



## Review article

# Biological control of bacterial leaf blight (BLB) in rice—A sustainable approach

Bestha Sai Teja<sup>a</sup>, Gayatri Jamwal<sup>a</sup>, Vishal Gupta<sup>a,\*</sup>, Mansi Verma<sup>a</sup>,  
Ayushi Sharma<sup>a</sup>, Akash Sharma<sup>b</sup>, Vinod Pandit<sup>c</sup>

<sup>a</sup> Division of Plant Pathology, Faculty of Agriculture, Sher-e-Kashmir University of Agricultural Sciences & Technology of Jammu, Chatha, 180009, India

<sup>b</sup> Division of Fruit Science, Faculty of Horticulture and Forestry, Sher-e-Kashmir University of Agricultural Sciences & Technology of Jammu, Chatha, 180009, India

<sup>c</sup> Centre for Agriculture and Bioscience International (CABI), New Delhi, 110012, India

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## ABSTRACT

Bacterial leaf blight (BLB) in rice, caused by the pathogen *Xanthomonas oryzae* pv. *oryzae*, is a significant agricultural problem managed through chemical control and cultivating rice varieties with inherent resistance to the bacterial pathogen. Research has highlighted the potential of using antagonistic microbes which can suppress the BLB pathogen through the production of secondary metabolites like siderophores, rhamnolipids, and hydroxy-alkylquinolines offering a sustainable alternative for BLB management. Additionally, the induction of plant immunity and defense-related enzymes in rice further enhances the resistance against the disease. Therefore, implementation of biological controls can complement chemical treatments in contributing towards the sustainability of rice production systems by aiming at host immunity improvement and killing of pathogen. It is crucial to continue exploring and understanding the complex interactions between various beneficial microbes, the rice plants, and the BLB pathogen to optimize and implement effective biocontrol strategies in future.

## 1. Introduction

**Bacterial Leaf Blight (BLB)** caused by the *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) is a widespread and devastating disease of rice affecting crops in both temperate and tropical regions. It is particularly destructive in tropical regions of Asia, causing substantial yield loss up to 74 percent [1]. The disease is perceived as vascular wilt during the early stages of plant growth and leaf blight during the flowering stage [1]. The gram-negative *Xanthomonas oryzae* pv. *oryzae* penetrates the host plant either through wounds or hydathodes, and invades xylem tissue which leads to a systemic infection [2]. This rod like motile bacteria produces yellowish slime and was first discovered as a bacterial cluster in dewdrops on rice leaves [3]. Subsequently it underwent various name changes from *Bacillus oryzae*, *Pseudomonas oryzae*, and *Bacterium oryzae* to finally *Xanthomonas oryzae* [3]. The pathogen networks with the parenchyma cells of xylem [4] and travels vertically along the primary veins and laterally through the commissural veins. In a few days, bacterial cells and extracellular polysaccharides (EPS) clog the xylem vessels, causing bacteria to ooze out from the hydathodes as distinctive exudate

\* Corresponding author.

E-mail addresses: [besthasaiteja@gmail.com](mailto:besthasaiteja@gmail.com) (B.S. Teja), [sci890@mail.com](mailto:sci890@mail.com) (G. Jamwal), [vishalgupta16@skuastj.org](mailto:vishalgupta16@skuastj.org) (V. Gupta), [mansiverma633@gmail.com](mailto:mansiverma633@gmail.com) (M. Verma), [ayushisharma485@gmail.com](mailto:ayushisharma485@gmail.com) (A. Sharma), [akashskuastj@gmail.com](mailto:akashskuastj@gmail.com) (A. Sharma), [v.pandit@cabi.org](mailto:v.pandit@cabi.org) (V. Pandit).

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strands [5]. Early onset destroys up to 80 percent of the yield, while even late-stage infections can greatly reduce both grain quality and yield. Infections during the tillering stage result in total crop failure. Significant yield reductions in rice yields in Southeast Asian countries viz., 25–30 per cent in Japan [6], up to 50 per cent in Malaysia [7], 20–80 per cent in Indonesia [8], 20–40 per cent in Bangladesh [9], 30–50 per cent in Philippines [10], 50–80 per cent in Mali [11] and 20–80 per cent in India [12] have been reported due to *Xanthomonas* infection. Jiang and co-workers reported a decrease in diversity of the rhizosphere bacterial community due to rice BLB [13].

Currently, different control measures are adopted for the management of BLB in rice and are broadly categorized into non-chemical cultural practices, chemical measures, biological control measures and use of resistant rice varieties. The field management practices aim at removing the potential sources of BLB pathogen at the time of cultivation. These sources, particularly infected plant material, irrigation water and weeds, if ignored can be detrimental for the health and yield of crop [12]. Therefore, a good drainage system, complete drying of fallow fields before sowing, avoiding overhead watering to keep leaves dry and timely weeding can help reduce the incidence of BLB considerably [12]. In addition to these, avoiding excessive use of nitrogen fertilizer, reducing canopy thickness, aerating soil and crop rotation also help in pathogen suppression [14]. However, with the current rate of re-emergence of *Xanthomonas oryzae* pv. *oryzae* (Xoo) infection, these measures remain inadequate in controlling disease occurrence and spread.

Cultivation of resistant rice varieties is another method employed for countering Xoo bacteria and is considered as the most effective strategy for BLB management [15]. Many BLB resistant rice varieties have been developed till date either through molecular marker assisted breeding (MAS) or genetic engineering [14]. The disease resistance genes (R genes) can confer race specific or broad-spectrum resistance in rice plants. Pyramiding of different combinations of *Xa4*, *xa5*, *xa7*, *xa13*, *xa21*, *xa23* and *xa33* genes and *Agrobacterium* mediated genetic transformations have proven successful in vesting rice varieties with broad-spectrum resistance against Xoo [14–16]. Also, CRISPR-cas9 mediated gene editing of susceptibility R genes has been used for developing rice BLB resistance [16]. Further, transgenic rice lines expressing defence related genes from other plant species have shown increased resistance against BLB pathogen [16]. However, since resistance genes also control other agronomic traits, the biggest downside with developing disease resistant rice varieties has been the compromise to be achieved between disease resistance and desired agronomic traits during breeding [16]. Further linkage drag and durability of resistance also remain an issue [12,14]. In certain cases, enhancement of resistance against one pathogen makes the plant susceptible to another pathogen [14]. Nevertheless, molecular breeding for disease control still remains an effective way of managing pathogen infections. Cultural practices and breeding resistant rice varieties are supplemented with chemical control measures on agricultural fields for managing BLB in rice. This is one of the most widely used methods of disease control in the form of soil treatments, seed treatments, and foliar sprays and exhibits significant reduction in disease incidence and yield losses in affected crops and improves its quality.

However, due to emergence of resistant strains, environmental concerns, toxicity to beneficial organisms and potential health hazards focus has shifted to the use of antagonistic microbes or biocontrol agents (BCAs) as part of integrated disease management for BLB. Plant pathogens can develop resistance against chemical pesticides and anti-microbial compounds by deploying mechanisms for efflux of pesticides, enzymatic degradation, target site mutation, target site overexpression and paralogue number variation [17,18]. BCAs are rhizosphere dwelling microbes that provide protection to plants against various pathogens. They are beneficial for overcoming pathogenic resistance as they attack on multiple fronts like competing for nutrients and space, secreting anti-microbial compounds and lytic enzymes, parasitism, forming biofilm, activating plant resistance and priming them, and producing phytohormones for triggering plant immune response [19]. These mechanisms alter pathogen cell morphology, increase anti-oxidant enzyme activity and generate ROS, thus increasing pathogen susceptibility [20–22]. Introduction of BCAs in crop cultivation reflects growing awareness of the risks posed by the leaching of toxic residues from chemical pesticides into the environment and their impacts on the food chain, highlighting the agricultural sector's necessity for alternatives to reduce reliance on pesticides [23]. BCAs serve as bio-insecticides, bionematicides, biopesticides and play a crucial role in mitigating phytopathogens by co-existing with the roots of the host [24]. These microorganisms, known as plant growth-promoting fungi (PGPF) and plant growth-promoting rhizobacteria (PGPR), in addition to enhancing the host plant's resistance to phytopathogens also improve plant growth and development [25]. They also promote systemic resistance in the host, offering sustainable and environmentally friendly protection against plant diseases [26]. These multifaceted benefits are not achievable through sole application of chemical pesticides.

