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An updated view of bacterial endophytes as antimicrobial agents against plant and human pathogens

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ABSTRACT

Bacterial endophytes are a crucial component of the phytomicrobiome, playing an essential role in agriculture and industries. Endophytes are a rich source of bioactive compounds, serving as natural antibiotics that can be effective in combating antibiotic resistance in pathogens. These bacteria interact with host plants through various processes such as quorum sensing, chemotaxis, antibiosis, and enzymatic activity. The current paper focuses on how plants benefit extensively from endophytic bacteria and their symbiotic relationship in which the microbes enhance plant growth, nitrogen fixation, increase nutrient uptake, improve defense mechanisms, and act as antimicrobial agents against pathogens. Moreover, it highlights some of the bioactive compounds produced by endophytes.

1. Introduction

Some microbes attached and lived on the surface of the plant and are called epiphytes while some others inhabit deeper inside the plant organs and are called endophytes (Hardoim et al., 2015). Endophytes in plants differ according to the microbes which involve bacteria, fungi, and endophytic actinomyces. However, bacteria and fungi are the most commonly found endophytes in plants (Stobel et al., 2004). Moreover, Microorganisms such as archaea, fungi, bacteria, lichens and algae commonly colonize or interact with the plant, mostly on the surface or within the tissues of the host (Krings et al., 2010). Endophytic bacteria are microorganisms that inhabit the plant tissues such as leaves, roots and stems. They spend the majority of their entire cycle inside the host plants' tissues by forming a biological association i.e., mutualistic symbiosis (Table 1). Endophytic bacteria are found across numerous phyla such as Firmicutes, Bacteroidetes, Proteobacteria, and Actinobacteria and some of its common examples include the genera *Bacillus, Pseudomonas,* and *Serratia.* Endophytes reside within the tissue of the host and benefit the plant in different ways by improving the nutrient uptake, increasing the availability of nutrients, enhancing nitrogen fixation, promoting plant growth and development, improving stress tolerance, and providing resistance against pests and pathogens (Chaudhary et al., 2022). However, some reports suggest few species tend to remain neutral without having any positive effects on the plant (Mendes et al., 2013). The symbiotic nature of interaction between the plants and bacteria relies on various biotic and abiotic factors such as environmental conditions, specificity of species (genotype), and complex processes occurring within the host tissues (Hardoim et al., 2015). Additionally, bacterial endophytes have the ability to produce siderophores and indole-3-acetic acid, two plant growth hormones (Gaiero et al., 2013); Rosenblueth, 2006), enhance the acquisition of nutrients, phosphate solubilization, and fixation of nitrogen (Singh et al., 2017). They carry genes essential for fixing nitrogen fixation which enables the conversion of dinitrogen gas (N_2) into nitrate and ammonium inside the host plant (Fig. 1).

It is known that 40–80 % of bacteria can mechanize biofilm formation, they can form biofilm on various surfaces such as synthetic or natural surfaces (Flemming and Stefan Wuertz, 2019). Bacterial interaction between the surrounding and substrate plays a crucial role which is the key source of biofilm formation (Van Houdt and Michiels, 2010). By establishing a conceptual framework, this review seeks to contribute to the understanding of endophytes and their intricate mechanism in

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enhancing plant systems. The bioactive compounds of endophytes could be further studied for future applications in the sectors of pharmaceutical, medical, agriculture and industry.

2. Association between plants and endophytic bacteria

The plants and endophytic bacteria have a mutualistic relationship which proves to be beneficial to both the organisms. These endophytes are abundantly found in almost all the known wild and cultivated varieties of plants. They are present inside the tissues of the different plant parts such as leaves, stems, seeds, or roots. Within this mutualistic association, the host plant supplies the bacteria with nutrients and a home, and the bacteria themselves support plant growth and development by improving nutrient uptake, atmospheric nitrogen fixation, and mineral and phosphate solubilization. Some of these microbes can also act as antimicrobial agents by producing compounds that protect the plants against pathogens. Additionally, few of them improve the capacity of the plants to tolerate environmental stresses such as cold, oxidative envelope, salinity, drought, etc.

The colonization of the host plants mainly depends on the bacterial battery which consists of various inherent traits of the microbe, commonly referred to as the colonization traits. These characteristics of the bacteria regulate the entire process of colonization which is a series of complex steps. This process normally begins at the roots and necessitates the use of specialized recognition chemicals released by bacteria (Weert et al., 2002; Rosenblueth & Martínez-Romero, 2006). Bacterial colonization requires a suitable environment and specific genetic factors that enable the bacteria to penetrate the surface of the plant and access the inner tissues (Compant, Christophe Clément, & Angela, 2010). The microbe’s entry point can vary across plant sections such as leaves, roots, flowers, seeds, and stems, and once inside, they create a symbiotic relationship with the plant. (Zinniel et al., 2002).

Superoxide dismutase (SOD) and glutathione reductase (GR), two ROS-deactivating genes, were more abundantly generated by the endophytic bacteria *Gluconacetobacter diazotrophicus* in the early stages of rice root colonization. Further evidence that the incapacity of GR and SOD mutants of *G. diazotrophicus* to colonize rice roots indicates that ROS-deactivating genes are essential during the initial stages of

Table 1
Some bacterial endophytes and their host plants.

