PLANT DISEASE FEATURE

Ecofriendly Control Strategies Against *Clavibacter michiganensis*, the Causal Agent of Bacterial Canker of Tomato

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Abstract

Bacterial canker of tomato, caused by the pathogenic Gram-positive bacterium *Clavibacter michiganensis*, represents a serious threat to tomato growers worldwide. Diverse approaches have been reported to control this infectious and aggressive bacterium. The current control strategy mostly relies on the application of copper-based products and, to some extent mancozeb and streptomycin, which are leading to growing concerns about resistance promotion, phytotoxicity effect, and environmental pollution. In this paper, we present a comprehensive overview on ecofriendly management strategies to control this phytopathogen. New technologies, including the application of biological and non-biological inducers integrated with conventional preventive measures, represent a new approach in plant protection to develop a sustainable strategy to fight this devastating disease.

Keywords: biocontrol, elicitors, induced systemic resistance, sustainable agriculture, systemic acquired resistance

History and Importance of the Phytopathogen *Clavibacter michiganensis*

Tomato (*Solanum lycopersicum*) is the second-most consumed vegetable crop in the world after potato, with an annual production of 186 million tons in 2022 (FAO 2022). It is rich in vitamins, minerals, sugars, essential amino acids, iron, dietary fibers, and phosphorus, providing an important nutrition source (Arah et al. 2015; Ayandiji and Adeniyi Omidiji et al. 2011). Bacterial canker of tomato (BCT), caused by the pathogenic Gram-positive bacterium *Clavibacter michiganensis* (*Cm*; previously named *Clavibacter michiganensis* subsp. *michiganensis*), represents a serious threat to the tomato-growing industry (Fig. 1). The disease was first described in 1910 on tomato plants in Michigan, U.S.A. (Smith 1910), and is currently widespread through all six continents (EPPO 2016). The European and Mediterranean Plant Protection Organization (EPPO) places *Cm* on the A2 list (pests locally present in the EPPO region) of quarantine pathogens (EPPO 2016). Solanaceous (e.g., *Datura stramonium*) and even nonsolanaceous plants (e.g., *Chenopodium album* and *Amaranthus retroflexus*) have been identified as reservoirs for survival and dissemination of the bacterium (Chang et al. 1992; Eichenlaub and Gartemann 2011).

The genus *Clavibacter* belongs to the phylum Actinobacteria, which is characterized by their unique genome with high guanine-cytosine content. It is an aerobic, nonmotile, and non–spore-forming actinomycete with optimal growth at 25°C in a pH between 7 and 8 (Nandi et al. 2018; Sen et al. 2015). Other than *Cm*, which infects tomato, two other species (*Clavibacter californiensis* and *Clavibacter phaseoli* [asymptomatic on tomato plant]) were recently isolated from tomato seeds (Arizala et al. 2022; Yasuhara-Bell and Alvarez 2015). In addition, *Clavibacter lycopersici* sp. nov. isolated from symptomless tomato plants in Iran was recently described by Osdaghi et al. (2023).

Disease occurrence has been reported in the United States (Quesada-Ocampo et al. 2012; Tancos et al. 2015; Thapa et al. 2017), Canada (Poysa 1993), Mexico (Borboa Flores et al. 2009; Holguín-Peña et al. 2006), Chile (Valenzuela et al. 2018), Uruguay (Croce et al. 2016), Argentina (Wassermann et al. 2017), Italy (Bella et al. 2012; Ialacci et al. 2016), Spain (De León et al. 2009), Belgium (Zaluga et al. 2013), Serbia (Milijašević-Marčić et al. 2012), Lithuania (Burokienė et al. 2005), Turkey (Basim et al. 2004; Baysal et al. 2011; Sen et al. 2018), Iran (Nazari et al. 2007; Osdaghi et al. 2018), Syria (Ftayeh et al. 2008), Japan (Kawaguchi et al. 2010), South Korea (Myung et al. 2008), India (Singh et al. 2017), Indonesia (Anwar et al. 2004), Israel (Kleitman et al. 2008), Morocco (Amkraz et al. 2010), and Egypt (Abd El-Sayed 2002). The presence of pathogen was also documented in Germany, the Netherlands, France, Austria, Greece, Bulgaria, Hungary, Cyprus, the Czech Republic, Latvia, Poland, and Romania (EFSA Panel on Plant Health 2014). Yield losses of 20 to 85% have been reported

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because of canker and wilting symptoms (Chang et al. 1992; Hausbeck et al. 2000; Poysa 1993; Rat et al. 1991).

The pathogenicity of *Cm* depends on several pathogenicity-determinant genes located on two circular conjugative plasmids (e.g., pCM1 [*celA*] and pCM2 [*pat-1*]) and a chromosomal pathogenicity island known as PAI (*tomA*, *ppaA*, *chpC*, *chpE*, *chpF*, *chpG*, *pelA*, and *sbtA*) (Gartemann et al. 2008; Jacques et al. 2012; Yim et al. 2012). The genomic features of *Cm* and interaction between *Cm* and tomato plants have been extensively described in several studies (Martínez-Castro et al. 2018; Nandi et al. 2018; Peritore-Galve et al. 2021).

Infection, Symptomatology, and Survival

Bacterial growth and disease severity are favored by higher temperatures (25 to 30°C) and humidity. *Cm* can cause various symptoms on infected tomato plants. The severity of the disease depends on the virulence of the bacterial strain, inoculum concentration, cultivar susceptibility, host plant age, cultural practices, and environmental conditions, including temperature, humidity, and composition of the microbiota (de León et al. 2011; Yin et al. 2020). Symptoms (Figs. 2 and 3) can be observed in leaves (wilting, shriveling, chlorosis, and necrosis of leaflet), stems (vascular discoloration, necrosis, and cankers) and fruits (necrotic bird's eye spots surrounded by white halos) (EPPO 2016; Vega and Romero 2016). Primary infections occur from seed contamination or from soilborne inoculum and affect the quality and quantity of fruit production. At the early stages of plant growth, systemic infections can cause unilateral wilting, vascular discoloration, and development of necrosis and cankers on the stems (Fig. 3), which ultimately can lead to total wilting and death. Secondary infections occur through wounds or

Fig. 1. Tomato plants, highly affected by *Clavibacter michiganensis* in greenhouse.

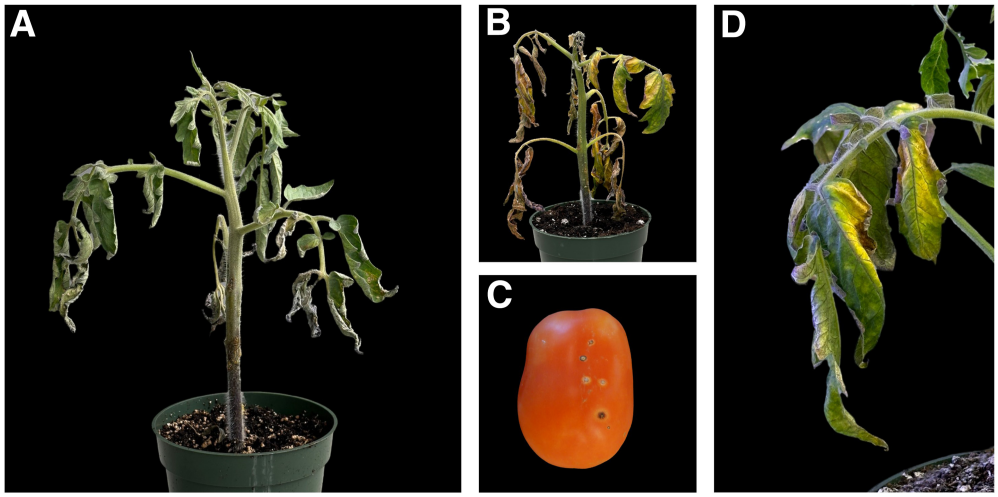

Fig. 2. A and B, Wilting, shriveling, and necrosis of leaflets. **C,** Fruit bird's eye spots surrounded by white halo. **D,** Marginal leaf necrosis and chlorosis.

natural openings, including stomata and hydathodes. These local infections found in older plants often result in foliar symptoms, such as leaf chlorosis or marginal necrosis of leaflets (Fig. 2D) (Carlton et al. 1998; Tancos et al. 2013). The life cycle and dissemination of *Cm* are represented in Figure 4.

Contaminated seeds are considered a primary source of infection for long-distance transmission and introduction of pathogen into previously disease-free areas. *Cm* can colonize the seed coat and endosperm (Quesada-Ocampo et al. 2012; Tancos et al. 2013). A transmission rate of 0.01% is considered sufficient to initiate a serious epidemic under favorable conditions (Chang et al. 1991). Plant debris acts as another source of inoculum for systemic infections. *Cm* can survive in plant debris for up to 2 years, influenced by both tissue exposure and geographical location (Fatmi and Schaad 2002). The pathogen is spread via the use of contaminated tools and by moving through a contaminated crop, in particular when the crop is wet. In open-field crops, the use of overhead irrigation can spread the pathogen via splashing or dripping water (Fig. 4) (Carlton et al. 1998; Chang et al. 1991; Xu et al. 2010).

Fig. 3. Canker symptoms on the stem at the site of artificial inoculation (**A to C**) and distal from the site of inoculation (**D**).