Certain beneficial microorganisms, such as *Pseudomonas* spp., *Bacillus* spp., and *Trichoderma* spp., have shown effectiveness in combating pathogens responsible for foliar and soil-borne diseases caused by *Xanthomonas* spp., *Rhizoctonia solani*, *Phytophthora* spp., and *Pythium* spp. [27,28]. The main advantage of BCAs is their target-selectivity and eco-friendliness with respect to harmlessness towards beneficial insects, and microbes, exhibiting no phytotoxicity, no leaching of residues in soil and water and therefore non-hazardous to animal and human health. These attributes can be useful when resistant varieties of rice are not available and soil health needs to be addressed. BCAs improve soil chemical characteristics by mitigating the effects of heavy metals and pollutants, maintain soil pH, and enrich micro diversity [29,30]. Their incorporation also reduces the build-up of chemical pesticide residues in soil. As with other disease control methods, there is a potential risk of development of resistance against BCAs overtime, although current data in this regard is sparse. Nevertheless, BCA resistance can be addressed through low application doses or using a combination of different BCAs. If at all resistance is reported a higher dose can be used for killing resistant pathogen [31]. Understanding the mechanisms used by BCAs for pathogen suppression is important for developing effective biological means of disease control. The present review, therefore, highlights the importance of BCAs as singular treatments or in the form of microbial consortias for controlling BLB in rice and the underlying mechanisms employed by these agents for suppressing *Xanthomonas oryzae* infection and their impact on plant growth.

## 2. Rice- *xanthomonas* pathosystem

*Xanthomonas oryzae* pv. *oryzae* is a soil borne pathogen capable of surviving for up to 3 months in soil and in tropical climatic conditions, throughout the entire year (Fig. 1A–E). Maximum chances of BLB occurrence are in monsoon season and specifically in India, maximum disease occurrence is noticed during June–September. *Xoo* infects the seed, stem and other plant parts of rice even after harvest [32]. The rain splash, birds, insects and other activities of humans can also spread the pathogen. *Xoo* can also survive in roots, stem and stubbles of various alternate hosts such as *Zizania* and *Leersia* spp. [33]. The rice-*Xanthomonas* system is the broader framework that involves both the mechanisms of bacterial infection and the defense strategies of host. Understanding these mechanisms is crucial for developing effective management practices and resistant rice varieties.

### 2.1. Mechanisms of bacterial infection

The infection process begins when *Xoo* bacteria enter the rice plant primarily through natural openings, such as hydathodes or wounds caused by insect activity or mechanical damage. Once inside the plant, *Xoo* rapidly colonizes the xylem vessels, the water-conducting tissues, where it multiplies and spreads throughout the plant. A key component of *Xoo*'s infection strategy is the Type III secretion system (T3SS) managed by the response of hypersensitivity and pathogenicity (Hrp) genes [34,35]. This gene cluster comprises of 26 genes regulated by the HrpX and HrpG proteins [36], and HrpG enhances the expression of HrpX [37]. T3SS acts like a syringe, allowing the bacteria to inject a variety of proteins known as effectors directly into the host plant cells. Among these effectors, transcription activator-like (TAL) effectors play a critical role in modulating the host's immune responses. By binding to specific DNA sequences within the plant's genome, TAL effectors can activate or repress genes that control the plant's defense mechanisms. This manipulation often leads to the expression of susceptibility (S) genes, which enhance the pathogen's ability to thrive within the plant. For instance, TAL effectors can alter the expression of sugar transporters, redirecting essential nutrients towards the bacteria and fostering their growth.

In addition to TAL effectors, *Xoo* secretes extracellular polysaccharides (EPS) that contribute to its virulence. EPS forms a protective biofilm around bacterial colonies, facilitating adherence to plant surfaces and shielding the bacteria from host defenses. This biofilm formation obstructs the xylem vessels, resulting in reduced water transport, which manifests as symptoms such as leaf wilting, yellowing, and the characteristic dry, brown streaks associated with bacterial blight. The accumulation of EPS and bacterial cells leads to significant water stress and nutrient deficiency in the plant, severely compromising its overall health and productivity.

### 2.2. Plant defense strategies

In response to *Xoo* infection, rice plants have evolved complex defense mechanisms that operate at cellular and molecular levels.



**Fig. 1.** (A) Healthy Crop, (B), Infected Crop (C), Symptoms of BLB, (D) Culture of *Xanthomonas oryzae* pv. *oryzae*, (E) *Xanthomonas oryzae* pv. *oryzae*'s microscopic view.

The first line of defense involves pattern recognition receptors (PRRs) located on the surface of plant cells. These receptors detect pathogen-associated molecular patterns (PAMPs), which are conserved molecular features common to many pathogens, such as bacterial flagellin and lipopolysaccharides. The recognition of these PAMPs triggers a broad-spectrum defense response known as PAMP-triggered immunity (PTI) [38]. This response includes the production of reactive oxygen species (ROS), fortification of the cell wall, and activation of signaling pathways that lead to the expression of defense-related genes (Fig. 2).

Despite this initial defense, *Xoo* employs its TAL effectors to undermine PTI, allowing the bacteria to persist within the plant. When *Xoo* successfully circumvents PTI, rice plants can initiate a more specialized immune response known as effector-triggered immunity (ETI) [38]. ETI is mediated by specific resistance (R) genes in rice that recognize the presence of TAL effectors or their actions within plant cells. Upon detection, these R genes activate a robust immune response characterized by the hypersensitive response (HR). The HR results in localized cell death at the infection site, creating a barrier of dead cells that limits the spread of *Xoo* and effectively deprives the bacteria of essential nutrients. PTI provides broad defense through recognizing conserved pathogen molecules, while ETI delivers race-specific resistance through R genes that detect specific effectors. Both R genes in ETI and pattern recognition receptors (PRRs) in PTI can confer qualitative resistance, regularly mentioned as major disease resistance (MR) gene's [39]. A total of thirty-seven major disease resistance (MR) genes have been observed in rice for their role in conferring resistance against *Xanthomonas* species [40]. It's worth noting that among the 37 MR genes identified for resistance against *Xoo*, 14 of them operate through a recessive regulatory mechanism [41].

In addition to local defenses, rice plants initiate systemic signaling pathways involving key plant hormones such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET). These hormones are crucial for regulating the plant's immune responses and coordinating the activation of defense genes throughout the plant. Salicylic acid plays a particularly important role in resistance against biotrophic pathogens like *Xoo*, enhancing the plant's capacity to mount long-lasting defensive responses.

### 3. Chemical management of bacterial leaf blight in rice

Farmers employ synthetic chemicals as a commercial method to mitigate BLB in rice (Fig. 3A–G). A chemical widely used against BLB is streptomycin, which includes streptomycin sulfate (90 %), and tetracycline hydrochloride (10 %) [42]. Kasugamycin, copper oxychloride, streptomycin sulfate, and a mixture of copper sulphate with lime and water have also been utilized against BLB. Copper oxychloride has shown 76.48 per cent effectiveness, while streptomycin sulfate has 92.23 per cent effectiveness in the management of BLB as compared to untreated controls. This resulted in yield increases of 2.31 per cent and 3.07 per cent, respectively [43]. Resin acid copper salt, an excellent copper based organic pesticide with minimum copper content have shown better control efficiency of 38.5 per cent over control with minimum phytotoxicity [44]. Similarly, copper nanoparticles (0.2 %) are able to inhibit the pathogen up to 15.1 mm as compared to control with 0 mm zone of inhibition [45]. Combined application of streptomycin and copper oxychloride resulted in a lower incidence of 22.33 per cent, whereas, control had a 55.53 per cent [46]. Application of copper hydroxide (77 % WP) have exhibited maximum control efficiency of 78.57 per cent after 14 days of inoculation [47]. The combination of antibiotics, chemical and biocontrol agents such as Streptomycin @0.01 % + CuOCl<sub>2</sub> @0.3 %, and 3rd spray with *P. fluorescens* @ 1.5 % have resulted minimum per cent disease index and maximum yield of 8.10 per cent and 43.00 q/ha, respectively as compared to control with