Endophyte species	Host plant	Properties of the endophytes	References
Azospirillum sp.	Maize	Increases drought tolerance, growth promotion	Riggs et al., 2001; Curá et al., 2017
Azoarcus sp.	Rice	Indole acetic acid production, nitrogen fixation, dissolve inorganic phosphate, foster plant growth under stress conditions	Reinhold-Hurek et al., 2006; Fernandez et al., 2014; Fernández-Llamosas et al., 2020
Bacillus siamensis	*Coriandrum sativum*	Antagonistic activity produces antifungal antibiotics like iturin, surfactin, fengycin,	Ibrahim *et at.*, 2019; Gorai et al., 2021
Stenotrophomonas maltophilia	*Panax ginseng*	Antifungal activity, plant growth promotion	Hong *et at.*, 2018; Rojas-Solís et al., 2018
Bacillus subtilis	Mulberry	Antagonistic activity against fungal pathogens, plant growth promotion	Ji et al., 2008; Xie et al., 2020
Kytococcus schroeteri	*Ephedra foliata*	Anticancer activity	Ghiasvand et al., 2020
Bacillus sp.	Wheat	Biocontrol agent, antagonistic activity, plant growth promotion,	Tao et al., 2014; Tian et al., 2017
Microbacterium sp.	*Coptis teeta,* Rice, *Halimione portulacoides*	Biocontrol agent of blast disease, production of phytohormones or enzymes, plant growth promotion	Liu et al., 2020; Patel et al., 2022
Gordonea terrae	*Avicena marina,* barley, rice	Produce surface-active compounds and pigments like carotenoids that allow survival under different conditions and stress, plant growth promotion	Sowani et al., 2018; Soldan et al., 2019;
Burkholderia phytofirmans	Grapevine, Switchgrass, *Arabidopsis thaliana,* White lupin, and maize	Growth promotion, promotes plant tolerance to biotic and abiotic stressors	Compant et al., 2008; Kim et al., 2012; Zuniga et al., 2013; Kost et al., 2014
Enterobacter sp.	Hybrid poplar	Growth promotion, hinders the activity of soil-borne pathogens, biofertilizer	Doty et al., 2017; Ludueña et al., 2019
Gluconacetobacter diazotrophicus	Sugarcane, rice, wheat, and sorghum	Promote plant growth in drought stress and low nitrogen conditions by fixing nitrogen, create indoleacetic acid to aid in the growth of plants.	Rouws et al., 2010;; Luna et al., 2010; Meneses et al., 2017;; Tufail et al., 2021
Herbaspirillum seropedicae	Maize, rice	Nitrogen fixation escalates photosynthetic capacity and nutrient uptake of the plants.	Balsanelli et al., 2014; Amaral et al., 2014; Brusamarello-Santos et al ., 2017; Ramos et al., 2020
Kiebsiella pneumoniae	Alfalfa	Boost plant growth and nutrient uptake, nitrogen fixation	Dong et al., 2003
Microbacterium sp.	Rape	Probiotic solubilization of plant nutrients, produces phytohormones, increases plant growth in stressful environments	Sheng et al., 2008; Sun et al., 2019
Pseudomonas fluorescences	Pea, rape, black nightshade, and tobacco, *Atractylodes lancea*	Increase nutrient level in soil and supply nutrients to the plants, increase biomass and boost plant height under greenhouse conditions, enhance assemblage of photosynthate	Long et al., 2008; Sheng et al., 2008; Oteino et al., 2015
Pseudomonas putida	Willow, potato, and pea	Produce antibiotics, manufacture plant hormone precursors, enhance plant development	Andreote et al., 2009; Germaine et al., 2006; Khan et al., 2014; Volke et al., 2020
Pseudomonas thivervalensis	Black nightshade and tobacco	Growth promotion, osmotic stress resistance (trehalose), chemotaxis, antibacterial and antifungal traits (2,4-diacetylphloroglucinol)	Long et al., 2008; Nascimento et al., 2021
Rahnella aquatilis	Hybrid poplar	Biocontrol agent, growth promotion, antagonistic activity, enhance nutrient procurement, boost production of biomass, increase yield production, enhance the production of phytohormones	Khan et al., 2009; Santhosh et al., 2023
Sphingomonas sp.	Rice, tomato	Reduce salinity stress, produce IAA and gibberellins thus promoting plant growth, tackle environmental contaminations, produce phytohormones such as gellan gum and sphingan	Kandel et al., 2015; Khan et al., 2017; Asaf et al., 2020
Curtobacterium sp.,	Hybrid poplar, sugarcane, grapevines, soybean, maize, sorghum, black pepper	Tackle plant salinity stress, phosphate solubilization, siderophores, growth promotion (IAA), stress relief, produce chitinase that helps in resistance of diseases, nitrogen fixation	Senthilkumar et al., 2007; Khan et al., 2016; Dimkić et al., 2021;
Acinetobacter calcoaceticas	Douglas-fir, *Lemna aoukikusa,*	Augmentation of phytoremediation of polluted soil, antagonistic activity, plant growth stimulation	Suzuki et al., 2014; Khan et al., 2015; Chen et al., 2015;
Paentbacillus spp.	Ryegrass, *Quercus robur*	Nitrogen fixation, procurement of iron in the soil, improved solubilization of phosphate, stimulation of plant development, and biocontrol agent against several diseases	Castanheira et al., 2017; Daud et al., 2019; Vaitiekūnaitė et al., 2021; Singh and Wesemael, 2022