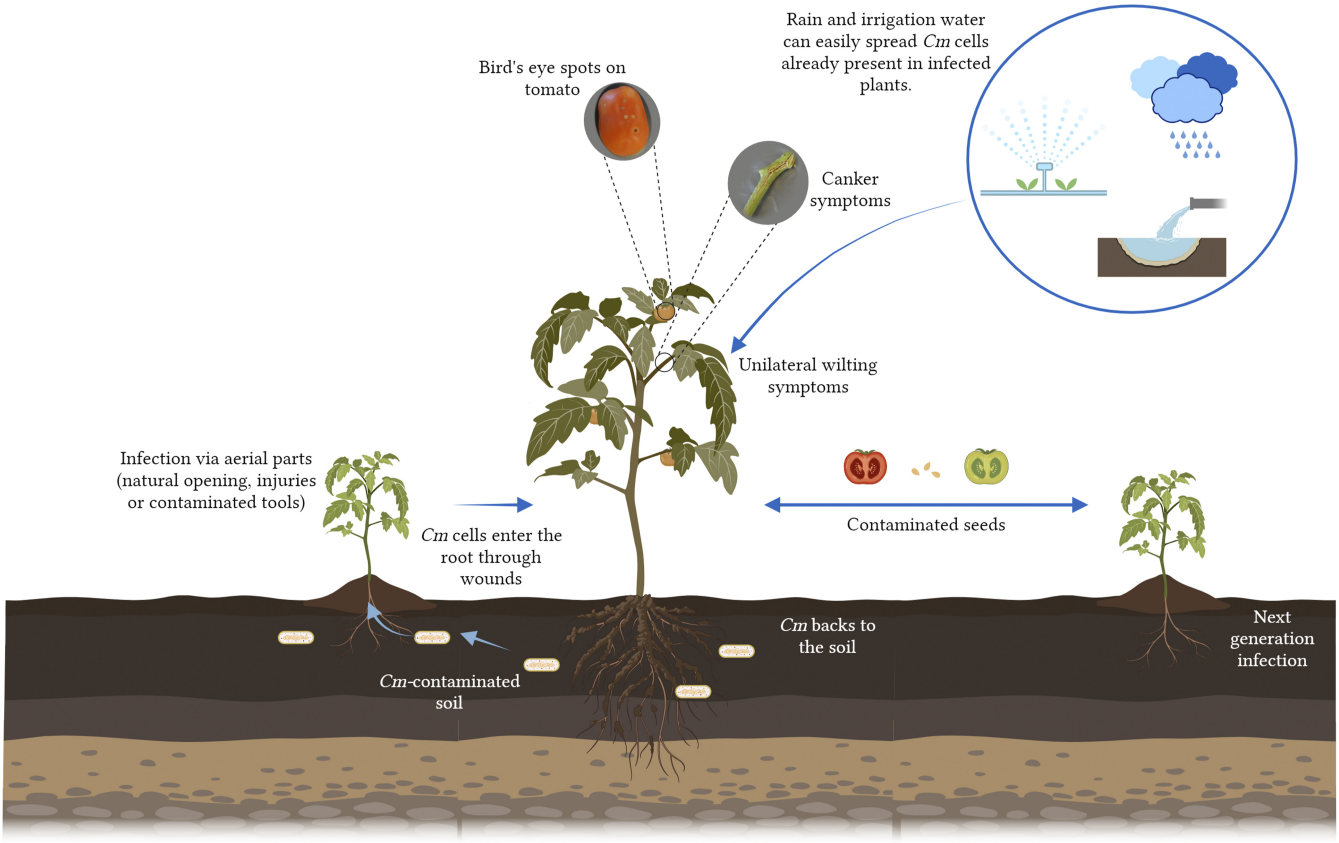

Fig. 4. Life cycle of *Clavibacter michiganensis* (*Cm*) causing bacterial canker of tomato. The infected soil or seeds act as a primary source of inoculum: *Cm* cells enter the host plant through the natural opening or injured plant tissues. After entering the host plant, they systemically multiply in xylem tissues and produce typical wilting symptoms. Infection can be spread from the disease to healthy plants through rain and irrigation water. Contaminated seeds and soils can provide the new source of inoculum for the next generation.

Control of *Cm*

Despite all attempts to manage this destructive disease, there are no methods to eradicate BCT (de León et al. 2011; Rani et al. 2021). The best strategy still relies on strict prevention (Sen et al. 2015). Several studies indicate that the use of chemical approaches (copper-based compounds or antibiotics) is only partially effective against *Cm* (Kasselaki et al. 2011; Sharma and Kumar 2000). In addition, the widespread application of chemical products has raised growing concerns about health problems (wildlife, livestock, and humans), environmental pollution, ecological disruption, and the development of resistance (Rani et al. 2021). For these reasons, many chemical products have been removed from lists of registered crop protection agents (Strobel et al. 2004). Therefore, a major priority in modern agriculture is to develop more effective and safer alternatives to fight plant diseases while improving crop quality and production (Glick 2020). Ecofriendly control strategies against *Cm* are presented in Figure 5.

Moreover, to prevent the introduction and spread of the pathogen, there is room for further improvement of methods to detect the pathogen in a fast, accurate, sensitive, and cost-efficient way. Such methods are also indispensable to prevent the introduction of infected plants for planting and contaminated materials and to monitor the effectiveness of management and control strategies. A loop-mediated isothermal amplification technique as a portable molecular diagnosis tool for on-site detection was developed in the previous decade (Yasuhara-Bell et al. 2013). Furthermore, multiplex TaqMan quantitative PCR assays and an enrichment in seed extracts followed by TaqMan quantitative PCR show high sensitivity and specificity in detecting *Cm* strains (Larrea-Sarmiento et al. 2019; Lelis and van der Wolf 2017; Ramachandran et al. 2021).

Importance of Biological Control Approaches

There is a growing demand for healthy food that is free of synthetic agrochemicals (Watanabe et al. 2020). Within this frame there is a continuous search for ecofriendly and sustainable approaches to control phytopathogens, generally based on biocontrol. In these approaches, organisms or products from biological origin are used, such as natural enemies or biobased products derived from animals, plants, or microbials to control pests. Biological control agents (BCAs), including bacteria, fungi, and viruses (mycoviruses or bacteriophages), can limit the growth of phytopathogens through either direct or indirect mechanisms. Direct mechanisms involve phytopathogen exclusion through means such as competition, siderophore production, and secretion of secondary metabolites, hydrolytic enzymes, and volatile compounds. Indirect mechanisms refer to induction of resistance (IR) in plants. Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are traditionally considered as the two main defense systems of plants (Grady et al. 2016; Sivasakthi et al. 2014). SAR is induced by necrotizing pathogens, whereas ISR is mediated by beneficial microbes living in the rhizosphere, such as bacteria and fungi. The involvement of plant hormones, such as salicylic acid (SA) for SAR and jasmonic acid (JA) and ethylene (ET) for ISR, has been reported for these two types of resistance pathways (Conn et al. 2008; Niu et al. 2011; Pieterse et al. 2014), although adverse results were also reported (De Vleesschauwer and Höfte 2009; Takishita et al. 2018). However, some concerns have been raised with this classification. First, observable defensive responses are often similar in both SAR and ISR. Second, physical injury, chemicals, and volatile organic compounds have been found to elicit resistance as well but as nonbiotic agents or actions. Therefore, De Kesel et al. (2021) proposed to use "induced

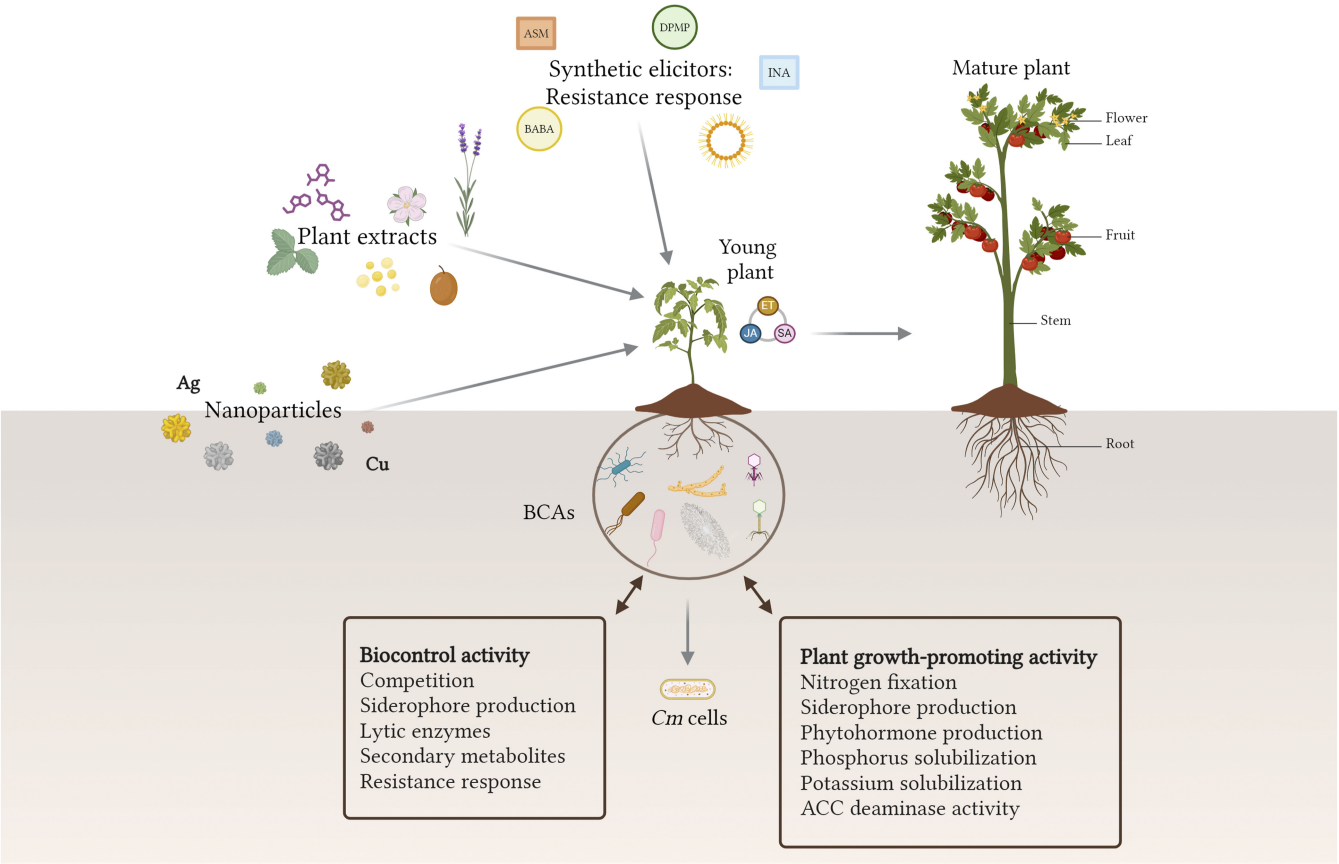

Fig. 5. Schematic illustration of control strategies used for the management of bacterial canker of tomato caused by *Clavibacter michiganensis* (*Cm*). ACC = 1-aminocyclopropane-1-carboxylate; ASM = acibenzolar-S-methyl; BABA = DL-β-aminobutyric acid; BCA = biological control agent; DPMP = 2,4-dichloro-6-{(E)-[(3-methoxyphenyl) imino] methyl} phenol; ET = ethylene; INA = 2,6-dichloroisonicotinic acid; JA = jasmonic acid; SA = salicylic acid.

resistance" (IR) as an umbrella term and "IR stimulus" as general reference for the evoking agent or action.