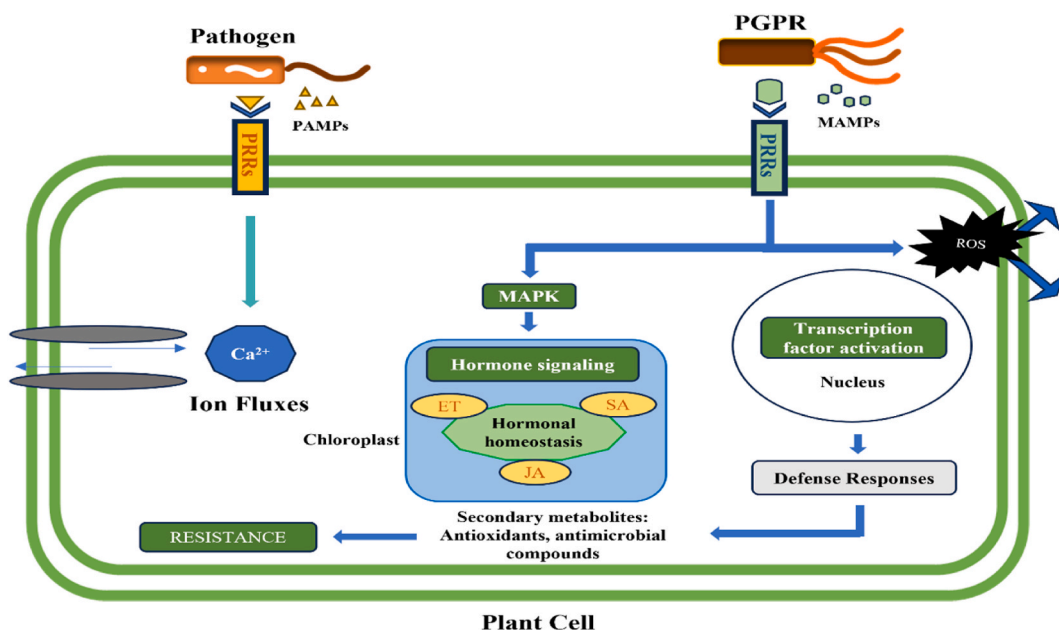
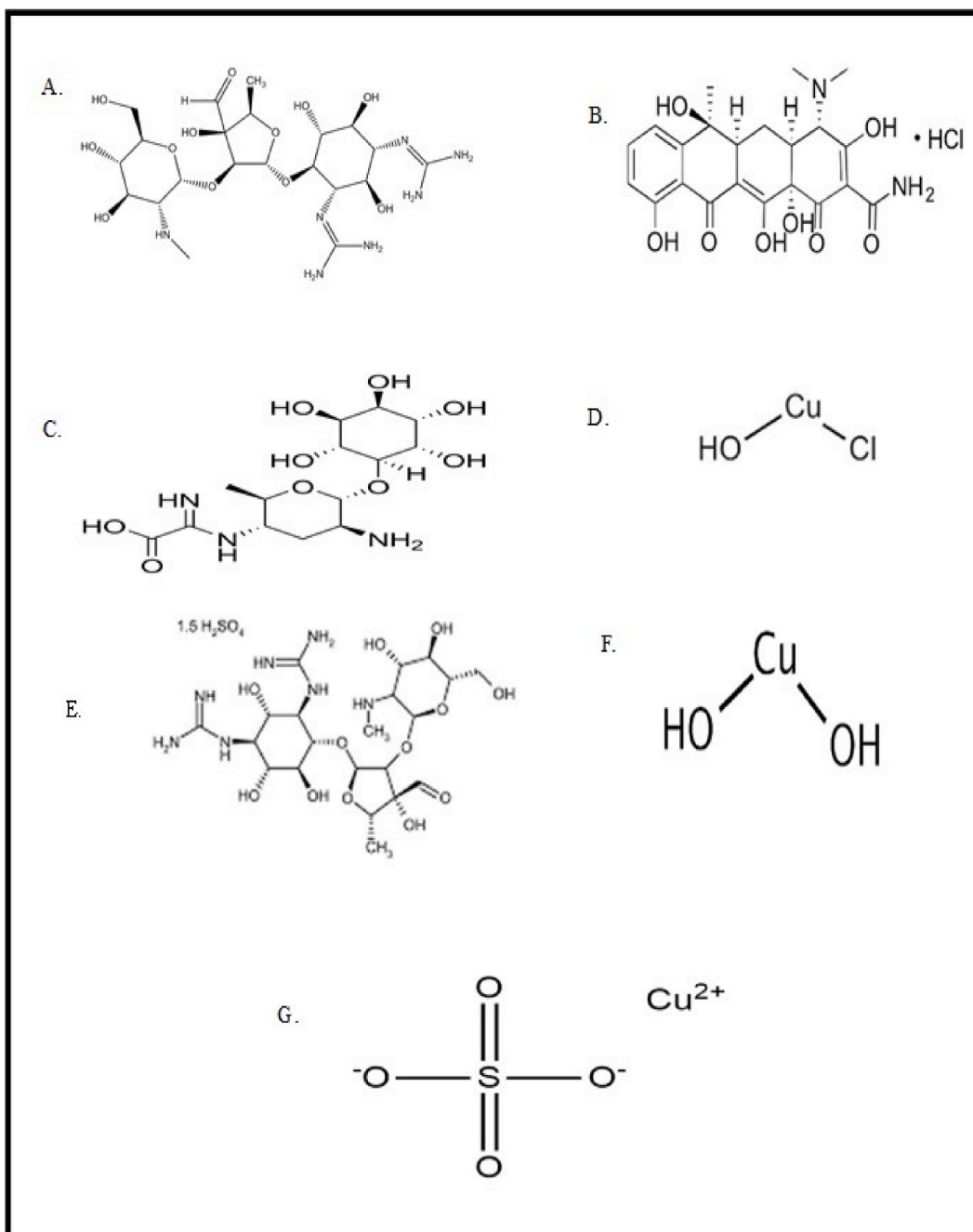


Fig. 2. Activation mechanisms of plant Défense responses.





**Fig. 3.** Common chemical compounds used for BLB management in rice. (A) streptomycin, (B) tetracycline, (C) Kasugamycin, (D) copper oxychloride, (E) copper hydroxide, (F) copper hydroxide, (G) copper sulfate.

74.81 per cent and 29.00 per cent, respectively [48]. Likewise, combination of agrimycin 100 and copper oxychloride exhibited minimum lesion length (4.26 cm) and per cent disease index (27.96 per cent) which led to maximum increase in growth parameters of plant such as plant height (54.19 cm), no. of tillers (4.60), root length (31.87 cm) and dry root weight (3.23 g/plant) [49]. Additionally, among several antibiotics used to manage BLB, streptomycin sulfate has shown higher efficacy, having colonies of 15.25 compared to 48.25 colonies in the control [50].

Tetracycline is another antibiotic used for *Xoo* suppression which prevents bacterial protein synthesis by blocking the binding of aminoacyl-tRNA to the bacterial ribosome [51]. To reach their targets inside bacteria, these molecules need to pass through membranes, requiring an understanding of how they are taken up and how they bind to ribosomes. In gram-negative enteric bacteria, tetracyclines enter through porin channels in the outer membrane, such as OmpF and OmpC. They often form complexes with

positively charged cations, such as magnesium [52]. These complexes are drawn into the periplasm by the interfacial potential across the outer membrane. Once there, they can break apart, releasing uncharged tetracycline. This neutral tetracycline can subsequently penetrate through a bilayer of lipids [53]. Afterward, tetracyclines bind to the ribosome, exerting a bacteriostatic effect against bacteria [51]. Despite its benefits, overuse of tetracycline poses several risks such as allergies, bacterial resistance, and harm to environmental microflora, impacting overall environmental health [54]. Tetracyclines are difficult to break down in both human and animal digestive systems [55]. Moreover, tetracyclines are stable but susceptible to degradation under extreme pH conditions, resulting in the formation of epi and anhydrous products due to their low Henry's constant, indicating low volatility and degradation potential. These traits underscore tetracycline's status as a significant environmental concern [56].

