005; Bora *et al.*, 2023). Bora *et al.* (2024) reported that *Bacillus* species can induce host tolerance through enhancement of defense enzymes such as PAL, PPO, peroxidase and also enhance phenol control. Noteworthy examples of the efficacy against *Foc* include *B. amyloliquefaciens*, recognized for  $\alpha$ -amylase production. The complex, multivariate relationships among plants, biocontrol agents, and pathogens, drawing on the extensive body of reports documenting the efficacy of *Bacillus* species against *Fusarium*. It synthesizes recent advances in *Bacillus-Fusarium* research and emphasizes the fundamental principles and mechanistic strategies by which plant-growth-promoting *Bacillus* strains operate (Khan *et al.*, 2017). Some more examples of *Bacillus* against *Fusarium* are listed in Table 1.

Another bacterial genera *Pseudomonas* spp. is also considered as a potential biocontrol solution against *Foc* and many pathogens. *Pseudomonas* strains can remain both as endos phyte and rhizospheric and phyllosphere microbe. *Pseudomonas fluorescens*, *P. aeruginosa*, *P. putida* have been reported to suppress different phytopathogens through production of antibiotics, triggering induced systemic defense and outcompeting pathogens through aggressive rhizosphere colonization (Sivamani and Gnanamanickam, 1988; Thangavelu *et al.*, 2001). Thangavelu *et al.* (2004) reported that banana rhizospheric *Pseudomonads* could inhibit mycelial growth of *Foc* and the strain upregulated plant

**Table 1: Biocontrol agents used against *Fusarium oxysporum* f. sp. *cubense***

Sl. No	Name of the bioagents	Mode of Application	Reference
1.	<i>Pseudomonas aeruginosa</i> FJAT-346-PA <i>Acremonium</i> sp. Q34	Root dripping	Yu <i>et al.</i> , 2010
2.	<i>Burkholderia cenocepacia</i> 869T2	Root dripping	Ho <i>et al.</i> , 2015
3.	<i>Pseudomonas putida</i> C4r4, <i>Achromobacterium</i> sp. Gcr1, <i>Rhizobium</i> sp. Lpr2, <i>Bacillus flexus</i> Tvpr1	Root dripping and soil drenching	Thangavelu and Gopi, 2015
4.	<i>Pseudomonas fluorescens</i> Pf1, <i>Bacillus subtilis</i> EPB 10 and EPB 56	<i>In vitro</i> co-culturing of plants with bacteria	Kavino <i>et al.</i> , 2016
5.	<i>T. viride</i>	Root dipping ( $10^6$ conidia mL <sup>-1</sup> ), followed by application of colonized wheat bran: saw dust mixture	Raguchander <i>et al.</i> , 1997

6.	<i>T. harzianum</i> TH UH and TH13 <i>T. harzianum</i> (ECO-T®)	Soil inoculation in the nursery	Mukhongo <i>et al.</i> , 2015
7.	<i>T. viride</i> NRCB1	Root dripping	Raguchander <i>et al.</i> , 1997
8.	<i>B. subtilis</i> TR21	Root dipping	Yu . <i>et al.</i> , 2010
9.	<i>B. subtilis</i> TRC 54	Soil application combined with <i>Pseudomonas fluorescens</i> Pfl and a plant extract-based fungicide	Akila <i>et al.</i> , 2011
10.	<i>B. amyloliquefaciens</i> NJN-6	bio-organic fertilizer	Xue <i>et al.</i> , 2015
11.	<i>B. amyloliquefaciens</i> W19	bio-organic fertilizer (10 <sup>9</sup> CFU g <sup>-1</sup> )	Wang <i>et al.</i> , 2016
12.	<i>T. harzianum</i> A34	Soil inoculation (10 <sup>9</sup> CFC g <sup>-1</sup> )	Pérez Vicente <i>et al.</i> , 2009
13.	<i>Trichoderma</i> sp. TR76	Soil drenching (10 <sup>6</sup> CFU mL <sup>-1</sup> )	Hima and Beena, 2016
14.	<i>B. amyloliquefaciens</i> WJ22	bio-organic fertilizer (10 <sup>8</sup> CFU g <sup>-1</sup> )	Wang <i>et al.</i> , 2015
15.	<i>Streptomyces</i> sp.	Fermentation broth ( <i>In vitro</i> study)	Wang <i>et al.</i> , 2022

defense enzymes PAL, POX, chitinase,  $\beta$ -1,3 glucanase and phenolics in inoculated banana plants. Other *P. aeruginosa* strains also showed bioefficacy against *Foc* *in vitro* and *in planta* (Yu *et al.*, 2010). Some of the successful bioagents evaluated against *Foc* are summarized in the Table 1.