A large proportion of BCAs belong to the group of plant growth-promoting rhizobacteria (PGPR). They colonize plant roots and interact with phytopathogens from the soil (Schroth and Hancock 1981; Weller 1988). In contrast to synthetic chemical compounds, phytopathogens do not easily develop resistance to biopesticides (Mnif and Ghribi 2015; Singh et al. 2022; Valdés et al. 2017). In addition, PGPR improve the general plant health status through a variety of mechanisms, including nitrogen fixation, siderophore production, indole-3-acetic acid (IAA) production, phosphate and potassium solubilization, and aminocyclopropane-1-carboxylate deaminase activity (Fig. 5). The mechanisms of action of various BCAs against *Cm* are presented in detail below.

Bacterial BCAs

Bacillus spp.

Strains of the Gram-positive genus *Bacillus* are the most frequently used biocontrol agents in agriculture. *Bacillus* isolates are not only potent BCAs, via IR and production of antagonistic secondary metabolites, but they also can stimulate plant growth (Olishevska et al. 2019; Shafi et al. 2017; Tamehiro et al. 2002). *Bacillus* spp. have also been identified to control several fungal and bacterial diseases on tomato plants (Agarwal et al. 2020; Amaresan et al. 2019; Olishevska et al. 2023).

Direct effect on *Cm*

Strains *B. velezensis* 1B-23 and *Bacillus* sp. 1D-12 produced a clear inhibition zone (antagonistic activity) against *Cm* in vitro and significantly reduced (as root drench) the incidence of BCT in the greenhouse (Laird et al. 2020). These bacteria produce surfactin-type lipopeptides [Leu^7] surfactin C_{13} (known as surfactin A), [Leu^7] surfactin C_{14} (surfactin B), and [Leu^7] surfactin C_{15} (surfactin C), of which surfactin B inhibited growth of *Cm* at all tested concentrations (1 to 10 mg/ml). These compounds are broad-spectrum antibiotics that function to disrupt bacterial membranes. Another notable aspect of these compounds goes back to their nonspecific interactions, which may help to prevent the development of resistance (Zhao et al. 2017).

In greenhouse experiments, significant reduction of bacterial canker by 74.4 and 53.3% was observed for *B. amyloliquefaciens* and *B. subtilis* strains, respectively, when they were used as talc-based formulations (Abo-Elyousr et al. 2019). These strains produced hydrogen cyanide (HCN), which can contribute to disease suppression (Voisard et al. 1989). These strains also showed plant growth promotion (PGP) properties (Table 1). In another study, the efficiency of *B. amyloliquefaciens* strain S1 as a biocontrol agent against *Cm* was confirmed both in vitro and in vivo. Minimum disease incidence (30.0%) was recorded for tomato plants inoculated (as root inoculation) with this strain compared with controls (98%) treated just with *Cm*. It exhibited produced lipase, protease, and chitinase (Gautam et al. 2019); these enzymes facilitate the release of breakdown products of plant cell wall components, acting as elicitors of plant defense responses (Van Loon 1997). Also, for this strain PGP functions have been demonstrated, including nitrogen fixation, inorganic phosphate solubilization, and production of siderophores and IAA (Gautam et al. 2019). The latter is a key phytohormone that improves plant growth, root development, and absorption of water and nutrients (Vega-Celedón et al. 2016). Siderophores are small molecules chelating Fe^{3+} with high specificity and efficiency. They are considered virulence factors by limiting iron availability to pathogenic bacteria. Phosphorus is an important micronutrient for plant growth because its deficiency in the soil delays maturation and decreases harvest yields (Sharma et al. 2013; Singh et al. 2022). Information regarding *Bacillus* spp. and mechanisms of action against *Cm* are provided in Table 1.

IR

In the case of BCT, Kolomiiets et al. (2019) reported a *Bacillus subtilis* strain (as aerial spray) that induced resistance in tomato plants against *Cm* by the action of phenolic compounds and peroxidase enzyme. It decreased disease incidence, increased the chlorophyll *a+b* and carotenoid content, and enhanced photosynthesis in tomato plants. Increased activity of antioxidant enzymes such as peroxidases induced initial reactions for the biosynthesis of phenolic compounds. These compounds play an important role in the regulation of metabolic processes, including lignin biosynthesis, accumulation of phytoalexins, and the formation of structural barriers. In general, biosynthesis of phenolic compounds appears to be an essential component of plant protection against phytopathogens (Baker et al. 2005; Farrag et al. 2017; Lewis and Yamamoto 1990; Nicholson and Hammerschmidt 1992).

A recent investigation conducted by Solano-Alvarez et al. (2021) revealed that the *Bacillus cereus* strain Amazcala exhibited significant antagonistic activity against *Cm* in vitro. Foliar spray and soil drench with strain Amazcala decreased the severity of BCT by approximately 50%. Higher activity of enzymes involved in reactive oxygen species (ROS) scavenging (superoxide dismutase and catalase [CAT]) as well as phenylpropanoid biosynthesis (phenylalanine ammonia-lyase [PAL]) was also observed in treated tomato plants, which is positively correlated with increase in plant tolerance to biotic stress and disease (Friend et al. 1973; García et al. 2015). In addition, this biocontrol agent respectively increased and decreased the relative expression of chalcone synthase gene *chs* (involved in flavonoids biosynthesis) and *PR1a* (SA gene marker), suggesting the activation of defense response of tomato plants through the SA-independent pathway (Solano-Alvarez et al. 2021). This strain displayed PGP factors, such as inorganic phosphate solubilization and gibberellic acid production. Application significantly increased height, stem width, dry weight, and total chlorophyll content in tomato plants. *Bacillus* spp. are active producers of several gibberellins, significantly increasing plant height in pepper plants (Kumar et al. 2015).

Extracts of *Bacillus* species

Jang et al. (2022) found that using bioactive aqueous extracts of *Bacillus* sp. strains H8-1 and K203 as soil drenches inhibited wilting caused by *Cm* and slowed colonization of tomato plants by the bacterium. These bioactive culture extracts inhibited the viability of *Cm* and decreased the relative expression of virulence genes, including *celA, celB, pat-1*, and *pelA* under in vitro conditions. These genes encode three major virulence-related enzymes of *Cm*, cellulase, serine protease, and pectate lyase, which are key virulence factors for host penetration, plant cell degradation, colonization, and infection promotion of entire plants (Hwang et al. 2019; Nandi et al. 2018). The ability of these extracts to induce resistance response was also evaluated. The results showed that treatment with the culture extracts of these strains increased the expression of SA-dependent (*PR-1a*) gene for strain K203 and JA-dependent (*PI2*) gene for strain H8-1 while decreasing the expression of ET-related gene (*ACO*) in *Cm*-infected tomato plants. A high accumulation of the plant's oxidative enzymes, including peroxidase, glutathione peroxidase, and CAT, was also observed in tomato plants inoculated with these bioactive extracts (Jang et al. 2022). Because ET is a stress hormone in plants, reduction in its expression resulted in resistance against phytopathogen (Binder 2020).

Pseudomonas spp.

Pseudomonas spp. are among the most beneficial microorganisms of the rhizosphere to control plant pathogens. They possess valuable features to suppress plant pathogens, such as biofilm formation, production of antimicrobial metabolites including phenazine-1-carboxylic acid, 2,4-diacetylephloroglucinol (DAPG), HCN, siderophores, and rhamnolipids (Haas and Défago 2005; Santoyo et al. 2012). Several *Pseudomonas* spp. express both PGP and biocontrol features to control plant pathogens and promote plant growth (Hashem and Abo-Elyousr 2011; Santoyo et al. 2012).

Direct effect on *Cm*

Pseudomonas brassicacearum LBUM300 exhibited antagonistic activity against *Cm* growth in both in vitro and in planta conditions (Lanteigne et al. 2012). The development of disease was significantly reduced in root-treated tomato plants. The level of reduction was

related to the production of antimicrobial compounds such as DAPG and HCN, because mutant strains LBUM300*phlD*$^-$ (DAPG deficient) and LBUM300*hcnC*$^-$ (HCN deficient) could not reduce the in planta symptoms significantly. These mutant strains also caused less or no inhibition zones against *Cm* under in vitro conditions, further supporting the idea that the production of DAPG and HCN contributed to control the growth of *Cm* (Lanteigne et al. 2012). In line with these observations, Paulin et al. (2017) reported that the presence of *Cm* significantly increased rhizosphere populations of *P. brassicacearum* LBUM300. They showed that in *Cm*-infected tomato rhizospheres, the populations of wild-type LBUM300 and strain LBUM300Δ*hcnC*, both producing DAPG, were significantly higher than the population of strain LBUM300Δ*phlD*. Additionally, in the presence of *Cm,* the expression of *phlD* was significantly upregulated, and biofilm formation was significantly reduced in strain LBUM300Δ*phlD* compared with the wild-type and LBUM300Δ*hcnC* strains.