colonization. (Alquéres et al., 2013). N-acyl-homoserine lactonase, or aiiA, is a gene that aids in the disruption of pathogen quorum sensing in bacteria like *Burkholderia* sp. KJ006; N-acyl-homoserine lactone synthase is a gene that aids in quorum sensing in *Burkholderia phytofirmans* PsJN (Cho et al., 2007; Zúñiga et al., 2013). *Burkholderia phytofirmans* PsJN have many genes for energy production, transcription control, cell redox homeostasis, general metabolism (lipids, sugars, nucleotide, amino acids), cellular homeostasis, cell redox homeostasis, and ECF group IV sigma factors (Sheibani-Tezerji et al., 2015). TonB-dependent siderophore receptor, Acds (ACC deaminase), ferritin, iacC, L-ornithine5-monooxygenase, and other significant genes involved in colonization (Sun et al., 2009; Zúñiga et al., 2013a; Zhao et al., 2016; Zúñiga et al., 2013b). The gene alkane monooxygenase (alkB), which is involved in the degradation of diesel, is present in *Rhodococcus* sp. and *Pseudomonas* sp (Andria et al., 2009). *Pseudomonas* sp. strain ITRI53, *Enterobacter ludwigii*, and *Pantoea* sp. strain BTRH7 possess CYP153 genes, which participate in the degradation of hydrocarbons found in petroleum. (Afzal et al., 2011; Yousaf et al., 2011). Genes like pectinase, endoglucanse (eglA, and eglS) are present in *Bacillus, Azoarcus* sp. strain BH72, and *Bacillus amyloliquefaciens*, respectively, allowing systemic colonization (Reinhold-Hurek et al., 2006; Fan et al., 2016). It was also discovered that the genes nifH (nitrogenase) for nitrogen fixation were present in *Herbaspirillum seropedicae, Bradyrhizobium, Pelomonas, Bacillus sp.*, and *Cyanobacteria*. Strain G of *Pseudomonas* sp. has gene carAB for disruption of pathogen cell-cell signaling (Roncato-Maccari et al., 2003; Terakado-Tonooka et al., 2008; Newman et al., 2008). Bacterial-plant interaction is also mediated by pilT, O-antigenic side chain, and numerous other genes (Duijuff et al., 1997; Rediers et al., 2003; Böhm et al., 2007).

2.1. Attachment and entry into the host plants

Bacterial adherence to the surface of the host plant is the first stage of endophyte colonization. Chemotactic affinities allow the bacteria in the soil to travel toward the roots in response to the chemical stimulus that the plant produces. Initially, they adhere to the rhizoplane to invade the entry sites towards the inner tissues of the plants, then attach to the plant's surface. Endophytic colonization is aided by exopolysaccharides (EPS), mostly in the early stage which promote the attachment of bacterial cell onto the surface of the roots. (Meneses et al., 2011). Flagella, polysaccharides, and fimbriae are other important microbial structures that serve as vital components for the attachment to the host surface (Balsanelli et al., 2010). The attachment is then followed by entry into the plants. Stomata, root pores, cuts, wounds, and hydathodes are the most typical points of entry for these microorganisms (Hardoim et al., 2015). Moreover, certain endophytic bacteria possess the capacity to alter the plant's cell walls by secreting enzymes like endoglucanases, xylanases, cellulases, and pectinases which promote the entry or access to the plant tissues (Compant et al., 2005).

During interaction (endophytic bacteria-plant interaction), detoxification of ROS occurred. For example, bacterial endophytes such as *Gluconacetobacter diazotrophicus* enter the host tissues, and it activated genes such as glutathione reductase and superoxide dismutase (SOD) which is a ROS- deactivating gene. This hypothesis indicates that ROS-deactivating genes are essential during the initial phases of plant colonization (Alquéres et al., 2013b). Some common types of bacterial genes involved in complex interaction have been shown in Table 2.