Due to development of bacterial resistance against these molecules, search for novel compounds for *Xoo* suppression is warranted. Recent reports have identified certain compounds which have shown promising *in vitro* and *in vivo* efficacy against *Xoo*. Xiang and co-workers have designed and synthesised thirty novel 1,3,4-oxadiazole sulfone compounds containing 3,4-dichloroisothiazolylamide moiety out of which two compounds showed excellent anti-*Xoo* and anti-*Xoc* activity [57]. Another novel Epipodophyllotoxin-Derived B2 compound which targets bacterial cell division protein FtsZ effectively controlled *Xoo* cell division *in vitro* and reduced BLB symptoms in pot experiments [58]. Several novel amide derivatives containing an imidazo [1,2-a] pyridine moiety were screened and one of them exhibited excellent bactericidal activities against *Xoo* and *Xoc* [59]. A novel pentacyclic tri-terpene acid amide derivative also exhibited inhibitory activity against *Xoo* and *Xoc* in pot experiments [60].

#### 4. Biological control of bacterial leaf blight in rice

Biocontrol agents (BCAs) adopt various mechanisms to combat the *Xanthomonas oryzae* pv. *oryzae* infection in rice. They directly inhibit *Xoo* by producing antimicrobial compounds, siderophores, and lytic enzymes, additionally competing for nutrients and spatial dominance [61]. Most studies on the Plant Growth Promoting Microbes's (PGPM) primarily focus on interaction among individual microorganisms and plants. These studies typically assess various growth and developmental parameters, including plant length or biomass, specific tissue characteristics, chlorophyll content, and the nutritional profile of plant tissues or grains [62]. These diverse microbes can occupy various niches, leading to a wide range of interactions [63]. Plants influence these interactions in the rhizosphere by releasing compounds that trigger competition for nutrients, space, and survival. Due to the complexity of these interactions, introducing a single microbial species may not consistently promote plant growth [64]. Combining compatible microbes from various strains or species can result in additional or harmonious benefits, enhancing their effectiveness in managing plant diseases, improving soil health and supporting plant growth [65]. The interactions of microbes in plant microbiome are intricate and responsive. When one microbe is lacking, others often step in to fill the gap, highlighting the resilience and adaptability of these communities. Innovative plant microbiome engineering leverages potent bioinoculants to deliberately shape these interactions, fostering well-organized biological networks in diverse soil environments. This approach revitalizes crucial microbial communities that may have been diminished

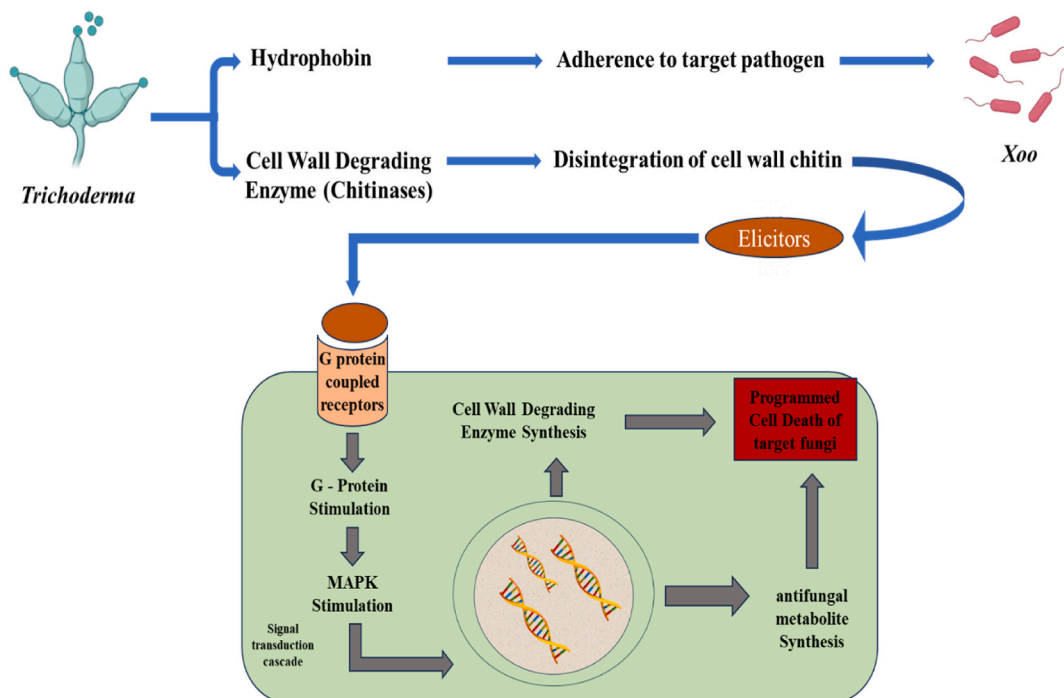


Fig. 4. *Trichoderma*'s Mode of action against phytopathogens.

by intensive agricultural practices, thereby boosting soil fertility. By incorporating diverse microbial consortia, these techniques enhance plant growth under various conditions, including challenges from pests, diseases, and environmental stresses. Overall, these advanced methods harness microbial communities to optimize soil health, increase crop productivity, and mitigate the environmental impacts associated with conventional farming practices [66]. A review by Dey and Raghuwansi [35], has discussed the aspects of biological control of *Xoo* species in several plant hosts. The present review focuses on the mitigation of *Xanthomonas oryzae* pv. *oryzae* infection in rice crop using these methods with emphasis on the use of microbial consortia for increasing the effectiveness of BCAs against *Xoo*.

#### 4.1. Effectiveness of trichoderma as biocontrol agent in BLB management

The biocontrol potential of *Trichoderma* spp. was first observed when it inhibited *Rhizoctonia solani*, leading to the identification of its mycoparasitic behavior. During mycoparasitism, *Trichoderma* coils around and penetrates the phytopathogen's hyphae, causing the dissolution of the host's cytoplasm [67] and activates host defenses, contributing to disease suppression. The combination of exclusion through competition, antibiosis, mycoparasitism, and ISR is vital for plant disease management mediated by *Trichoderma* [68]. As an aggressive biocontrol agent, *Trichoderma* protects germinating seeds from various plant diseases in the sperm sphere and rhizosphere [69]. Synthesis and secreting pathogenesis-related enzymes, such as cell wall degrading enzymes (CWDEs), and toxic secondary metabolites like peptaibols, which serve as potent chemical agents to eradicate bacteria, are mechanisms of biocontrol exhibited by *Trichoderma* [70] (Fig. 4). A *Trichoderma* isolate T6 from rice rhizosphere was reported to be effective in reducing lesion length and promoting plant growth under greenhouse conditions in *Xoo* infected rice [71]. The isolate produced key inhibitory metabolites like indole acetic acid (69.73 mg/ml), siderophores (92.70 % siderophore units), chitinases (32.52 min<sup>-1</sup> mg<sup>-1</sup> Protein),  $\beta$ -1,3-gucanases (1.93 nmol/s/ml) against *Xoo* and also harbored phosphate solubilization capability (153.16  $\mu$ g/ml) and showed maximum plant growth promotion among all fungal and bacterial isolates [71]. In another study secondary metabolites from mono cultures of *Trichoderma harzianum* (PGT4), *Trichoderma reesei* (PGT5 and PGT13) and their co-cultures were used for the synthesis of ZnO nanoparticles which had a dose-dependent inhibitory effect on *Xoo in vitro* [72].

##### 4.1.1. Mycoparasitism

It is a multi-step process involving complex events. Initially, when *Trichoderma* confronts a pathogen, it releases cell wall-degrading enzymes (CWDEs) and engages in direct interaction [73]. First, carbohydrates from the cell wall of *Trichoderma* bind to the target pathogen's lectin, initiating primary identification and attachment. This is followed by hyphal coiling, where hydrophobins aid in adhesion to the host fungi, facilitated by the expression of the Vell1 gene [74]. Infiltration into the hyphae develops the appressoria, which concentrates osmotic solutes like glycerol to generate mechanical pressure. Fungitoxic CWDEs, including chitinases and glucanases, in combination with the appressorial strength to enable successful penetration. Once inside the target hyphae, *Trichoderma* utilizes CWDEs to dissolve the cell wall of the host, which leads to parasitization & ultimately becomes the reason for the pathogen's death [75] (Fig. 4). This mechanism has been used for mycoparasitism of fungal pathogens of rice and other crops [76].