Table 1. Overview of the modes of action of biocontrol agents to enhance tomato growth parameters and control of *Clavibacter michiganensis* (*Cm*)

Biocontrol agent	PGP[a] properties	Control *Cm*[c]	References
Bacillus sp.	ND[b]	Inhibitory effect (culture and extract) against *Cm* growth in vitro Reduction of disease severity and disease incidence in planta Removal of *Cm* from tomato seeds Production of surfactin A, B, and C Inhibition of wilting caused by *Cm* Decrease of the relative expression of virulence genes coding factors, such as cellulase and pectate lyase, in *Cm* High accumulation of antioxidant enzymes, including peroxidase, glutathione peroxidase, and catalase, in tomato plants IR (SA and JA signaling pathways)	Kasselaki et al. 2011 Laird et al. 2020 Jang et al. 2022
Bacillus amyloliquefaciens	Increase the seed germination and seedling vigor Grow on nitrogen-free medium Improve tomato growth parameters Solubilize inorganic phosphorus Produce siderophores and indole acetic acid	Inhibitory effect (culture and extract) against *Cm* growth in vitro Reduction of disease severity and disease incidence in planta High accumulation of phenylalanine ammonia-lyase and total phenol contents in tomato plants	Girish and Umesha 2005 Gautam et al. 2019 Abo-Elyousr et al. 2019
Bacillus velezensis	ND	Inhibitory effect (culture and extract) against *Cm* growth in vitro Reduction of disease incidence *in planta* Production of surfactin A, B, and C	Grady et al. 2019 Laird et al. 2020
Bacillus cereus	Improve tomato growth parameters and yield Solubilize inorganic phosphorus Produce gibberellic acid Increase total chlorophyll content in tomato leaves	Inhibitory effect (culture) against *Cm* growth in vitro Reduction of disease severity and disease incidence in planta High accumulation of stress response antioxidant enzymes, including superoxide dismutase, catalase, and phenylalanine ammonia-lyase, increase in expression of *chs* (contributed to flavonoid biosynthesis) in tomato plants	Moustaine et al. 2019 Solano-Alvarez et al. 2021
Bacillus subtilis	Increase the seed germination and seedling vigor Improve tomato growth parameters Produce siderophores and indole acetic acid Improve photosynthesis Increase chlorophyll and carotenoid content in tomato leaves	Inhibitory effect (culture and extract) against *Cm* growth in vitro Reduction of disease severity and disease incidence and delay in progression of the disease in planta High accumulation of peroxidase, phenylalanine ammonia-lyase, and total phenol contents (phenol and catechin) in tomato plants	Utkhede and Koch 2004 Girish and Umesha 2005 Jung et al. 2014 Abo-Elyousr et al. 2019 Kolomiiets et al. 2019
Brevibacillus brevis	Increase the seed germination and seedling vigor	Reduction of disease incidence in planta High accumulation of phenylalanine ammonia-lyase and total phenol contents in tomato plants	Girish and Umesha 2005
Pseudomonas entomophila	Improve tomato growth parameters Solubilize inorganic phosphorus Produce siderophores and indole acetic acid	Inhibitory effect (extract) against *Cm* growth in vitro Delay in progression of the disease Production of anti-*Cm* compounds IR (SA signaling pathway)	Takishita et al. 2018 Takishita et al. 2021

(*Continued on next page*)

[a] PGP = plant growth-promoting activity.
[b] ND = not determined.
[c] DAPG = 2,4-diacetylphloroglucinol; HCN = hydrogen cyanide; IR = induced resistance; JA = jasmonic acid; PCA = phenazine-1-carboxylic acid; SA = salicylic acid.

Table 1. (*Continued from previous page*)

Biocontrol agent	PGP[a] properties	Control *Cm*[c]	References
Pseudomonas fluorescens	Increase the seed germination Improve tomato growth parameters Produce siderophores and indole acetic acid Improve photosynthesis Increase chlorophyll and carotenoid content in tomato leaves	Inhibitory effect (culture) against *Cm* growth in vitro Reduction of disease severity and disease incidence and delay in expression of disease symptoms in planta High accumulation of peroxidase and phenol contents (phenol and catechin) in tomato plants	Boudyach et al. 2001 Umesha 2006 Amkraz et al. 2010 Singh et al. 2017 Abo-Elyousr et al. 2019 Kolomiiets et al. 2019
Pseudomonas brassicacearum	ND	Inhibitory effect (culture) against *Cm* growth in vitro Reduction of disease severity in planta Production of PCA, DAPG, and HCN	Lanteigne et al. 2012 Paulin et al. 2017
Pseudomonas aeruginosa	Improve tomato growth parameters Solubilize inorganic phosphorus and potassium Produce siderophores, indole acetic acid, and ammonia	Inhibitory effect (culture) against *Cm* growth in vitro Reduction of disease severity and disease progression in planta	Abo-Elyousr et al. 2019 Ghadamgahi et al. 2022
Pseudomonas putida	Improve tomato growth parameters Produce siderophores	Inhibitory effect (culture) against *Cm* growth in vitro Reduction of disease severity and disease incidence in planta High accumulation of the phenolic compounds (catechin and chlorogenic acid) in tomato leaves	Aksoy et al. 2017 Hamidi Banayem et al. 2020
Pseudomonas chlororaphis	ND	Inhibitory effect (culture) against *Cm* growth in vitro	Deng et al. 2015
Pseudomonas corrugata	ND	Inhibitory effect (culture) against *Cm* growth in vitro	Strano et al. 2017
Pseudomonas mediterranea	ND	Inhibitory effect (culture) against *Cm* growth in vitro	Strano et al. 2017
Pseudomonas sp.	Improve tomato growth parameters and yield Produce indole acetic acid	Inhibitory effect (culture) against *Cm* growth in vitro	Bouizgarne et al. 2023
Streptomyces sp.	ND	Inhibitory effect (culture and extract) against *Cm* growth in vitro	Yuan et al. 2009 Zhang et al. 2010
Streptomyces lividans	ND	Inhibitory effect of antimicrobial protein against *Cm* growth in vitro	Calderón-de la Sancha et al. 2022
Pantoea agglomerans	Improve tomato growth parameters and yield	Inhibitory effect (culture) against *Cm* growth in vitro Reduction of disease incidence in planta	Moustaine et al. 2019 El Kinany et al. 2017
Serratia proteamaculans	Improve tomato growth parameters and yield	Inhibitory effect (culture) against *Cm* growth in vitro Reduction of disease incidence in planta	Moustaine et al. 2019
Serratia sp.	Solubilize inorganic phosphorus, potassium, and zinc Improve tomato growth parameters and yield	Inhibitory effect (culture) against *Cm* growth in vitro	Bouizgarne et al. 2023
Alcaligenes faecalis	Improve tomato growth parameters	Inhibitory effect (culture) against *Cm* growth in vitro Reduction of disease incidence in planta Delay in canker symptoms development	Oloyede et al. 2021
Acinetobacter sp.	Improve tomato growth parameters	Inhibitory effect (culture) against *Cm* growth in vitro Reduction of disease incidence in planta Delay in canker symptoms development	Oloyede et al. 2021
Azotobacter chroococcum	Improve photosynthesis Increase chlorophyll and carotenoid content in tomato leaves	Delay in progression of the disease in planta High accumulation of peroxidase and phenol contents (phenol, catechin, and flavonoid) in tomato plants	Kolomiiets et al. 2019
Rhodosporidium diobovatum	ND	Reduction of disease incidence in planta	Utkhede and Koch 2004
Aureobasidium pullulans	Increase chlorophyll content in tomato leaves	Inhibitory effect (culture) against *Cm* growth in vitro Reduction of disease incidence in planta	El Kinany et al. 2017
Trichoderma koningii	ND	Inhibitory effect of Trichokonins against *Cm* growth in vitro	Song et al. 2006

(*Continued on next page*)

IR

Kolomiiets et al. (2019) found a *P. fluorescens* strain that, as an aerial spray, protected tomato plants against *Cm* and promoted the accumulation of phenolic compounds, chlorophylls, and carotenoids; photosynthesis productivity; and peroxidase enzyme activity. Takishita et al. (2018) reported that *Pseudomonas entomophila* 23S, with several PGP properties (Table 1), promoted (as soil drench) tomato seedling's growth and delayed the progression of bacterial canker in tomato plants by inducing resistance response through SA signaling pathways (*PR1a*). Plants treated with strain 23S 5 days before *Cm* inoculation significantly limited disease severity. In addition, 23S was a moderate producer of HCN, which inhibits *Cm* growth (Lanteigne et al. 2012). Following the next research, two other anti-*Cm* compounds, $C_{15}H_{16}N_2O$ and $C_{16}H_{18}N_2O$ (containing isoquinoline ring as the base component of their structure), were identified in cultures of this strain, inhibiting growth of *Cm* in vitro. These compounds could possibly be synthesized and used as new biocontrol agents under in planta condition (Takishita et al. 2021).

Aksoy et al. (2017) showed that *Pseudomonas putida* strain CKPp9 induced resistance in root-inoculated tomato plants through high accumulation of phenolic compounds, such as chlorogenic acid, caffeic acid, catechin, and rutin. A direct relationship between total phenolic concentration and percentage of tomato plant mortality (seedling survival) was observed. CKPp9 also inhibited the growth of *Cm* in vitro.

Recently, the survey conducted by Hamidi Banayem et al. (2020) showed that strains of *P. putida* (strains M1R1 and H1R1) applied as seed and root treatments significantly reduced the severity of bacterial canker on tomato plants. Information regarding *Pseudomonas* isolates and their mechanisms of action against *Cm* is provided in Table 1.

Other bacterial genera

Streptomycetes are Gram-positive, filamentous soil bacteria belonging to class Actinomycetia like *Cm,* which can modulate plant growth through nutrient uptake or the production of secondary metabolites (Kunoh 2002). Several studies reported the antagonistic activity of *Streptomyces* spp. against Gram-positive bacteria and fungi (Araújo et al. 2000; Sabaratnam and Traquair 2002; Sardi et al. 1992). Regarding BCT, *Streptomyces* sp. HL-12 inhibited the growth of *Cm* in pure culture exposed to low concentrations of cadmium (Cd) (Yuan et al. 2009). Results of another study demonstrated the antimicrobial activity of a low molecular weight protein produced by *Streptomyces lividans* TK24 against *Cm*. The results of protein fractionation and transcriptional expression analyses indicated 50S ribosomal protein L19 as the main responsible candidate for antimicrobial activity (Calderón-de la Sancha et al. 2022).

Several works suggest using the combinations of different biocontrol agents. El Kinany et al. (2017) found that the combined spray application of *Aureobasidium pullulans* and *Pantoea agglomerans* reduced the incidence of BCT more effectively than a single treatment, particularly when tomato plants were treated at 15-day intervals. Thus, the combination of BCAs appears promising, possibly because of their different mechanisms of action, although in the study of El Kinany et al. (2017) no mechanistic work was conducted.