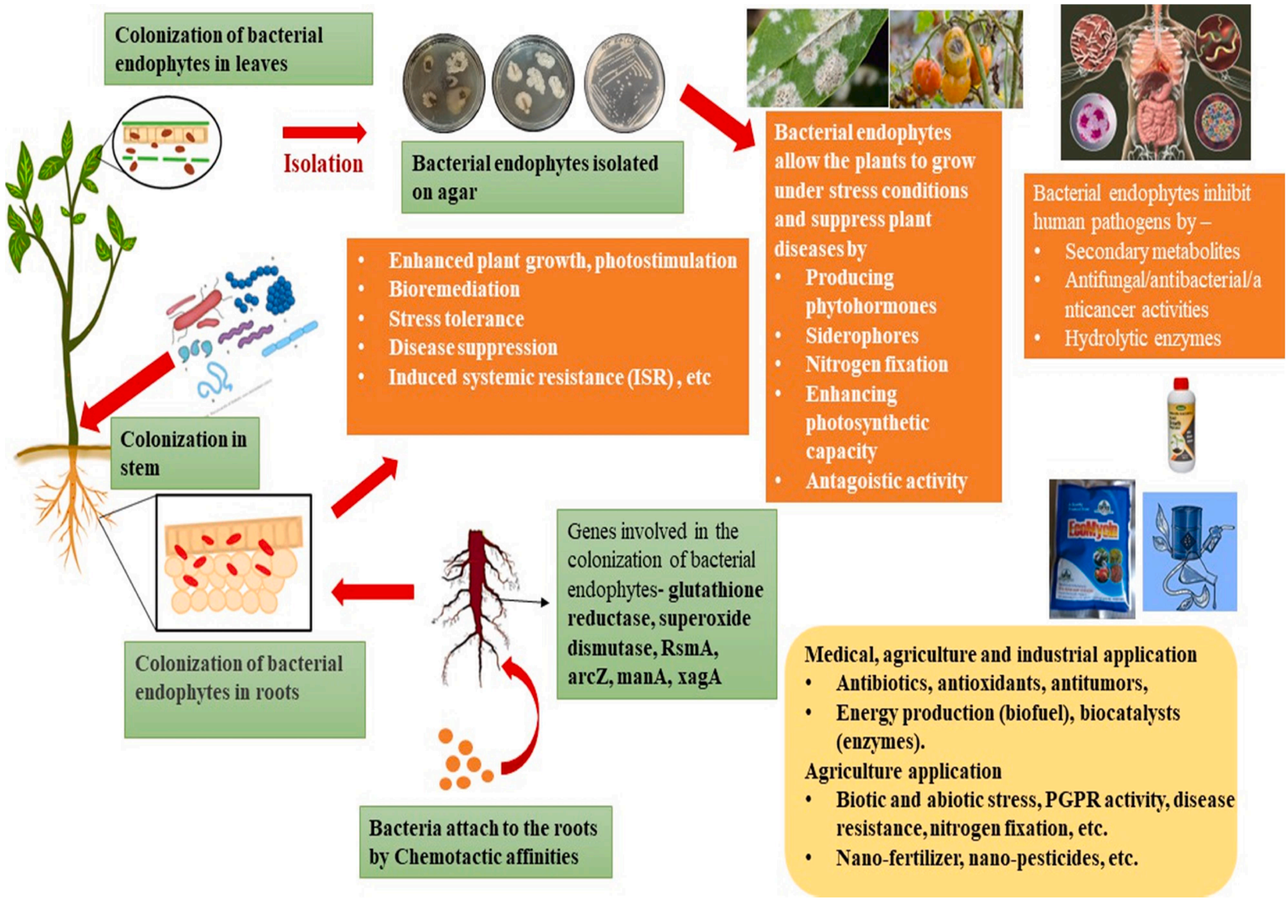

Fig. 1. Overview of bacterial endophytes in plants and the benefits.

Table 2
Mechanisms for regulation of biofilm formation by secondary messengers.

Mechanism	Bacteria	Genes involved	Reference
Cyclic GMP	*Xanthomonas campestris*	RsmA modulates the formation of biofilms	Lu et al., 2012; An et al., 2013
Small RNAs and RNAbinding proteins	*E.amylovora*	Repression of attachment to solid by hfq-dependent ArcZ sRNA and cellular aggregation promotion	Zeng et al., 2013; Zeng and Sundin 2014
Small RNAs and RNAbinding proteins	*X.campestris*	RsmA negatively regulates the production of biofilms and lowers c-di-GMP levels.	Lu et al., 2012
Small RNAs and RNAbinding proteins	*X. oryzaepv. oryzae*	Negative regulation of biofilm by RsmA	Zhu et al., 2011
Cyclic-di-GMP	*E.amylovora*	edc genes positively modulate Amylovoran activation and pdeA, pdeB, and pdeC enhance biofilm formation	Edmunds et al., 2013; Kharadi et al., 2019
Cyclic-di-GMP	*Pseudomonas fluorescens*	RsmA and RsmE are the regulatory genes produced by cyclic-di-GMP that regulates the quorum sensing of PcoI/PcoR system and polyketide antibiotic 2,4-diacetylphloroglucinol. This, in turn, aids the bacterium in protecting the plants from diseases.	Xiao-Gang et al., 2010
Cyclic-di-GMP	*X.fastidiosa*	Regulation of genes manA, and xagA involved in biofilm formation EPS biosynthesis repression	Chatterjee et al., 2010

2.2. *Biofilm formation*

The process via which bacteria produce biofilms is intricate, the bacterial communities are held together by a matrix of polymer which mainly consists of secreted proteins, extracellular DNAs, and polysaccharides. The process of biofilm formation can be characterized into five phases: (i) reversible phase (non-specific interaction of bacteria with the surface), (ii) irreversible phase (bacteria-host interaction by surface adhesion using lipopolysaccharides and fimbriae, (iii) exopolysaccharides (EPS) production phase, (iv) maturation phase (interaction through signal molecules), (v) dispersion phase (modification of surface adhesion and degradation of polysaccharides and matrix) (Muhammad et al., 2020). Fig. 2 depicts the different stages of biofilm formation in bacteria.

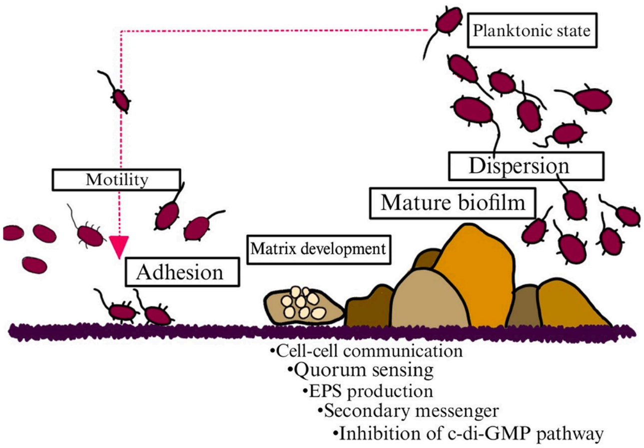

Fig. 2. Different stages of biofilm formation in bacteria.