##### 4.1.2. Antibiosis

It is a process, where a low-molecular-weight compounds capable of diffusion as secondary metabolites (SMs), inhibit the growth of pathogens [77]. Various (180) kinds of secondary metabolites have been isolated from the genus *Trichoderma*, each with similar or distinct functions. These functions include biochemically inhibiting protein synthesis, promoting mycoparasitism to block key pathways of phytopathogens, and enhancing the host's cell growth, reproduction, and nutrient uptake [78]. Based on their biosynthetic nature, these SMs have been categorized into peptaibols, polyketides, and terpenes. *Trichoderma* is particularly known for producing peptaibols, which are non-proteinogenic amino acids with antimicrobial properties. These metabolites undergo significant transformation in the pathogen, leading the host to release reactive oxygen species, which convert them into antimicrobial oxidized forms such as 1,5-dihydroxy-3-hydroxymethyl-9,10-anthraquinone, 1,7-dihydroxy-3-hydroxymethyl-9,10-anthraquinone, and emodin. These processes enhance *Trichoderma's* competitiveness as a robust antimicrobial agent and reinforce the host's immune system against pathogens [79]. Peptaibols are linearly formed peptide antibiotics typically comprising of five to twenty residues of amino acids, presenting an acetylated N-terminus, C-terminal amino alcohol, and a notable presence of  $\alpha$ -amino isobutyric acid. Trichokonin A (TKA) and Trichokonin B (TKB), have 20 and 12 amino acids, respectively, and usually show antimicrobial activity against gram positive bacteria. TKA and TKB have also demonstrated antimicrobial activity against gram negative bacterium like *Pectobacterium carotovorum* subsp. *carotovorum* and *Xanthomonas oryzae* pv. *oryzae*. These peptaibols can cause distortions and irregularities in the morphology of bacterium, like separation of the membrane and envelope of the cell, rough surface texture, decreased height, and discharge of intracellular substances like nucleic acids and proteins. A study by Zhang and co-workers reported that *Trichoderma longibrachiatum* strain SMF2 against *Xanthomonas oryzae* pv. *oryzae*, showed an 82.2 per cent reduction in lesion length in plants treated with 27  $\mu$ g/mL of TKA compared to untreated diseased control [22]. Also, TEM and AFM analysis revealed changes in cell morphology and damage to the pathogens cell permeability [22].

Additionally, polyketides are a distinct class of defence metabolites catalysed by polyketide synthases. Several *Trichoderma* strains synthesize different kinds of polyketides such as trichotoxins A & B, trichodecenins, trichorovins, trichocellins, trichorzianins A & B, trichorzins isolated from *T. viride*, *T. harzianum*, and atroviridin A to C and neatroviridins A to D from *T. atroviride*. This metabolite plays a dual role by acting as antibiotics and enzymes that disintegrate the cell wall of phytopathogen [79].

#### 4.1.3. Competition

In the rhizosphere *Trichoderma*, acts as an aggressive root colonizer competing for space, nutrients, and energy. It mobilizes soil nutrients and can outcompetes other microorganisms in nutrient absorption from various root secretions of host plant [80]. *Trichoderma* outperforms in competition by releasing a variety of compounds that counteract phytopathogens, combined with its rapid growth and colonization. This enhances plant growth in the rhizosphere while inhibiting the proliferation of potential pathogens [81]. The ATP-binding cassette (ABC) transporters present in *Trichoderma* enhances its competitive edge by providing resistance to several toxic metabolites produced by phytopathogens [75].

#### 4.1.4. Induction of plant immunity

Beneficial microbes like *Trichoderma* spp. induce plant immunity against phytopathogens by activating various components of the defense network. Samal and co-workers reported that biopriming of rice seeds with *T. erinaceum* reduced bacterial blight by inducing catalase enzyme activity against *Xoo* [82]. Rice plants primed with beneficial *T. paraviridescens* (BDISOF67), *T. erinaceum* (BDISOF91), *T. asperellum* (BDISOF08), and *T. asperellum* strains isolated from rice rhizosphere showed higher activity of defense-related enzymes and genes related to salicylic acid and jasmonic acid pathways. They also reduced lesion length of rice leaves (31.25 %–87.5 %) and increased the activity of defense-related enzymes, which in turn lead to the production of signaling molecules, like salicylic acid and jasmonic acid and increased the expression of marker genes of these pathways viz., OsWRKY45, OsWRKY62, OsWRKY71, OsHI-LOX, and OsACS2 [83]. In a study with tobacco plants, *Trichoderma asperellum* strain T42 modulated the activity of reactive oxygen species and nitric oxide molecules as a defense response against *Xoo* [20].

### 4.2. *Pseudomonas* spp. biocontrol mechanisms against *xoo*

*Pseudomonas* spp. is characterized by its gram-negative nature, polar flagella, and rod-shaped morphology [84]. The genus of bacteria belongs to the phylum Proteobacteria, class Gamma proteobacteria, and family Pseudomonadaceae. *Pseudomonas* species, along with their derivatives, find extensive use in various large-scale biotechnological applications [85] and are widely distributed in various kinds of soil exhibiting numerous beneficial traits that enhance host growth. The non-pathogenic fluorescent *Pseudomonas* is a well-known PGPR commonly detected in the root region of paddy fields [86,87]. Several strains of *P. fluorescens* solubilize phosphate, aid in siderophore production, hydrogen cyanide, indole-3-acetic acid (IAA),  $\beta$ -1, 3-glucanase, cellulase, and salicylic acid, all of which contribute to mitigating phytopathogens.

This PGPR can also promote host growth through rapid colonization and dominance in the spermosphere, rhizosphere, and within plants. They produce several bioactive metabolites, efficiently utilize seed and root exudes, and engage in intense competition with other deleterious microbes for nutrients while displaying resistance to abiotic stress. These characteristics significantly contribute to their role in promoting plant growth and enhancing innate resistance to various soil-borne pathogens. The *Pseudomonas aeruginosa* BRp3 exhibited a minimum severity of BLB (50 per cent) while untreated control, had an 80 per cent severity attributed to secondary metabolite production and induction of defence related enzymes. Furthermore, BRp3 showed an increase in straw weight (120 g per plant), and grain weight (35 g per plant), in contrast to the untreated control, which had 80 g of straw weight and 20 g of grain weight per plant [88]. In an earlier *in vitro* study with *P. putida* A1, it was reported that the strain could form biofilms and harboured antimicrobial activity against several phytopathogenic bacteria, including *Xoo* [89].

**Biological Nitrogen Fixation:** Despite the atmosphere containing 78 per cent nitrogen, it remains unavailable to plants. Using nitrogen-fixing microorganisms as biofertilizers is an efficient and eco-friendly method to enhance crop growth [90]. Biological nitrogen fixation by the rhizobacterium *Pseudomonas fluorescens*, produces plant-friendly ammonia from atmospheric nitrogen with the help of nitrogenase [91]. Multiple strains of *Pseudomonas fluorescens* were tested on rice crop challenged by *Xoo*. Among these, seed treatment with Pf6 exhibited an average root length of 14.4 cm and an average shoot length of 6.61 cm compared to control. Another strain Pf9 under controlled conditions showed significant enhancement in seed germination and vigour index [92].

**Solubilization of phosphorus:** Phosphorus is a crucial macronutrient for plant growth, after nitrogen. While a significant quantity of phosphorus is present in insoluble form, plants can only utilize phosphorus in monobasic and dibasic forms [93]. Fluorescent *Pseudomonas* utilize organic acids with a low molecular weight like citric and gluconic acids, to dissolve insoluble phosphorus into an available form for plants [94]. Yasmin and co-workers reported that *P. fluorescens* strain BRp3 solubilized phosphate (97  $\mu$ g/ml) and promoted growth and yield of rice plants under greenhouse conditions [88].