Fungal BCAs

Some fungal strains also have biocontrol effects against *Cm*. The ascomycete *Trichoderma harzianum* (order Hypocreales) is very effective in combating various microbes (Grondona et al. 1997; Sallam et al. 2019). Biocontrol mechanisms of *Trichoderma* spp. include antibiosis, competition, mycoparasitism, and IR (Segarra et al. 2010). Trichokonins extracted from *Trichoderma koningii* SMF2 showed high inhibitive effect against several bacterial pathogens, including *Cm*, under in vitro conditions (Song et al. 2006). This compound was stable over a wide pH range and at every temperature tested. Moreover, it was insensitive to proteolytic enzymes, suggesting a potential for the development of a new biopesticide (Song et al. 2006). In another study, the use of the endophyte *T. harzianum* KABOFT4 resulted in the maximum protection against *Cm* in tomato plants and reduced disease severity as foliar spray combined with soil drench treatment (disease severity 29%), single soil drench treatment (disease severity 45%), and single foliar treatment (disease severity 55%) compared with nontreated control (disease severity 75%) (Abo-Elyousr and Marei Almasaudi 2022). This fungal biocontrol agent also showed PGP properties (Table 1) and increased tomato seed germination. Total phenol and flavonoid contents were also increased in tomato seedlings, indicating activation of the resistance response (Abo-Elyousr and Marei Almasaudi 2022).

Barda et al. (2015) showed that extracellular metabolites secreted by the epiphytic fungus *Pseudozyma aphidis* can inhibit the growth of several bacterial phytopathogens, including *Cm*, under in vitro condition. The fungus reduced the occurrence and severity of BCT (as soil

Table 1. (*Continued from previous page*)

Biocontrol agent	PGP[a] properties	Control *Cm*[c]	References
Trichoderma harzianum	Solubilize inorganic phosphorus and zinc Produce siderophores and indole acetic acid Increase seed germination Improve tomato growth parameters High accumulation of phenol and flavonoid contents in tomato plants	Inhibitory effect (culture and extract) against *Cm* growth in vitro Reduction of disease incidence and disease severity in planta High accumulation of phenol and flavonoid contents	Utkhede and Koch 2004 Anwar and Iqbal 2017 Abo-Elyousr and Marei Almasaudi 2022
Trichoderma asperellum	ND	Bacteriostatic and bactericidal activity of crude extract against *Cm* in vitro	Leylaie and Zafari 2018
Trichoderma brevicompactum	ND	Bacteriostatic and bactericidal activity of crude extract against *Cm* in vitro	Leylaie and Zafari 2018
Trichoderma koningiopsis	ND	Bacteriostatic and bactericidal activity of crude extract against *Cm* in vitro	Leylaie and Zafari 2018
Trichoderma longibrachiatum	ND	Bacteriostatic and bactericidal activity of crude extract against *Cm* in vitro	Leylaie and Zafari 2018
Alternaria sp.	ND	Inhibitory effect of crude extract against *Cm* growth in vitro Production of alterperylenol	Zhao et al. 2018
Alternaria alternata	ND	Inhibitory effect of extract against *Cm* growth in vitro	Wu et al. 2019
Pseudozyma aphidis	ND	Inhibitory effect of extract against *Cm* growth in vitro Reduction of disease incidence and disease severity in planta, IR	Barda et al. 2015

drench) and induced a resistance response in tomato plants by activating SA resistance pathways, through the upregulation of *PR1a* expression. In other words, the efficacy of *P. aphidis* for control of *Cm* in tomato plants correlated with the activation of *PR1a* in *P. aphidis*–treated plants that were inoculated with *Cm*. Surprisingly, reduction in disease severity was also observed in *P. aphidis*–treated *NahG* transgenic tomato plants, which do not accumulate SA and do not activate *PR1a* expression. There is a possibility that other, as-yet-unidentified, PR genes and hormonal pathways are involved in the defense response against *Cm* after treatment with *P. aphidis* (Barda et al. 2015).

In another study, alterperylenol extracted from *Alternaria* sp. (isolated from marine plants) showed strong anti-*Cm* activity with a minimum inhibitory concentration (MIC) of 1.95 µg/ml, which was twofold lower than streptomycin. This compound caused significant cell membrane hyperpolarization without altering cell membrane integrity, indicating an inhibitory effect against *Cm* proliferation (Zhao et al. 2018). Characterization of compounds derived from marine fungi may represent a promising strategy for finding potential biopesticides with novel structures and notable bioactivities. Because multiple fungal species have been reported to control bacterial plant pathogens (Le Dang et al. 2014; Wang et al. 2023), further in-depth investigations will be needed to evaluate their effect against *Cm*.

Bacteriophages

Bacteriophages are viruses that can cause lysis and death of bacterial cell hosts (Parisien et al. 2008). They have been used to combat human, animal, and plant pathogens (Jones et al. 2007; Kutter and Sulakvelidze 2004). In recent years, interest in the use of bacteriophages to fight plant pathogens has significantly increased (Wittmann et al. 2010). In tomatoes, for example, phages can control bacterial spot and wilt diseases, caused by *Xanthomonas* spp. and *Ralstonia solanacearum*, respectively (Balogh et al. 2003; Álvarez et al. 2019). Phage therapy could control BCT (Echandi and Sun 1973). This is notably the case for bacteriophage CMP1, a member of the *Siphoviridae* viral family that specifically infects *Cm*, originally isolated from overwintering tomato stems infected with *Cm* (Echandi and Sun 1973). Its specificity of action is related to the production of an endolysin with a peptidase activity, capable of hydrolyzing the murein (peptidoglycan) of *Cm*. The bacteriophage CN77, which infects *Clavibacter nebraskensis* (causal agent of Goss's bacterial wilt and leaf blight of corn), has also been identified as a specific active producer of endolysin (Wittmann et al. 2010, 2011). The genus *Clavibacter* possesses a rare and specific murein of type $B2_\gamma$ (Schleifer and Kandler 1972). CMP1 can therefore inhibit *Cm* without influencing the bacterial community in the soil, rhizosphere, and phyllosphere (Wittmann et al. 2016). Accordingly, external application of phage endolysins to tomato plants controls *Cm* without disrupting microbial diversity (Wittmann et al. 2010).

Nevertheless, the use of bacteriophages against plant pathogens faces several obstacles. Indeed, only a few *Cm*-specific phages have yet been reported. Phages are highly specific for their host, and often this specificity can be strain-specific; thus, more research will be required to determine the host range of known *Cm* phages. Furthermore, phages can be influenced by various environmental factors, including UV light, physicochemical properties of water and soil, pH, temperature, and fertilizers (Frampton et al. 2012). To overcome these problems, a transgenic tomato plant was recently developed, expressing the endolysin (*lys*) gene of the CMP1 phage (Wittmann et al. 2016). These transgenic tomato plants showed no symptoms after being infected with *Cm*. However, small amounts of *Cm* were detected in xylem and leaf tissue. According to Hausbeck et al. (2000), 10^7 CFU/g of fresh tissue are required to affect plant survival and yield, whereas most transgenic plants did not reach this concentration (Wittmann et al. 2016).

Plant/Insect Extracts for Control of *Cm*

Essential oils (EOs), naturally found in many plants, have insecticidal, fungicidal, and bactericidal activities against certain phytopathogens (Isman 2000; Yihune and Yemata 2019). Wang et al. (2023) reviewed the antibacterial effect of several plant species against BCT. Many aromatic plants have been also tested for their antibacterial activity against *Cm*. Pure EOs, such as thyme oil, oregano oil, cinnamon oil, clove oil, and Biosept (extract of grapefruit containing EOs and organic acids) inhibited *Cm* in low concentrations in in vitro assays, whereas for organic acids extracted from plants the MIC values were much higher (van der Wolf et al. 2008). Kotan et al. (2013) demonstrated that indirect application of EOs, direct or indirect use of hexane/methanol extracts, and pure metabolites of *Satureja hortensis* such as thymol and carvacrol showed antibacterial activity against *Cm*. Disease severity was reduced (as seed treatment) without affecting seed germination or growth of tomato plants under in vitro and in vivo conditions. The mechanism of action is probably related to the outer membrane–disrupting properties of thymol and carvacrol. Some investigations suggest that these compounds penetrate the cells and disturb the structure of the membrane (Karami-Osboo et al. 2010; Ultee et al. 2002). Cai et al. (2019) studied the antibacterial activity of *Polygonum orientale* extracts against *Cm*. They demonstrated that the extracts had a strong antibacterial activity against *Cm* in a survival test, and surviving cells were damaged, with virtually no resistance or adaptability. The *P. orientale* extracts damaged the cell wall and membrane, causing a significant reduction in intracellular ATPase activity.

A study of antibacterial activity against *Cm* and the characterization of phytoconstituents was performed by Sánchez-Hernández et al. (2023) using leaf and fruit extracts of *Ginkgo biloba* L. Even though fruit extracts had no antibacterial activity in vitro, leaf extracts inhibited *Cm* at minimum concentrations of 500 µg ml^{-1} that can be attributed to the presence of 2,4-dimethyl-3-hexanol and catechol. It is noteworthy that these extracts (as aerial spray at a concentration of 1,000 µg ml^{-1}) completely protected *Cm*-infected tomato plants from stem decay, with no phytotoxicity (Sánchez-Hernández et al. 2023).

Aksoy et al. (2021) studied the phenolic profile and the effects of extracts of *Calendula officinalis* and *Echinacea purpurea* on tomato plants infected with *Cm*. They observed that those from *E. purpura* (as root inoculation) showed greater results in terms of not only the height and weight of plants but also the roots. Both extracts also showed inhibitory activity toward *Cm.* High accumulation of phenolic compounds, such as chlorogenic acid, was also observed in tomato seedling leaves treated with *E. purpura* + *Cm* and *C. officinalis* + *Cm,* indicating the importance of phenolic compounds in plant defense response (Aksoy et al. 2017, 2021). Siddique et al. (2020) also studied the ability of medicinal plants and weeds to control BCT caused by *Cm*. For this, they tested aqueous extracts of *Peganum harmala*, *Allium sativum*, *Withania somnifera*, *Melia azedarach*, *Calotropis procera*, *Mentha piperita*, and *Nerium oleander*. Extracts of *P. harmala* and *M. piperita* were very effective against *Cm* in vitro. These results were confirmed in vivo, as the highest dose of dried powder (mixed with soil) from these two plants significantly reduced the disease. No phytotoxicity was observed by the application of these powders, and some parameters contributing to crop yield were improved. Moreover, alkaloids, tannins, glycosides, flavonoids, and saponins were detected in aqueous extracts of these plants and were likely involved in diverse mechanisms of action against pathogens (Siddique et al. 2020).