2.2.1. *Reversible phase*

The reversible phase is initiated with non-specific between the cells and the surfaces through interaction hydrophobic interaction, van der Waals force or electrostatic forces. The bacteria move to the surface by random motion (Brownian movement), convection, or sedimentation (Palmer et al., 2007). Direct movement of bacteria towards nutrient sources such as sugar or amino acids is directed by chemotaxis which can be likely found in all micro-organisms and it plays an important role in enhancing the plant'splant's growth by cell-surface interaction (Vladimirov and Sourjik, 2009; Porter et al., 2011). The interaction between cells and their surroundings relies on the total sum of attractive or repulsive forces (the greater the attractive force, the greater the bacteria have the affinities to attach to the surfaces) (Carniello et al., 2018).

2.2.2. *Irreversible attachment*

Irreversible attachment is loosely adherent with the cell surface, involving hydrophobic and dipole-dipole interaction, ionic, covalent and hydrogen bond (Bos et al., 1999). Fimbriae, pili, flagella and non-fimbrial adhesions which are part of the adherent structure are found to be involved in the formation of biofilm which helps them to connect with the substrate (Berne et al., 2015). The repulsive forces that can obstruct cell-surface interaction can be reduced or controlled by the flagella (Terashima et al., 2008; Lemon et al., 2007; Haiko and Westerlund-Wikstrom, 2013). Quorum sensing (QS) which is a intercellular signaling technique also play a vital function in biofilm formation. In QS, the bacteria (both gram-negative and gram-positive) synthesize and excrete chemical molecules that transmit signals such as autoinducers for cell-to-cell communication (Abraham, 2016; Li and Tian, 2012; Papenfort and Bassler, 2016).

2.2.3. *Secondary messenger molecules*

Secondary messenger molecules act as signaling molecules between endophytes and the host plants. Cyclic di-GMP, or c-di-GMP, is an essential secondary messenger in *Gluconacetobacter xylinum* because it functions as an allosteric activator of cellulose synthase (Ross et al., 1987). It controls the expression of genes related to bacterial differentiation, EPS production, and the cell cycle (Römling and Galperin, 2015). The protein domains such as diguanylate cyclases, phosphordiesterases with either HD-GYP or EAL domain, GGDEF domain synthesize c-di-GMP control the catalytic action of the self-regulation process of these molecules (Ryjenkov et al., 2006; Schmidt et al., 2005). *Pseudomonas syringae pv.* tomato DC3000 was recently shown to activate biofilm formation by c-di-GMP upon engagement with host cells and to evade immune response.. GGDEF-EAL protein Chp8 expressed by this pathogen is accountable for the plant signal, degradation activity, and c-di-GMP biosynthesis (Engl et al., 2014). Table 2 shows the different mechanisms for the regulation of biofilm formation.

2.2.3.1. Mechanism of C-di-GMP. The c-di-GMP pathway operates through different molecular mechanisms such as regulation of enzyme or proteins, gene expression by modulation of transcription factor (TF), and non-coding RNA molecules by direct interaction (riboswitches). The regulation relies on the different c-di-GMP receptors and effectors. Observations have shown that this receptor detects c-di-GMP's level and translates the information into the signal pathway. Meanwhile, C-di-GMP effectors are proteins that change its activity (allosterically) upon binding of the c-di-GMP and regulate the target protein (Chou and Galperin, 2016; Hengge, 2009, 2013).

In Fig. 3, diguanylate cyclases synthesize the c-di-GMP having GGDEF region and are broken down by the phosphodiesterases (HD-GYP or EAL domains) which then undergo hydrolysis with oligoribonuclease to produce 2 GMP molecules. C-di GMP mechanism relies on the diversity of binding receptor and effectors and occurred at different levels i.e., transcription phase, post-transcription and post-translational phase (Valentini and Alain Filloux, 2016).

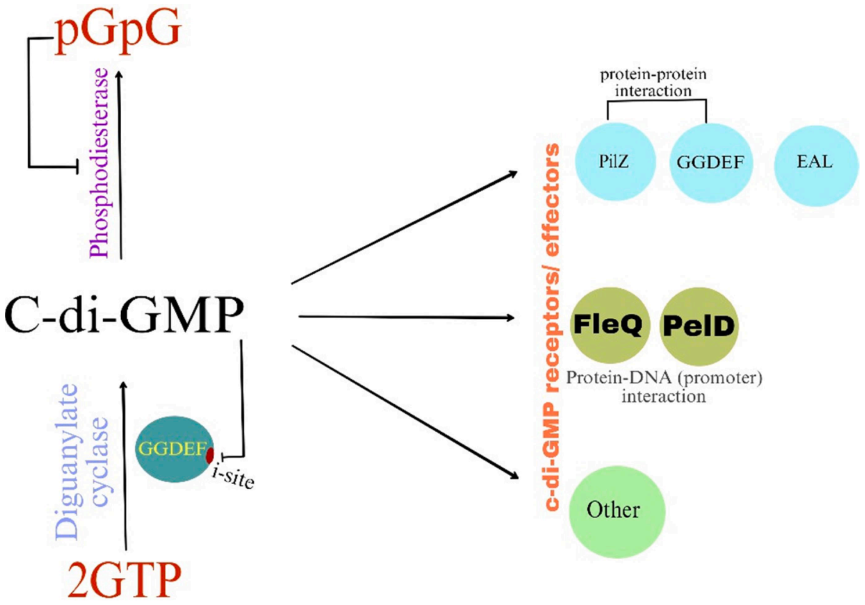

Fig. 3. Molecular mechanism of c-di GMP.