**Siderophore Production:** Iron exists in its elemental form as ferric ions ( $\text{Fe}^{3+}$ ), with poor solubility. Consequently, plants and microorganisms are unable to utilize these poor soluble forms. Some extracellular compounds, commonly referred to as siderophores, have been identified as being secreted by fluorescent *Pseudomonas*. These siderophores will limit the accessibility of iron molecules to pathogenic microbes [95]. Various bacteria and fungi, like *Pseudomonas*, *Agrobacterium*, *Erwinia*, *Enterobacter*, and *Rhizobium*, produce various forms of siderophores, such as pyoverdins, catechols, hydroxamates, and rhizobactin [96]. The *P. fluorescens* strain BRp3 was shown to produce siderophores (15 mg/ml) which inhibited *Xoo* growth [88].

**HCN Production:** Hydrogen cyanide (HCN), known for its antibacterial properties, is a highly toxic compound used against phytopathogens. Most Plant Growth-Promoting Rhizobacteria (PGPR) produce HCN to inhibit phytopathogens and enhance crop yield [97]. *Pseudomonas fluorescens* is particularly renowned for its disease-inhibiting ability due to HCN production [98].

**Phytohormone Production:** Phytohormones, including gibberellins, IAA, and cytokinins, are essential for development. IAA, a well-studied auxin, is crucial for tuber and seed development, cell division, vegetative growth, and the formation of lateral and adventitious roots [99]. Auxins support the growth and development of plants, while cytokinins has important role in the enlargement, expansion, and division of cells [100]. Gibberellins alter plant morphology by promoting cell elongation, especially in stems. Ethylene,



known as the "wounding hormone" due to its gaseous form, is produced in response to physical or chemical stress and inhibits root growth. PGPR is important for reducing the production of ethylene by modulating plant hormones, maintaining ion balance, and regulating stress-responsive gene expression [101]. The *P. fluorescens* BRp3 strain was reported to produce 30 µg/ml of indole acetic acid *in vitro* which aided in plant growth promotion [88].

**Antibacterial action:** PGPR help plants to grow & prevent dispersal to plant pathogens by producing antifungal antibiotics. *P. fluorescens* produces 2,4-diacetylphloroglucinol (DAPG), which serves as an effective biocontrol agent, inhibiting *Xoo* growth and suppressing BLB up to 59%–64 % in greenhouse and field experiments [102]. A recent study demonstrated that *P. fluorescens* can protect host from various diseases like BLB of rice, black root rot of tobacco, root rot of wheat, and root rot of peas [103]. A natural pyrazolotriazine pseudodiodinine compound from *Pseudomonas mosselii* 923 was reported to inhibit rice phytopathogens including *Xoo* [104].

**Induced Systemic Resistance (ISR):** In the plant rhizosphere, beneficial microbes induce systemic resistance to defend against pathogenic attacks. Microbes such as *Pseudomonas fluorescens* promote defense mechanisms by imparting structural changes and accumulating biochemical and phenolic compounds in the host [105]. ISR in plants leads to significant modifications in plant structure and functions, and mitigates the invading pathogens [105,106]. For example, *Pseudomonas fluorescens* Pf1 was tested against *Xanthomonas oryzae* pv. *oryzae*. Pf1 have shown intensity of 1.2 at 30 days after inoculation (DAI) and 6.8 at 60 DAI, as compared with control exhibiting intensity of 6.8 at 30 DAI and 7.1 at 60 DAI [107].

**Volatile compounds:** Volatile organic compounds (VOCs) with low-molecular-weight promote development, and induces resistance in host plants [108]. These microbially derived VOCs hold antimicrobial properties, enhance the growth of host, and function as signalling molecules [109]. Predominantly VOCs produced by *Pseudomonas chlororaphis* such as 3-methyl-1-butanol, phenylethyl alcohol, and 2-methyl-1-butanol exhibited inhibition of *Ceratocystis fimbriata*, responsible for black rot disease in sweet potatoes [110].

#### 4.3. *Xoo* suppression and plant growth promotion by spore-forming *Bacillus subtilis*

*Bacillus subtilis*, a gram-positive bacterium that forms spores and is widespread in the environment, has gained attention as a biological control agent. It is noted for its production of diverse biologically active compounds, its ability to form resilient endospores under stress conditions, and its ease of isolation and cultivation [111]. Its application has the capability to enhance the growth of the

**Table 1**

*Bacillus* species used for biocontrol of *Xoo*.

Bacterial BCA	Biocontrol mechanism		Plant Growth Promotion	References
	Direct control	Indirect control		
<i>Bacillus</i> strain D13	Secondary metabolite production of decyl alcohol and 3,5,5-trimethylhexanol Altered surface morphology in the majority of <i>Xanthomonas</i> cells	Transcriptional expression of virulence-associated genes repressed by decyl alcohol and 3,5,5-trimethylhexanol.	Not studied	113
<i>Bacillus subtilis</i> GBO3 and SE34	Increased accumulation of phenylalanine ammonia lyase, peroxidase and polyphenol oxidase	Not studied	Germination of 85–86 % and increase in vigour index after seed treatment	114
<i>Brevibacillus laterosporus</i> SN19-1	Produced cellulase, protease, and siderophores, and IAA.	Not studied	Ability to fix nitrogen, detoxify organic phosphorus	115
<i>B. subtilis</i> A15, <i>B. amyloliquefaciens</i> D29 and <i>B. methylophilicus</i> H8	Biofilm formation ability and induced changes in <i>Xoo</i> cell morphology.	Not studied	Phosphorus compounds solubilization	116
<i>Bacillus velezensis</i> strain Bv-303	Not studied	Not studied	No effect on rice seed germination and seedling growth observed.	117
<i>B. velezensis</i> BR-01	Production of protease, cellulase, β-1,3-glucanase, chitinase, indoleacetic acid, siderophore, and 1-aminocyclopropane-1-carboxylate (ACC) deaminase, and lipopeptide antibiotics- surfactin, iturin, and fengycin.	Not studied	Not studied	118
<i>Bacillus oryzicola</i> sp. nov.	Not studied	Not studied	Promoted the growth of rice seedlings with higher germination rates and more tillers	119
<i>Bacillus albus</i> (CWTS 10)	Production of siderophore (methanolic and diethyl ether) and antimicrobial compounds such as 2-deoxystreptamine, miserotoxin, fumitremorgin C, piperidine, piperonaline, gingerone A, and deoxyvasicinone.	Not studied	Significant increase in root and shoot length. Increase in wet and dry weight.	120
<i>Bacillus amyloliquefaciens</i> FZB42	Production of antibiotic compounds difficidin and bacilysin.	Down regulation of virulence related genes	Not studied	121

host and increase the yield of the crop by increasing nitrogen uptake, phosphate solubilization, and the production of siderophores and phytohormones [112]. Table 1 shows a comparison between various species of *Bacillus* used for biocontrol of *Xoo*.

The utilization of *Bacillus subtilis* in plant disease management can significantly impact the plant-pathogen interaction by improving the growth of the host, ISR, forming biofilms, competing for essential nutrients or colonization sites, exerting cell lysis effects, and producing antibiotics [122]. Recent research demonstrates that, this beneficial bacterium has the capability to affect several factors of the disease triangle in a roundabout way. Consequently, *B. subtilis* can have a domino effect on the environment, host plants, and pathogens, affecting both plant development and disease progression [123]. *Bacillus subtilis* (D13) demonstrated efficient suppression of *Xoo*, by reducing the lesion length (5 cm) compared to the control's lesion length [113].

One of the mechanisms that contribute to the antagonistic activity of *B. subtilis* is its competition for iron through siderophore production. This process is key to controlling various fungal and bacterial pathogens, such as *Clavibacter michiganensis*, *Fusarium oxysporum*, and *Rhizoctonia solani*. In environments with limited iron availability, *B. subtilis* synthesizes catecholate siderophores viz., 2,3-dihydroxybenzoate and 2,3-dihydroxybenzoyl glycine. The initial structurally characterized siderophore, itoic acid, was discovered in *B. subtilis* cultures grown under low-iron conditions. Additionally, the *B. subtilis* strain CAS15 produces the catecholic siderophore bacillibactin, a trimeric ester made up of 2,3-dihydroxybenzoate, glycine, and threonine, which serves as a growth promoter [124].