#### MECHANISTIC AND GENETIC BASIS OF BIOLOGICAL CONTROL AGAINST FOC

The biological suppression of *F. oxysporum* f. sp. *cubense* (*Foc*) is driven by highly coordinated molecular and ecological strategies deployed by rhizospheric and endophytic biocontrol agents (BCAs) (Saikia *et al.*, 2023). Beneficial microbes including *Trichoderma*, *Bacillus*, and *Pseudomonas* spp. possess diverse genetic determinants enabling direct antagonism, niche competition, and modulation of host immunity to prevent *Foc* invasion. Antifungal activity is largely attributed to secondary metabolite biosynthetic gene clusters such as *ituA*, *fenA*, *srfAA*, and *bmyB* in *Bacillus* and *phlD*, *pltB*, *hcnA* in *Pseudomonas*, responsible for the synthesis of potent lipopeptides and antibiotics that disrupt fungal membranes and inhibit hyphal growth (Damodaran *et al.*, 2023). Mycoparasitism, a hallmark of *Trichoderma* spp., is facilitated by hydrolytic enzyme genes such as *ech42*, *chi18-5*, *bgn13.1*, and *prb1*, enabling targeted sensing, coiling, and enzymatic degradation of *Foc* cell walls. In the rhizosphere, BCAs effectively outcompete *Foc* through iron sequestration using siderophore biosynthetic

pathways (*pvdA*, *fpvA*, *dhbA*) and through biofilm-forming genes (*epsA-O*, *tasA*) that enhance persistent root colonization (Rahman *et al.*, 2023). Beyond direct antagonism, BCAs trigger induced systemic resistance (ISR) in banana by activating jasmonic acid (JA) and ethylene (ET)-mediated signaling networks that elevate phenylpropanoid pathway enzymes such as peroxidases, phenylalanine ammonia-lyase, and polyphenol oxidase, alongside defensive chitinases and  $\beta$ -1,3-glucanases, strengthening vascular tissues against fungal ingress (Shen *et al.*, 2015). Soil microbiome restructuring through bio-organic amendments further establishes *Foc*-suppressive microbial communities, reducing pathogen proliferation and enhancing beneficial diversity. Moreover, endophytic BCAs modulate host gene expression and root exudate chemistry to minimize pathogen entry and neutralize key *Foc* effectors during latent colonization. Collectively, these genetic and mechanistic interactions form a multilayered defense system in banana, showcasing microbial biocontrol as a robust and adaptive strategy in sustainable management of Fusarium wilt.

#### CONCLUSION

Fusarium wilt of banana, driven by the formidable *Fusarium oxysporum* f. sp. *cubense* (*Foc*), continues to threaten global banana production. The emergence and rapid dissemination of Tropical Race 4 (TR4) have rendered conventional management approaches inadequate, underscoring the urgency for

integrated, sustainable, and region-specific solutions. Microbial allies-particularly rhizospheric and endophytic bioagents such as *Trichoderma*, *Bacillus*, *Pseudomonas*, and *Streptomyces*-offer promising avenues by combining direct pathogen suppression with plant growth promotion and induced systemic resistance. Yet, the transition from experimental success to large-scale field adoption demands deeper mechanistic insights, robust formulation technologies, and coordinated implementation frameworks. Future research must prioritize host-microbe-pathogen interaction studies, the development of bioagent consortia tailored to local agroecologies, and the integration of molecular diagnostics with on-farm disease surveillance. Exploring the synergistic potential of beneficial microbes within holistic management systems could transform *Fusarium* wilt control from reactive crisis management to proactive, eco-smart resilience building-safeguarding both banana biodiversity and the livelihoods dependent on this globally vital crop.

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#### AUTHORS CONTRIBUTION

PB - developed and designed the concept, prepared and edited. BS and AS researched and reviewed the existing literature on the topic and prepared the initial manuscript. All authors read and approved the final manuscript.

#### CONFLICT OF INTEREST

The authors don't have any conflict of interest.

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