RsmY and RsmZ, small regulatory RNAs which are promoted by the GacS/GacA are known to modulate the translational respressor activity of the RsmA. In addition, the Gac/Rsm system is further regulated by RetS and LadS (hybrid sensors) and histidine phosphotransfer protein (HptB) and the titration of RsmA acts as a determinant for the production of biofilm. The modulation of Gac/Rsm biofilm formation is largely dependent on the SadC which is repressed by RsmA. This confirms that the Gsc/Rsm system and c-di GMP network play a crucial role and rely on each other for the formation of biofilm (Valentini & Alain Filloux, 2016).

3. Contribution of bacterial endophytes against pathogens

The endophytes play an important role in combating the pathogens, both in plants and humans. Some endophytic bacteria have the ability to produce antimicrobial compounds which provide protection by inhibiting the growth of pathogens. Bioactive compounds are commonly used as synthetic medicines to treat various diseases with less negative effects (Chang et al., 2013). Additionally, the endophytes function as biocontrol agents, preventing the growth of pathogens and helping in increasing crop yields. The secretion of secondary metabolites such as antifungal agents, hydrolytic enzymes, and siderophores protects the plant and improves antioxidant activity. Endophytes can also suppress the plant defense mechanism by ISR and SAR system (Muthu Narayanan et al., 2022). Table 3 displays some plant pathogen-opposing endophytic activities.

It is estimated that approximately 70 % of plant infections can be attributed to fungi and bacterial pathogens, leading to a significant loss of crop yields (Savary et al., 2019; Hussain et al., 2019). Some notorious bacterial plant pathogens include the genera Xanthomonas, Ralstonia, Pseudomonas, *Bacillus, Clavibacter, Agrobacterium, Xylella, Burkholderia, Erwinia, Streptomyces,* and *Pantoea.* These bacteria commonly cause blights, leaf spots, cankers, overgrowths, wilts, scabs, galls and soft rots (Nazarov et al., 2020). Endophytes such as *Bacillus thuringiensis* SY33.3, *Pseudomonas fluorescens* obstruct the pectinolytic enzyme activities of *Fusarium oxysporum*, which causes vascular wilt in plants (Zheng et al., 2019). Shorter exposure to pesticide is effective against pathogens but prolonged use of chemical pesticides such as

Table 3
Some activity of bacterial endophytes against the plant pathogen.

Bacterial endophytes	Plant pathogens	Activity against plant pathogen	References
Bacillus subtilis XZ18-3	*Rhizoctonia cerealis*	With the accumulation of reactive oxygen species (ROS), the endophyte exhibits antagonistic antifungal activity that leads to wheat rot and blight.	Yi et al., 2022
Bacillus velezensis Bs006	*Fusarium oxysporum f. sp.*	The endophyte exhibits antagonistic activity by producing antimicrobial cyclic lipopeptides such as surfactants, turnins and fengycins, suppresses the microorganism that causes *Fusarium* wilt in goldenberries.	Velandia et al., 2021
Bacillus thuringiensis SY33.3	*Aspergillus niger, Verticillium dahlia, and Fusarium oxysporum f. sp. niveum*	The bacterial endophytes creates an extracellular chitinase enzyme	Azizoglu et al., 2021
Bacillus velezensis strain J.K.	*Magnaporthe oryzae*	Antagonistic activity	Jing et al., 2020
Bacillus circulans GN03	*Verticillium dahliae* strain V991	Promotes plant growth and enhance disease resistance by producing hormones such as brassinosteroids, IAA, gibberellic, etc.	Qin et al., 2021
Streptomyces roseoverticillatus 63 (Sr-63)	*Xanthomonas oryzae pv. oryzae*	The endophytes produce carbazomycin B which confers antagonistic activity. It inhibits the protein expression of the pathogen and reduces the malate dehydrogenase activity	Shi et al., 2021
Streptomyces angustmyceticus NR8-2	*Colletotrichum sp., and Curvularia lunata*	Suppressing the activity of the pathogens by producing β-1, 3-glucanase antifungal metabolites	
C. vaccinii MWU328, MWU300, and MWU205; *Chromobacterium vaccinii*	*Coleophoma sp., Phoma sp.*	Antifungal activity	Ebadzadsahrai et al., 2020
Pseudomonas sp. LBUM300	*Clavibacter michiganensis*	Produce antibiotics such as hydrogen cyanide (HCN) and 2,4-diacetylphloroglucinol	Paulin et al., 2017