Numerous *Bacillus* strains (*B. pumilus* INR7, *B. pumilus* SE34, *B. subtilis* GBO3, *B. subtilis* IN937b, *Brevibacillus brevis* IPC11, *B. pumilus* T4 and *B. amyloliquefaciens* IN937a) were used to challenge *Xoo* in rice. Among these strains, SE34 showed the minimum incidence of 22 per cent, followed by GBO3 (31 %), T4 (35.7 %), IN937b (40.2 %), IPC11 (44 %) and IN937a (51.3 %), whereas, control, had an incidence of 75 per cent [114]. A *Brevibacillus laterosporus* SN19-1 strain produced cellulase, protease, and siderophores *in vitro* and in pot experiments, it controlled BLB up to 90.92 %. The inhibitory mechanism was revealed to the biofilm formation. Respiratory and the energy metabolism enzymes of *Xoo* were significantly inhibited, and there was an increase in ROS production. Scanning electron microscopy observations showed folds on the surface of *Xoo*. *B. laterosporus* SN19-1 increased *Xoo* cellular permeability resulting in cell death [115].

*Bacillus subtilis* also enhances plant growth by regulating phytohormones and enzymes, facilitating the mineralization of nutrients, nitrogen fixation, and improving the absorption capability of roots. Among these plant growth-promoting (PGP) traits, phytohormones and siderophores are particularly noteworthy in *B. subtilis* isolates. The production of phytohormones viz., auxins, gibberellins, cytokinins, and ethylene contributes to growth promotion [125]. Indole-3-acetic acid (IAA), a phytohormone, is widely acknowledged as the predominant endogenous auxin, acting as a vital signalling molecule in the regulation of plant development. *B. laterosporus* SN19-1 was reported to fix nitrogen, detoxify organic phosphorus and produce IAA [115]. *In vitro* assays of *Bacillus velezensis* LS123N revealed that it inhibited phytopathogen *B. oryzae*, produced hydrolases, siderophores, and IAA, while harbouring the ability to solubilize phosphorus compounds highlighting it as a potential biocontrol candidate in rice plants [126].

Microbial consortium consisting of *B. subtilis* (GBO3) and *B. amyloliquefaciens* (IN937) was tested against cucumber mosaic virus in *Arabidopsis thaliana*. The consortium shown maximum growth of *Arabidopsis*, with foliar fresh weight to 568 mg compared to the control with 268 mg [127]. Similarly, different isolates of *B. subtilis* were isolated and tested in rice. Among the several isolates PGB4 shown maximum seed germination (94.15 %) and shoot dry weight (9.40 mg) over the control with seed germination (82.10 %) and shoot dry weight (7.20 mg) [128]. *B. subtilis* A15, *B. amyloliquefaciens* D29 and *B. methylotrophicus* H8, showed strong biofilm formation ability and inhibited *Xoo* and changed its morphology [116].

*B. subtilis* (A15), *B. amyloliquefaciens* (D29) and *B. methylotrophicus* (H8) when evaluated against bacterial leaf blight, *B. amyloliquefaciens* D29 shown better results with spike of SOD (350 units/g FW) and better inhibition rate of 60.36 per cent as compared to control with SOD (150 units/g FW) [128]. Similarly, SOD spike was observed while mitigate the *spl40* and wild type strains of *Xanthomonas oryzae* pv. *oryzae*. The results have reported that, SOD levels are far higher in *spl40* (60–65 units/g FW) as compared to wild type (30–35 units/g FW) during the tillering stage [129].

The rise of SOD levels is the reason of programmed cell death which is the main step while controlling the spread of pathogen. Several antioxidant profile such as total phenolic content and content of flavonoid was observed in Pusa basmati-1. The treated samples resulted maximum total phenolic content ( $12.23 \pm 0.06$ ), and total flavonoid content ( $22.20 \pm 0.02$ ) as compared with control with total phenolic content ( $10.14 \pm 0.01$ ), and total flavonoid content ( $12.20 \pm 0.06$ ) at 5th day after infection [130]. Similarly, various isolates of endophytic bacteria were tested their efficiency against *Xoo*. Out of various isolates, the isolates of *Bacillus subtilis* var. *amyloliquefaciens* FZB 24, EPB 9, EPB10, EPCO 29 and EPCO 78 shown maximum inhibition with 20 mm of inhibition in above well performed isolates as compared to control with 0 mm of inhibition [131]. A *Bacillus velezensis* strain Bv-303 was reported to increase disease resistance to BLB up to 62.7 % *in vivo*. However, no effect on rice seed germination and seedling growth was observed [117]. Secondary metabolite production in *B. velezensis* BR-01 was reported by Zhou and co-workers. Spraying of its fermentation broth reduced BLB incidence up to 66.16 % and controlled BLB up to 55.51 % respectively [118]. A novel species *Bacillus oryzicola* sp. nov. was reported to promote rice growth [119]. Another *Bacillus* species, *B. albus* strain CWTS 10 produced siderophores and several anti-microbial compounds and promoted plant growth [120]. *Bacillus amyloliquefaciens* FZB42, was previously reported to secrete antibiotic compounds diffidin and bacilysin which distorted *Xoo* cell walls and had protective rates of 58.82%–72.31 % [121].

## 5. Microbial consortia for enhancing bioefficacy of BCAs against *xoo*

Several studies demonstrated that microbial consortium typically surpass individual inoculants in management of plant diseases. The microbial consortium offers numerous benefits, including participation in carbon exchange, absorption of excess water and nutrients, acting as probiotics, and simultaneously mitigating both biotic and abiotic stresses [66]. Microbial consortia-based

bioinoculants typically consist of various species of bacteria, and some formulations also incorporate beneficial fungi [132]. Utilizing multiple species of PGPM's with diverse mechanisms is anticipated to provide a vast series of benefits for plants, including promoting growth, enhancing overall health, and increasing yields. Additionally, such diverse PGPM applications are expected to reduce plant diseases caused by pathogens [133]. Swarna rice treated by WBB70 and WBF4 strains of *Bacillus amyloliquefaciens* and *Aspergillus spinulosporus*, either individually or in combination, against *Xanthomonas oryzae* pv. *oryzae*, the consortium (WBB70 + WBF4) outperformed the individual treatments. The leaf lesion of *Xoo* was 5 per cent for the consortium, compared to 10 per cent for WBB70 and 13 per cent for WBF4 [134]. *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) encounters significant inhibition when confronted with *Trichoderma* consortia (TAIK-1 to 5), *Bacillus* consortia comprising *B. velezensis*, *B. subtilis*, and *B. paralicheniformis*, then singular inoculants. The findings reveal superior efficacy in pathogen control by *Trichoderma* consortia, manifested by a reduced lesion length of 7 per cent. Whereas, *Trichoderma* inoculants demonstrate suboptimal performance, exhibiting lesion lengths (TAIK-1 at 9 %, TAIK-2 at 15 %, TAIK-3 at 16 %, TAIK-4 at 11 %, and TAIK-5 at 13 %) Similarly, *Bacillus* consortia exhibit heightened effectiveness, with a lesion length reduction of 3 per cent compared to *Bacillus* singular inoculants with *B. velezensis* at 5 per cent, *B. subtilis* at 4 per cent, and *B. paralicheniformis* at 5 per cent [135].

The concurrent administration of biocontrol agents not only exerts antagonistic effects against pathogens but also positively impacts various growth parameters in plants by enhancing nutrient assimilation. The combined application of *Trichoderma harzianum* (Th3) and *Pseudomonas fluorescens* (RRb11) significantly exhibited BLB severity of 13.5 per cent, whereas, individual inoculants (*T. harzianum* Th3) showed severities of 18.2 per cent and 21.4 per cent for *P. fluorescens* (RRb11), compared to the untreated control (27.1 %). Moreover, the consortium not only mitigated BLB but also enhanced plant morphological attributes. Plants treated with the consortium showed increased plant height (90.1 cm), root length (22.5 cm), and number of grains per plant (297.3), surpassing those treated with individual inoculants (85.3 cm, 18.5 cm, and 278 grains per plant for *T. harzianum* Th3, respectively; 85 cm, 18.5 cm root length, and 268.7 grains per plant for *P. fluorescens* RRb11, respectively) [136]. Similarly, in a study an endophytic bacterial consortium used against BLB of rice have demonstrated superior results with lowest intensity of BLB (26.6 %) and notable increase in morphological parameters such as plant height (104.42 cm), fresh weight of plant (46.33 g) as compared to control with highest intensity (42.5 %) and lowest growth of morphological parameters such as plant height of 98.40 cm and fresh weight of 32.76 g [137].