Valencia-Hernandez et al. (2022) showed that synthetic capsaicinoid oleoresin (CO) containing 70% nonivamide and 30% dihydrocapsaicin, in two concentrations of 0.05 and 0.1%, had an inhibitory effect against certain phytopathogens, including *Cm* in vitro and decreased significantly the damage index (according to the scale of Baysal et al. 2003) in tomato plants both in preventive and curative treatments compared with nontreated controls. Postharvest tests on tomato fruits displayed a significant reduction in weight loss and fruit damage in the treatment of CO 0.05 and 0.20% compared with control. Moreover, several plant extracts have been reported to be effective against species of *Clavibacter* other than *Cm*, suggesting the need to verify their effect against this phytopathogen. All plant species and their products active against *Clavibacter* spp. are presented in Table 2.

Finally, regarding the activity of insect extracts, piperidine and piperideine alkaloids extracted from the red imported fire ant

(Solenopsis invicta) had an inhibitory effect on *Cm* grown in vitro (Li et al. 2013). The growth of *Cm* was negatively correlated with the concentration of piperidine alkaloids in culture medium. Under greenhouse conditions, this compound (as foliar spray) significantly reduced symptom development on two tomato cultivars, Better Boy and DRK7018F1. From a biochemical point of view, piperidine alkaloids were stable at 4°C and 22°C for 12 weeks and 54°C for 4 weeks. This stability may provide a solid basis for further product processing and commercialization (Li et al. 2013).

Biobased Nanotechnological Approaches to Control *Cm*

Nanotechnology is an emerging innovative approach that has provided a plethora of nanomaterials for potential applications in the

Table 2. Antibacterial potential of several plant species extracts against *Clavibacter* spp.[a]

Product	Plant source	Phytopathogen	Consequence	Reference
Fragarin	*Fragaria ananassa*	*Cs*	Inhibition of *Cs* growth by dispersing membrane potential	Filippone et al. 2001
Essential oils from	*Lavandula angustifolia* *Mentha pulegium* *Origanum dictamnus* *Origanum majorana* *Origanum vulgare* *Rosmarinus officinalis* *Salvia fruticose* *Thymus capitatus*	*Cm*	Inhibition of bacterial colony formation and growth in vitro	Daferera et al. 2003
Potide-G (antimicrobial peptide)	*Solanum tuberosum*	*Cm*	Inhibition of *Cm* growth in vitro	Kim et al. 2006
Essential oils from	*Abies sibirica* *Artemisia absinthium* *Citrus aurantifolia* *Eugenia caryophyllata* *Ocimum basilicum* *Origanum compactum* *Origanum vulgare* *Thymus vulgaris*	*Cs* and *Ci*	Reduction in colony size	Pauvova et al. 2008
Essential oils from extracts of	*Thymus vulgaris* *Origanum vulgare* *Syzygium aromaticum* *Cinnamomum verum*	*Cm*	Inhibition of *Cm* growth in vitro	van der Wolf et al. 2008
Extracts of	*Citrus* × *paradisi*			
Extracts of	*Cistus monspeliensis* *Lavandula coronopifolia* *Rubus ulmifolius*	*Cm*	Inhibition of *Cm* growth in vitro, reduction in colony size, and improvement of germination rate in tomato seeds	Talibi et al. 2011
Carvacrol essential oils from	*Satureja hortensis*	*Cm*	Reduction of disease severity in vitro and in planta	Kotan et al. 2013
Extracts of	*Laminaria japonica*	*Cs*	Degradation of the *Cs* cell structure, rupture of the envelope, deformation of the cell, formation of vacuoles, and separation of the cell wall from the cell membrane in vitro	Cai et al. 2014
Caffein	ND	*Cs*	Inhibition of *Cs* growth in vitro	Sledz et al. 2015
Extracts of	*Cyperus rotundus*	*Cm*	Inhibition of *Cm* growth in vitro	Özdemir and Erincik 2015
Essential oils from Methanolic extracts of	*Satureja hortensis* *Tamarix ramosissima* *Rosmarinus officinalis* *Chelidonium majus* *Silybum marianum*	*Cs*	Reduction in growth and biofilm formation of *Cs* in vitro	Ichim et al. 2017
Essential oils from	*Eucalyptus citriodora*	*Cm*	Inhibition of *Cm* growth in vitro	Ünlü and Elçi 2019
Extracts of	*Polygonum orientale*	*Cm*	Damage to *Cm* cell wall and membrane, significant reduction in intracellular ATPase activity, and sensitization in vitro	Cai et al. 2019
Essential oils from	*Allium aromaticum* *Trametes versicolor*	*Cm*	Inhibition of *Cm* growth in vitro	Orzali et al. 2020
Extracts of	*Thymus vulgaris* *Origanum vulgare*			
Extracts of	*Allium sativum* *Calotropis procera* *Melia azedarach* *Mentha piperita* *Nerium oleander* *Peganum harmala* *Withania somnifera*	*Cm*	Inhibition of *Cm* growth in vitro, reduction of disease severity, and improvement of crop yields in planta	Siddique et al. 2020
Extracts of	*Cistus ladanifer* subsp. *ladanifer*	*Cm*	Increase germination rate in tomato seeds infected with *Cm* in vitro	Benali et al. 2020

(*Continued on next page*)

[a] *Ci* = *Clavibacter insidiosus*; *Cm* = *Clavibacter michiganensis*; *Cs* = *Clavibacter sepedonicus*; ND = not determined.

field of agriculture. Nanotechnology helps in exploring the biological properties of antimicrobial compounds by controlling their size-to-boost performance. The development of nano-based pesticides has been integrated into the agriculture industry, offering a range of cost-effective control strategies (Das and Patra 2017; Elmer and White 2018). The bactericidal effect of silver is well demonstrated and the World Health Organization listed silver sulfadiazine as a vital anti-infective topical human medicine (Chernousova and Epple 2013; Lara et al. 2010). Several studies have confirmed the efficacy of silver nanoparticles (AgNPs) against Gram-positive and Gram-negative bacteria, fungi, and certain viruses (Elechiguerra et al. 2005; Iniyan et al. 2017; Jo et al. 2009; Lara et al. 2010; Lu et al. 2008). Rivas-Cáceres et al. (2018) found a bactericidal effect of AgNPs against *Cm*.

Synthesis of AgNPs using microorganism or plant extracts (known as biosynthesized AgNPs) is an important subtype of the green nanotechnology approach. Oloyede et al. (2017) found that using biosynthesized AgNPs derived from leaf extract of *Azadirachta indica* and *Vernonia amygdalina* and fungal filtrate of *Cladosporium cladosporioides* inhibit the growth of *Cm*. Biosynthesized AgNPs with fungal extracts of *T. harzianum* and *Aspergillus fumigatus* not only were bactericidal in in vitro assays but also significantly reduced (mixed with soil) the incidence of BCT even at the lowest concentration of 0.088 mg/liter. It also enhanced seed germination and tomato growth parameters under greenhouse conditions (Noshad et al. 2019). Similarly, biosynthesized AgNPs assisted with a mycelial aqueous extract of the beneficial oomycete *Pythium oligandrum*, exhibited a large in vitro inhibition zone against several bacterial pathogens including *Cm*, decreased the incidence of BCT (mixed with soil), and improved tomato growth parameters (Noshad et al. 2020).

Biosynthesized AgNPs containing leaf extracts of *Larrea tridentate* (as aerial spray, at a concentration at 50 mg/liter) decreased BCT incidence up to 20% and disease severity by 36%, which was correlated with up to 95% inhibition of bacterial growth in the tissue. Moreover, nanoparticle treatment increased growth, total phenol, and flavonoid concentrations in leaves, and activity of CAT, ascorbate peroxidase, and peroxidase enzymes, indicating IR response (Méndez-Andrade et al. 2022). In addition, fructose-stabilized AgNPs showed in vitro antibacterial properties against some plant pathogenic bacteria, including *Cm* (Dzimitrowicz et al. 2018).

Smirnov et al. (2023) recently reported that biosynthesized AgNPs, obtained with *Capsicum annuum* fruit extracts, showed excellent in vitro antibacterial activity against *Cm* compared with the antibiotic gentamycin (Smirnov et al. 2023). Phytochemical screening of aqueous extracts of *C. annuum* pericarps showed the presence of capsaicinoids, phenolic compounds, flavonoids, and phenolic acids. These results are in congruence with the above-described Valencia-Hernandez et al. (2022) results, which showed that this compound had an inhibitory effect against *Cm*. The exact mechanism of antimicrobial activity of AgNPs is unknown, but based on several reports it could be due to disturbance of permeability and respiration function of the cell, cell decomposition, formation of ROS, and disruption of ATP production and DNA replication (Abdullah and Hamid 2013; Mohamed et al. 2014).

Results of another study revealed that mesoporous silica nanoparticles loaded with antimicrobial peptides (human β-defensin-2 [hβD2]) and two variants (TRX-hβD2-M and hβD2-M) inhibited the growth of *Cm* in solid and liquid media (Marcelino-Pérez et al. 2021). The exact mode of action of hβD2 is unknown, but it could be due to the electrostatic interactions between the positively charged residues in hβD2 with the polar head groups of the cell walls of bacteria (Järvå et al. 2018; Li et al. 2021; Zhuang et al. 2021). Bibi et al. (2021) have shown that carbon-coated copper oxide nanosheets (CuO NS) with aqueous extract of *Rhazya stricta* have enhanced antibacterial potential against both solanaceous crops' wilt-causing bacteria (*Ralstonia solanacearum* and *C. michiganensis*). Interestingly, both selected bacteria developed resistance against streptomycin more readily than toward CuO NS.

Although apparently promising, the integration of nanotechnologies into biocontrol practices is still currently at the laboratory level, and further studies are required to assess the health hazards and possible side effects of these compounds in the environment and the food chain.