dichlorodiphenyltrichloroethane (DDT) may cause residual toxicity and harm human health by resulting in seizures or acute poisoning, which may also lead to death. Moreover, it may result in the emergence of mutant or resistant fungal pathogenic strains like *Ustilago, Verticillium, Botrytis, Penicillium, Aspergillus, Colletotrichum, Phytophthora* and others. This necessitates the need for natural management approaches to control plant pathogens and certain endophytic microbes such as fungi and bacteria have the potential to act as promising biocontrol agents by inhibiting or combating the pathogens (Agrios, 2009; Collinge et al., 2019; Narayanan, 2022). According to Mei et al., (2021), bacterial endophytes can act as novel approaches or tools to control pathogens, improve stress tolerance in plants and enhance plant growth. Their work observed that endophytic bacteria, *Bacillus velezensis* strains IALR619, IALR308 and IALR585 can successfully inhibit or suppress the growth of the fungal pathogen, *Colletotrichum gloeosporioides* (strawberry pathogen) under greenhouse conditions. *Paenibacillus* and *Bacillus* have been reported to produce antimicrobial compounds called lipopeptides. Lipopeptides serve as a key class among antimicrobial compounds. It has also been found that *Bacillus amyloloquefaciens* are effective producers of lipoproteins among the *Bacillus* strains White et al., 2014).

Several research works have demonstrated that the bioactive metabolites of endophytes are good sources of drugs to treat a wide range of diseases and may find use in the sector of food and pharmaceutical industries, agriculture, medicine, and cosmetics (Godstime et al., 2014; Shukla et al., 2014). Medicinal plants are likely to be colonized by some microbes which have anti-microbial activity (Wang et al., 2019). For example, Cordia dichotoma also called Lasura is a widespread plant commonly found in India. It is used as a medicinal plant to treat chest pain and stomach aches. Some native people have been known to use all parts of the species to treat different diseases such as tumors, cough, jaundice, dysentery, wounds and for its analgesic, and antihelminthic effects (Ragasa et al., 2015).

Table 4 shows some responses of bacterial endophytes to pathogens in humans. About 75 % of the known bacterial endophytes are Streptomyces species which are filamentous, gram-positive bacteria with high potential for biocontrol agents and belong to the class of actinomycetes (de Lima Procópio et al., 2012). Furthermore, uncontrolled proliferation of aberrant cells is a defining characteristic of cancer, a disease that, if left unchecked, kills people. The medications used to treat cancer have non-specific harm to healthy cells that grow, and several adverse effects remain inactive in the fight against some types of cancer (Pasut and Veronese, 2009). Novel metabolites that may act as anticancer agents and other illness-causing factors are reportedly produced by endophytes (Rajamanikyam et al., 2017).

4. Endophytes of agricultural significance

Endophytes are organisms that display a wide range of plant growth-promoting activities. These include activities like nitrogen fixation, phosphate solubilization, siderophore synthesis, IAA synthesis, and even ammonia synthesis. (Hashim et al., 2020; Zamin et al., 2020). Enzymes that aid in the extraction of biofuels are reported to be produced by *Keteleeria davidiana varchienpeii, Sabina chinensis* cv. *Kaizuca, Cupressus torulosa* D. Don, *Taxus chinensis* var. *mairei* Mast, and Keteleeria evelyniana Mast. These plants yielded the endophytes Phomopsis, Cephalosporium, Microsphaeropsis, and Nigrospora (Tiwari et al., 2023). Instead of toxic chemicals, the textile industry utilizes a mixture of pectinase, lipase, amylase, cellulase, and hemicellulase to break down cotton and eliminate sizing agents. Pectinase's role in the extraction of oil from a variety of sources, including flaxseed, dates, and olives, has been well studied (Haile and Ayele, 2022). In addition, proteases have application in numerous other sectors such as the food industry, leather tannery, paper production, bioremediation processes, silver extraction from photographic film, and the treatment of inflammation and potentially dangerous lesions (Abdel Wahab and Ahmed, 2018; Othman et al., 2018). It has been determined that endophytic fungi and bacteria are potent biofactories for the synthesis of metal-based nanoparticles along with therapeutic applications (Rahman et al., 2019; Rana et al., 2020; Eid et al., 2020). Microorganism-based green synthesis of metal-based nanoparticles has become a viable and appealing alternative approach to producing NPs in a more sustainable and clean manner, hence reducing their harmful impacts on the environment and human health (Pal et al., 2019).

Compared to microstructured materials, nanoparticulate materials can offer a plethora of advantages. The efficacy of these materials in the health and wellness sectors depends on several aspects, including their size, shape, and chemical makeup. When using green biosynthesis from endophytic bacteria, the microbes used, how these microorganisms are used in the biosynthesis, and the normal synthesis settings are the defining elements for the synthetic process (Shariq Ahmed et al., 2019), Ag nanoparticles produced from a *Pennisetum setaceum* endophytic bacteria, a tropical plant, were discovered to prevent the growth of many bacteria, such as *Pseudomonas aeruginosa* (ATCC 27853), *Salmonella typhimurium* (ATCC 14028), *Staphylococcus aureus* (MTCC 1430),

Table 4

Some secondary metabolites produced from the bacterial endophytes and their activity against human pathogens.