Under in-vitro conditions, the sixteen isolates of *Streptomyces* (S1 to S16), twenty isolates endophytic bacteria (EB1 to EB20) and six isolates of fungal endophytes (EF1 to EF6) exhibited effective suppression of *Xoo* in dual culture assay. Among various combinations, EB8 + S2 + S15 demonstrated the most promising results with 52.58 per cent inhibition, followed by EF2 + S2 + S15 (47.60 %), EB8 + S15 (48.29 %), and EB8 + S2 (45.11 %), as compared to the control [138]. Similarly, various combinations of bacteria, including *Bacillus cereus* (E15), *Lysinibacillus fusiformis* (E18), *Escherichia coli* (E27), *Delftia lacustris*, and bacterium clone SN\_IN\_327 (P124), were employed to assess their efficacy against *Xoo*. The outcome demonstrated that, combination of P55 and E27 exhibited the greatest inhibition zone (2.76 cm), whereas, P124 + E18 (1.47 cm), P124 + E27 (0.30 cm), P165 + E15 (2.32 cm), P165 + E18 (0.66 cm), P55 + E15 (3.05 cm), P55 + E18 (2.56 cm), and P124 + E15 (2.45 cm), also displayed varying degrees of inhibition [139].

The synergistic utilization of chemical compounds and beneficial microorganisms as a consortium has the potential to yield optimal outcomes in disease mitigation. The synergistic effect of *Trichoderma harzianum* and carbendazim (with different concentrations) was investigated for disease mitigation at various concentrations. Among these combinations, *T. harzianum* + Carbendazim at 1000 ppm exhibited higher efficacy, with a colony diameter of 60.33 mm and an inhibition percentage of (22.6 per cent after 48 h of incubation, compared to control [140]. Similarly, in a study various combination of beneficial microbes includes consortium-A (consisting of *A. vinelandii*, *Azospirillum* sp., *B. cereus*, *Bradyrhizobium* sp., and *Methylobacterium* sp.) and consortium-B (comprising *A. chroococum*, *A. vinelandii*, *Azospirillum* sp., *P. cepacia*, *Penicillium* sp., and *Acinetobacter*) were tested efficacy against BLB in three rice varieties including Inpari 9, Inpari 33, and Ciherang. Among the two combinations of beneficial microbes, Consortium B demonstrated high compatibility with both Inpari 33 and Ciherang rice varieties, resulting in reduced disease intensity of 14.44 per cent at 10 weeks after transplanting as compared with untreated check with intensity of 17.50 per cent [141]. A study on the rice variety Ciherang assessed the efficacy of the microbial consortium Mikrobat (comprising *Azotobacter* sp., *Lactobacillus* sp., *Pseudomonas* sp., *Streptomyces* sp., and *P. polymyxa*) and a single inoculant (*Trichoderma asperellum*), in mitigating bacterial leaf blight. Mikrobat demonstrated a lower severity of 3.67 per cent, while the single inoculant (*T. asperellum*) showed a severity of 5.27 per cent, whereas, control had a severity of 4.50 per cent [142].

## 6. Future prospects and conclusion

Agricultural and environmental sustainability are paramount when devising strategies for disease control in plants. Bacterial leaf blight, caused by *Xanthomonas oryzae* pv. *oryzae*, is a significant disease of rice which threatens global food security. Traditionally, BLB is managed through the use of chemical pesticides which pose environmental risks and, in many cases, lead to development of bacterial resistance. As a result, there is a growing interest in exploring sustainable alternatives of disease control such as antagonistic microbes or biocontrol agents, which compete for space and nutrients, produce antimicrobial compounds, and induce plant defense responses for suppressing the pathogen. Compared to the conventional use of single inoculants, the application of multi-strains demonstrates significantly enhanced control efficacy. The microbial consortium not only effectively suppresses the proliferation of *Xoo* but also induces a robust activation of plant defence mechanisms. Although BCAs show promising results under controlled conditions, their biggest limitation is poor efficacy during field application as compared to chemical pesticides. The field efficacy of BCA's is subjected to abiotic factors such as temperature and moisture, seasonal variations, area of cultivation, availability of nutrients and presence of chemical residues [143]. Therefore, in order to achieve a consistent field performance, these factors need to be taken into consideration. Bonaterra and co-workers have reviewed some strategies that can be adopted for improving BCA efficacy including nutrient

enhancement and improving methods of delivery [143]. Compatible microbial strain mixes can be designed where each microbe exhibits complementary mechanisms of action and can thrive under hot and humid soil conditions of rice cultivation for improving BCA efficacy. They can also be supplemented with traditionally used anti-microbial compounds specific for *Xoo* to enhance the potency of the formulations and avoid long applications. However, reports have shown that extensive use of antibiotics have increased *Xoo* resistance against such compounds [144]. In this regard quinazolines and sanguinarine derived antibiotics with novel mechanisms of action can be used in conjunction with BCAs which would simultaneously counter drug resistance and suppress pathogen activity [145, 146]. One potential reason cited for pathogen resistance is the secretion of quorum sensing molecules which help them evade unsuitable environmental conditions. In addition to using novel antibiotics, naturally derived quorum sensing inhibitors can also be of potential benefit to rice production when used alongside BCAs as they are target specific and block pathogen growth and metabolism [147]. Also combined usage of biocontrol agents and chemical pesticides, which falls in line with integrated pest management (IPM), have shown significant reduction in disease symptoms while simultaneously improving plant growth. Therefore, the two can be used together for rice BLB managements as it will considerably reduce the burden on chemical usage.

Poor performance of BCAs in agricultural fields is also attributed to certain biotic factors such as predation and competition by other non-target species residing in rhizosphere and pathogen inoculum density. In addition to them, the tripartite relationship between plants, pathogens and BCAs plus interaction between plants and other rhizosphere microbes manifest their own influence on BCA activity. Understanding the biocontrol mechanisms used by BCAs and their regulation during interaction with plants and pathogens holds the key for improving existing strains of these agents. Molecular biology, genomics, transcriptomics and proteomics can further help in identifying high efficacy strains of bacterial and fungal biocontrol agents possessing anti-bacterial activities against *Xoo*. However, continuous application of the same BCA should be discouraged so as to avoid development of resistance against them [19]. Shelf-life enhancement and time of application should also be focused upon. One can also use broad spectrum BCAs to counter other bacterial and fungal pathogens in addition to *Xoo* which have devastating effects on rice production and productivity. A robust comparison between field efficacy of chemical and biocontrol agents would be helpful in highlighting the shortcomings of BCA treatments and devise strategies for their improvement. Also impact of BCAs on indigenous microbes in rice rhizosphere and on human health needs assessment. In conclusion, the efficient management of the highly infectious bacterial leaf blight (BLB) in rice, can be mitigated through the strategic application of biocontrol agents as part of IPM. This approach holds promise as an innovative and sustainable strategy for combating BLB and ensuring the health and productivity of rice crops.

#### **CRedit authorship contribution statement**

**Bestha Sai Teja:** Writing – review & editing, Writing – original draft. **Gayatri Jamwal:** Writing – review & editing. **Vishal Gupta:** Writing – review & editing, Supervision, Project administration, Conceptualization. **Mansi Verma:** Writing – original draft. **Ayushi Sharma:** Writing – review & editing. **Akash Sharma:** Resources. **Vinod Pandit:** Resources.

#### **Ethical approval statement**

The study did not involve usage of any plant cultivar, voucher specimen of plant material and plant extracts. No conduction of plant transformation experiments and field, green house or lab experiments was required for the study.

#### **Data and code availability statement**

No new data was generated for the research described in the article.

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#### **Declaration of competing interest**

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

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