Activation of Resistance Response in Tomato Plants Against *Cm* Through Synthetic Elicitors

IR by synthetic elicitors has been reported in many plants against a wide range of fungal, bacterial, and viral pathogens (Bektas et al. 2016; Cohen 2002; Lopez and Lucas 2002). Therefore, this alternative provides a promising tool to reverse the negative effect of *Cm* on plant performance. Synthetic elicitors are small molecules capable of inducing plant immune responses against phytopathogens (Bektas and Eulgem 2015). To date, several synthetic elicitors have been reported to improve crop defense against plant pathogens (Archana et al. 2020; Bektas et al. 2016; Oostendorp et al. 2001; Ryals et al. 1996) by inducing a resistance response. In the case of BCT, priming tomato seedlings with acibenzolar-S-methyl as a foliage spray significantly reduced disease severity by up to 76% (Baysal et al. 2003; Soylu et al. 2003). This resistance correlated with high activity of plant defense enzymes such as peroxidase, glutathione peroxidase, and pathogenesis-related protein chitinase. Moreover, treatment of tomato plants with synthetic, nonprotein, amino acid DL-β-aminobutyric acid (BABA) as a foliar spray significantly suppressed BCT development by up to 54% in BABA-treated plants compared with control plants. Bacterial populations were also reduced by 84%. This

Table 2. (*Continued from previous page*)

Product	Plant source	Phytopathogen	Consequence	Reference
Carvacrol	*Origanum vulgare*	*Cm*	Inhibition of *Cm* growth in vitro owing to its interaction with the bacterial expansin protein	Yılmaz et al. 2021
Extracts of	*Calendula officinalis* *Echinacea purpurea*	*Cm*	Inhibition of *Cm* growth in vitro, increase of tomato growth and weight, and high accumulation of phenolic compounds in tomato leaves in planta	Aksoy et al. 2021
Leaf and fruit extracts from	*Ginko biloba*	*Cm*	Inhibition of *Cm* growth in vitro and in planta	Sánchez-Hernández et al. 2023
Extracts of	*Heliotropium arbainense*	*Cm*	Inhibition of *Cm* growth in vitro, reduction of disease severity and disease incidence in planta, high accumulation of antioxidant enzymes including peroxidase, glutathione peroxidase, and catalase in tomato plants	Eid et al. 2023

resistance was related to increased concentrations of defense-related enzymes, such as PAL and peroxidase, together with higher H_2O_2 concentrations (Baysal et al. 2005). Hassan and Buchenauer (2008) demonstrated that the combined application of a resistance inducer (BABA) with a BCA (fluorescent *Pseudomonas* isolate CW2) as a soil drench was more effective than single treatments in reducing bacterial canker symptoms. This combined application also increased root and shoot weight and SA content in tomato plants.

In another study, Utkhede and Koch (2004) showed that using lysozymes as a foliar spray reduced the disease severity of bacterial canker up to 63% and inhibited the in vitro growth of *Cm*. Moreover, the study conducted by Bektas (2021) revealed that the application as foliage spray of 2,6-dichloroisonicotinic acid and 2,4-dichloro-6-{(E)-[(3-methoxyphenyl) imino] methyl} phenol reduced the severity of BCT and induced the SA-dependent systemic resistance in tomato plants through the expression of *PR-1*, *PR-5, PAL, WRKY33b,* and *WRKY70* (Bektas 2021).

Cultivation Measures and Hygiene to Control *Cm*

Cm can survive in plant residues, soil, and water for extended periods of time. Yield loss was insignificant if the bacterium infected plants at the 18 to 19 leaf stage or later (Sharabani et al. 2013). To prevent yield loss in the field, the pathogen population must be suppressed below 10^7 CFU/g of tissue at the time of transplanting (Hausbeck et al. 2000). Cultural practices, for example tying, clipping, pruning, harvesting, or physical contact between infected and healthy plants, rain splash, irrigation water, and chemical spraying, can spread the bacterium to nearby *Cm*-free plants (Carlton et al. 1994; Gleason et al. 1993; van der Wolf et al. 2012). Thus, the use of hygienic materials and procedures, for example propagation (seed and transplant), soil, irrigation water, and gardening tools, is crucial to prevent any introduction of the pathogen into a new growing area. In addition, removal of plant debris and crop rotation are highly important to eradicate the source of inoculum for the next season (Aksoy et al. 2021; Sen et al. 2015).

Infected seeds are considered the main sources of inoculum for long-distance dissemination of the bacterium. Transmission rates through the infected seeds can vary from 0.25 to 85% (Strider 1969). The most appropriate seed treatment for the least damage to germination appears to be hot water soaking. This is highly recommended for several vegetables, such as pepper, tomato, eggplant, cucumber, spinach, and carrot (Singh et al. 2020). Mtui et al. (2010) demonstrated that preheating tomato seeds in water at 37°C for 10 min, followed by another warming step in water bath at 50°C for 25 min, increased yield parameters and reduced seed contamination by *Cm*, *Xanthomonas vesicatoria*, and *P. syringae* pv. *tomato*. Still, the optimal temperature together with exposure time should be considered for each seed variety to reach the best efficacy (Divsalar et al. 2014). Ganiyu et al. (2021) reported that the use of ethanol (70%) and NaOCl (2%) for 5 min would be effective as tomato seed surface-sterilizing agents to reduce *Cm* population and improve seedlings quality and vigor.

Soil solarization has also been applied to control soilborne fungal and bacterial pathogens (Stapleton and DeVay 1982). Zanón and Jordá (2008) tested the effect of soil mixture of peat moss and sand mix (amended with artificially *Cm*-infected fresh tomato debris) at two different temperature, 25 and 45°C. Their results revealed that the incidence of BCT was lower in enclosed pots in the plastic bag at 45°C (for 4 weeks) than open pots at 25°C. Bibi and Ahmad (2016) demonstrated that the growth of tomato plants in silt loam soil (owing to its optimum water-holding capacities) with 10 days interval in irrigation resulted in the highest tomato yield while keeping BCT damage below the threshold. They recommended that tomato growers use this type of cultural practice, especially for greenhouses and tunnel farming. Mtui et al. (2010) found that soil treatment with dry grass (*Panicum* sp.) mulch resulted in a higher number of marketable fruits per tomato plant, a higher marketable yield, and larger and less sunscald fruits compared with the nonmulched treatment. These findings are consistent with other studies indicating the benefits of mulching on tomato growth and yield (Agele et al. 1999; Ramalan and Nwokeocha 2000).

Utkhede and Koch (2004) found that vermicompost tea (as foliar spray) significantly reduced the severity of BCT under greenhouse condition. Using composts based on tomato or pepper residues in combination with chicken or cattle manure was reported to be effective to reduce disease severity caused by *Cm* by between 79 and 100% under either natural infection or intentional inoculation. In the compost substrate, the bacterial population was reduced to undetectable levels within 15 to 20 days whereas those in peat remained high for 35 to 40 days. In addition, the colonization of compost-grown tomato plant tissues by *Cm* was lower than those grown in peat or perlite (Yogev et al. 2009). Using an immunofluorescent assay, Kasselaki et al. (2011) demonstrated that treatment of seed vacuum-infiltrated with *Cm* using several compost extracts eliminated 100% of *Cm* cells from inoculated tomato seeds. Moreover, a combination of cultural controls, including treatments with cow manure, compost, micronutrient mixtures, and NPK fertilizers, reduced the incidence of bacterial canker on tomato plants compared with untreated control plants (Chinnadurai et al. 2018). Belgüzar (2023) reported that the use of vermicompost (mixed with soil) was highly effective to reduce disease severity caused by *Cm* on tomato plants. However, the mode of action of composts is poorly understood. Their effectiveness may be due to competition between antagonistic microorganisms present in the compost or their antimicrobial compounds (Kasselaki et al. 2011).

The addition of a low dose of heavy metals, such as Cd, has recently been considered in plant science to enhance plant performance as well as protect against biotic or abiotic stresses (Carvalho et al. 2020; Vázquez-Hernández et al. 2019). Valencia-Hernandez et al. (2023) showed that a low dose of Cd (60 µg/kg) in the soil increased the tolerance of tomato plants against *Cm* infection and improved growth parameters. This treatment also significantly induced the activity of the oxidative enzyme PAL. Moreover, an increase in *PR1a* gene expression was detected in the preventive treatment with Cd, indicating the induction of plant defense mechanism.

Resistant Cultivars

One of the most ecofriendly strategies to control bacterial canker is the use of *Cm*-resistant cultivars. Attempts have been made to introgress resistance against *Cm* in commercial cultivars using a number of wild *Solanum* species, including *S. arcanum*, *S. chilense*, *S. habrochaites*, *S. lycopersicum*, *S. pennellii*, *S. parviflorum*, *S. peruvianum*, and *S. pimpinellifolium* (Francis et al. 2001; Sen et al. 2013; Sotirova and Achkova 1989; Şanver et al. 2022). However, these have never resulted in the release of commercial tomato cultivars with complete resistance (Gleason et al. 1993; Liedl et al. 2013). The absence of resistance may be due to the relatively low level of genetic diversity in tomato cultivars. In other words, domestication has increased tomato productivity while narrowing its genetic diversity, causing a limitation in conventional genetic improvement via breeding with wild species (Lin et al. 2014). Next-generation sequencing of various wild tomato species (*S. arcanum*, *S. habrochaites*, and *S. pennellii*) revealed that genome variability is up to 20 times greater than in commercial cultivars (The 100 Tomato Genome Sequencing Consortium et al. 2014).

Nevertheless, tolerant cultivars, differing in susceptibility to bacterial canker, do exist (Coaker 2003; Rivera-Sosa et al. 2022; Sen et al. 2013; Tripathi et al. 2018; Wang et al. 2022). Unfortunately, *Cm* still can multiply to high densities in tolerant cultivars (Koseoglou et al. 2023b; Şanver et al. 2022), bearing a risk for dissemination of the pathogen to susceptible cultivars during cultivation practices. The absence of symptom expression may even be considered as a negative plant trait in case of pathogens with a quarantine or regulated non-quarantine status, as symptomless plants can become a source of unnoticed spread.

Marker- and genomics-assisted breeding techniques would enhance the introgression of single or multiple *Cm* resistance in commercial cultivars. Combining two or more resistant genes would facilitate an increased level of resistance. Several quantitative trait loci have been identified for *Cm* resistance. van Heusden et al. (1999)

found loci for resistance mapped on chromosomes 5, 6, and 7 in F2 populations derived from crosses between *S. esculentum* and *S. peruvianum*. Abebe et al. (2022) identified loci on chromosome 6 using 909 F2 individuals of a cross between a susceptible and resistant cultivar of *S. lycopersicum* involved in tolerance. Further analysis revealed the presence of mutations in and differential expression of nucleotide-binding leucine-rich repeat, receptor kinase, and receptor-like proteins in the quantitative trait loci, which may explain the difference in susceptibility. Whole-genome sequencing in combination with a bulk segregant analysis enabled the identification of loci on chromosomes 2, 4, and 7 involved in tolerance to *Cm* in near-isogenic lines of *S. lycopersicum* containing a fixed *S. arcanum* LA2157 introgression on chromosome 7 (Koseoglou et al. 2023a).