Bacterial endophytes	Bioactive compound	Human pathogens	Activity against human pathogen	References
Bacillus atrophaeus, Bacillus mojavensis	Bis(2-ehtylhexyl) ester, 1,2-bezenedicarboxyl acid, methyl ester, and decanodioic acid, BmB 4, fengycin, surfactin	Klebsiella pneumoniae, Salmonella typhi, Escherichia coli, Staphylococcus aureus	Antifungal, antiviral, antibacterial	Jasim et al., 2016; Mohamad et al., 2018
B. subtilis	Subtilin, 4-(4-cinnamoyloxy)phenyl)butanoic acid, cyclo-(L-Val-L-Phe), cyclo-(L-Pro-D-Tyr), cyclo-(L-Pro-L-Val)	*Bortrytis cinerea, Enterococcus raffinosus, Xanthomonas axonopodis pv. citri, Ralstonia solanacearum, E. coli*	Antimicrobial, antifungal	Singh et al., 2017; Bolivar-Anillo et al., 2021; Numan et al., 2022
Streptomyces hygroscopicus	Valinomycin	*Vibrio cholerae*	Antibacterial, antioxidant, antifungal	Golinska et al., 2015
B. subtilis	Subtilin		Antibacterial	Singh et al., 2017
Streptomyces sp.	Pentalenolactone, geosmin, β-unsaturated ketone, 2-methylisoborneol, albaflavenone	Multi-drug resistant bacteria	Antibacterial	Takahashi et al., 1983; Lin and Cane, 2009
Bacillus thuringiensis, Bacillus licheniformis	Alkaloids (inosine and guanosine), oocydin, pseudomycins, ambuic acid	*Escherichia coli, Staphylococcus aureus, Apergillus niger, Aspergillus flavus, Listeria monocytogenes*	Antibacterial, antifungal, antioxidant activities	Liu et al., 2015; Nisa et al., 2022
Streptomyces xiamenensis, Bacillus sp., Bacillus cereus subsp. thuringiensis	cyclo-(L-pro-D-tyr)	*Enterococcus raffinosus, Xanthomonas axonopodis pv. citri, Ralstonia solanacearum*	antimicrobial activities, anti-cytotoxicity	Kumar et al., 2013; Qian et al., 2018; *Al*-Hosni et al., 2020
Bacillus cereus	β-sitosterol acetate, 2-Piperidinone, N-(4-Bromo-N-Butyl)-, Cholest 5-en-3-ol- 3-beta acetate, Phthalic acid, Dimethyl phthalate, Tricosanal	*Pseudomonas aeruginosa, Bacillus spizizenii, Salmonella typhimurium and Klebsiella pneumoniae*	Anti-cancer, anti-fungal, antibacterial, antioxidant, anti-inflammatory	Nisa et al., 2022;

Escherichia coli (ATCC 25922), and *Acinetobacter baumannii* (ATCC 19606). Additionally, the production of biofilms could be inhibited by these nanoparticles, which is a pathogen inhibition mechanism ascribed to the NPs' interaction with the indicator cells.

The most common method of inoculation in agriculture is endophytes; the culture is mixed with the artificially produced sticky seeds and sown, assisted by a carrier. Additionally, several commercial formulas involve the direct administration of liquid cultures, either in conjunction with granular fertilizer or seed treatments. Additional methods such as direct soil application, foliar spraying, root dipping, pelleting, seed priming, and seed coating have also been employed (O'Callaghan, 2016). Numerous bacterial and fungal endophytes generate antimicrobial substances that have potent antibacterial and antifungal properties and may be hostile to plant diseases (Khalil et al., 2021). For instance, endophytes Pseudomonas sp. have been identified from the roots of Artemisia sp. (Asteraceae) and reputed to generate the antibiotic DAPG which can make plants resistant to pathogens like *Phytophthora capsici, Colletotrichum gloeosporioides, Verticillium dahliae*, and *Fusarium oxysporum* (Chung et al., 2008).

5. Conclusion and future perspective

The rapid rise of antimicrobial resistance in the environment is due to the overuse and misuse of antibiotics. Currently, antimicrobial resistance is a global threat that has alarmed the WHO to initiate preventive measures and develop compounds or drugs to fight the diseases while tackling drug resistance. Moreover, researchers all over the world are investigating underexplored areas to discover novel compounds to overcome this issue. In this scenario, endophytic bacteria can be explored in this quest for alternative antimicrobial agents as they play an important role in the prevention of pathogenesis. They are mutually associated with the plants and promote solubilization of minerals, nutrient availability, siderophore production, and phytoremediation. They can act as novel tools to enhance plant growth, and induce the synthesis of gibberellins, ethylene, auxin, and cytokinins, which are plant growth hormones. They also protect the plants against stress and increase their tolerance to environmental stressors such as salinity and drought. Most importantly, they serve as natural antibiotic producers and can prevent antibiotic resistance developed by the pathogens. The secondary metabolites which include terpenoids, lipids, flavonoids, saponins, alkaloids, and flavonoids play an important role in their antimicrobial activity . Thus, endophytes could be a potential source for the derivation of natural bioactive antimicrobial compounds.

CRediT authorship contribution statement

Lalhmangaihmawia Hnamte: Conceptualization, Writing – original draft. **Vanlallawmzuali:** Conceptualization, Writing – review & editing. **Ajay Kumar:** Resources. **Mukesh Kumar Yadav:** Resources. **Zothanpuia:** Resources. **Prashant Kumar Singh:** Conceptualization, Resources, Writing – review & editing, Funding acquisition.

Declaration of competing interest

Authors declare no competing interest.

Data availability

No data was used for the research described in the article.

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