Another approach to identify genes contributing to *Cm* resistance is by studying gene expression of resistant and susceptible cultivars. Lara-Ávila et al. (2012) analyzed the gene expression of several wild tomato species resistant to *Cm* (i.e., *S. peruvianum* LA2157, *S. peruvianum* LA2172, and *S. habrochaites* LA2128) as well as the susceptible species *S. lycopersicum*. One of the genes differentially expressed was the conjugation enzyme SUMO E2 SCE1 (SCEI). Using virus-induced gene-silencer, it was shown that SCEI plays an important role in the innate immunity of *S. peruvianum* to *Cm* (Esparza-Araiza et al. 2015). Similarly, proteomic analyses have resulted in the identification of tolerance in genotypes of *Lycopersicon hirsutum* (Coaker et al. 2004). In this way, enzymes involved in hydrogen peroxide accumulation and pathogenesis-related proteins associated with tolerance were found.

It is expected that studies on the molecular interactions between pathogen and host will also contribute to the identification of resistance genes and selection of markers useful in resistance breeding. Balaji et al. (2008) demonstrated that the Never ripe mutant of tomato plants impaired in the ET perception character, and transgenic plants with reduced ET biosynthesis capacity, exhibited significant delay in the appearance of wilt symptoms compared with wild-type plants inoculated with *Cm*. These results indicate that ET plays an important role in the susceptibility of tomato plants and consequently in the development of diseases. Koseoglou et al. (2023b) found that tomato gene *SlWAT1* is a susceptibility gene for *Cm* infection. Inactivation of this gene (by RNAi and CRISPR/Cas9) reduced free auxin contents and ET synthesis in tomato stems and suppressed the expression of *Cm* virulence factors (transcriptional factor *vatr2* and its target *phpA* gene). Genes involved in resistance may be tracked down in populations of wild *Solanum* species or in ethyl methanesulfonate populations (Garcia et al. 2016; Yan et al. 2021).

Concluding Remarks and Future Trends

BCT caused by *Cm* is considered one of the most devastating plant diseases worldwide. Health and environmental concerns, as well as increased demand for pesticide-free products, have been encouraging producers and growers to use alternatives to respect sustainable agriculture. This review presented the large variety of research and development performed to face the challenge represented by this phytopathogen and exposed several effective environmentally eco-friendly management strategies to control *Cm*. Biopesticides are considered an attractive alternative to chemical pesticides because of their low toxicity and biodegradability. In general, the key benefit of biopesticides focuses on humanity, providing a healthier environment and safer nutritious food in the markets. In other words, it minimizes the pollution and nuisances associated with the use of synthetic chemicals and will reinforce food security and sustainable production in agriculture industry. Application of biopesticides can also reduce the risk of resistance development, particularly within an Integrated Pest Management (IPM) strategy combined with different control measures. Compared with synthetic chemical pesticides, biopesticides have lower toxic effects on nontarget organisms and can reduce negative impact on biodiversity (Hezakiel et al. 2024). As a point of economic issue, biological control can therefore be a cost-effective alternative compared with traditional pest control methods. It can create new employment opportunities through the research and development, production, commercialization, and distribution of BCAs, and can improve the living conditions of farmers in rural communities. Biological control also brings economic profit to landholders, such as increased yield and lower production costs. In addition, it can provide monetary benefits through natural pest control services within the agroecosystem (Colmenarez and Vasquez 2024).

The identification of new BCAs effective against *Cm* opens the way to the development and commercialization of novel biocontrol products. This will require careful assessment of eco-toxicological risks for safe treatment and effective stability in the environment (Anckaert et al. 2021; Lengai and Muthomi 2018). Even though there is just one approved biobased product (Agriphage CMM) against *Cm* currently commercialized, several BCAs have been formulated and commercialized to control other plant diseases. For instance, the products BSF4, Cease, Companion, Serenade OPTI, and BACSTAR derived from *B. subtilis* are available to control tomato fungal diseases as well as apple fire blight cause by *Erwinia amylovora* (Anckaert et al. 2021). In addition, various *Pseudomonas*-based bioprotectants are registered for commercial use (Höfte 2021). For instance, strain *P. fluorescens* A506 is the active ingredient in Blightban (Frostban B) and is widely used to suppress frost damage on various crops and to suppress fire blight caused by *E. amylovora* (Höfte 2021). Moreover, several EOs are identified for various biocide usages (herbicide, fungicide, bactericide, and insecticide) in agriculture industry (Raveau et al. 2020). Hence, the commercial product PathoCURB (thyme EO–based) is available for use as a fungicide or bactericide for foliar pathogens on several agriculture crops and food crops. Several neem (*Azadirachta indica*) oil–based products (Ecozin and Agroneem) are commercially available as fungicides, acaricides, insecticides, and nematicides (Saroj et al. 2020). It is possible that some of these products could present a still-unexploited potential to control *Cm*.

However, translating the strategies presented here into practical applications for commercial tomato cultivation faces substantial challenges. There is still a gap between the consistency of the results between controlled environments and commercial tomato-growing conditions. Despite the abundant literature identifying potential biocontrol agents, only one product is commercialized as a bioprotectant (Agriphage CMM). Formulation of biopesticides constitutes a crucial link between production and application (Hezakiel et al. 2024). Indeed, more data on stability, toxicity, chemistry, and compatibility of products are needed to improve and facilitate the formulation and commercialization. To assess the effectiveness of biocontrol, it is critical to choose agents that are effective in a variety of situations, including temperature extremes, soil texture, wetness, and competition (He et al. 2021). Collaboration between research institutions, private companies, and government agencies is essential to facilitate innovation and commercialization in the field of biopesticides.

Because of the complexity of the disease, an IPM strategy is required that would combine several of the approaches presented here, including both biological and cultural methods. More field studies are recommended to examine the efficiency of biocontrol agents in different conditions. A disease-suppressive soil enriched with BCAs may also provide a condition that can improve host immunity against *Cm*. Application of BCAs as seed treatment (preventive), interval root inoculation, and foliar spray are also suggested. Further research on the efficiency of derived antimicrobial compounds may help to develop biopesticides against this phytopathogen.

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Nasim Sedighian

Dr. Nasim Sedighian holds a PhD degree in plant pathology (plant pathogenic prokaryotes). Currently, she is a postdoctoral researcher at the Institut National de la Recherche Scientifique (INRS) in Laval, Québec, Canada. She obtained her BSc in plant protection at Shahrekord University in Iran (2008). She continued her research in plant pathology, and she received an MSc (Tarbiat Modares University, Iran) in 2012. Nasim completed her PhD at Shiraz University (Iran) in 2020. During her PhD, she gained admission (sabbatical leave) into the Wageningen University and Research in the Netherlands to do research on rose plants (2019). Dr. Sedighian has over 10 years' experience of working with bacterial phytopathogens. She has worked on bacterial diseases of Cucurbitaceae, Solanaceae, and Rosaceae. She is experienced in working with beneficial (PGPR) and phytopathogenic bacteria in the phyllosphere and the rhizosphere. Her program at INRS specializes in biological control of tomato bacterial canker caused by *Clavibacter michiganensis*. Her research has been conducted toward development of alternative management strategies to control this devastating disease.

Anaëlle Guineheux

Anaëlle Guineheux was born in Reims, France. She graduated from the University of Reims Champagne-Ardenne in 2021 with a bachelor's degree in life sciences. In 2023, she obtained her master's degree in biology and agro-sciences, specializing in biotechnologies, plant chemistry, and biorefineries, as well as a double master's degree in engineering focusing on biotechnologies and agro-resources from the same university. Her studies focused on the production, protection, and sustainable use of agro-resources. In particular, she had the opportunity to work on the research of beneficial microbiota against pathogens in *Arabidopsis thaliana*, such as *Pseudomonas syringae* or *Botrytis cinerea*, within the laboratory of induced resistance and bioprotection of plants located in Reims. She has also studied the use of phytosanitary products to reduce or even eliminate the action of mildew and powdery mildew in various vineyard plots in the Champagne region.

Jan van der Wolf

Prof. Jan van der Wolf is working as senior scientist in the field of phytobacteriology at Wageningen University and Research in the Netherlands. He started his career in 1986 and is currently involved in projects on diagnostics, ecology, and disease management of various plant pathogenic bacteria, including *Clavibacter michiganensis*, soft rot Pectobacteriaceae (SRP), *Candidatus* Liberibacter species, *Ralstonia (pseudo)solanacearum*, and blotch-causing *Pseudomonas* species in mushrooms. He was coordinator of an EU project on bacterial ring rot and of several EU Euphresco projects on SRP. He described RNA- and DNA-based methods for the detection of plant pathogenic bacteria, patented the use of an endophytic biocontrol strain (*Serratia plymuthica*) for control of SRP, and conducted various studies on the dissemination and colonization of bacterial pathogens in open-field crops. In recent projects, the role of the microbiome in the suppressiveness of plants against plant pathogenic bacteria was investigated. With colleagues from Wageningen Plant Breeding, projects on resistance against plant pathogenic bacteria are carried out. Most of his work is conducted in close collaboration with stakeholders in Dutch agriculture and horticulture and financially supported by the Dutch Ministry of Economic Affairs via so-called "Topsector" programs. He is (co)author of over 100 publications in peer-reviewed journals.

Eric Déziel

Prof. Eric Déziel holds a PhD in environmental engineering from École Polytechnique de Montréal, Canada. Following 3 years as a postdoctoral research associate at the Massachusetts General Hospital (Boston, MA, U.S.A.) he joined the faculty of the Centerre Armand-Frappier Santé Biotechnologie at the Institut National de la Recherche Scientifique (INRS), Québec, Canada, in 2005. As a microbiologist with expertise in microbial physiology and functional genomics, research in his group focuses primarily on how social functions (e.g., intercellular communication) shape the behavior of bacteria. His research team has a particular interest in the secondary metabolites produced by certain bacteria as well as how bacteria benefit from the production of these molecules. A priority area of his research group is the identification of new approaches to inhibit the virulence or survival of pathogenic bacteria, notably through the discovery of new antibiotics or adjuvants, and the development of biocontrol and PGPR agents. He is (co)author of over 160 publications in peer-reviewed journals and holds several patents on the development of biocontrol agents against various phytopathogens.

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