Exploring the bioefficacy of Endophytic Bacteria against Important Plant Pathogens

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ABSTRACT

The biological management of plant diseases has developed into a separate scientific and technological discipline, and in recent years, this change has happened quickly. A form of bacterium known as a bacterial endophyte may colonize any portion of a plant without causing any symptoms or harm to the host plant. Endophytic bacteria have been discovered by several researchers, and there is growing evidence that they can stop a variety of plant diseases from growing and functioning. Endophytes have a variety of benefits including growth-increasing and disease-hampering properties. Researchers’ interest in this field is growing as a result of its potentially to be utilized as an alternative to synthetic fungicides. This review's main objectives are to chart the development of endophytic bacterial research and give scientists access to current knowledge that will spur further investigation. Endophytic bacteria are employed to control plant diseases including wilt, rot and post-harvest damage, as well as nematode infestation. Endophytic bacteria are also used to control nematodes and postharvest diseases. With an emphasis on endophytic bacteria, this review explains the diverse mechanisms of bacterial endophytes to shield the plant from biotic infection.

Keywords: Antibiotics, Bacteria, Endophytes, Management, Phytopathogens

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INTRODUCTION

Plant diseases create tremendous biotic stress in plants, causing farmers to lose a lot of money and tainting food by creating toxins while it is kept. Farmers' purposeful determination to combat illness resulted in the development of a variety of pesticidal molecule, the use of which destroys the environment and eventually, harms human health. Plant health management has gotten more difficult as certain plant diseases have developed resistance to these treatments (Dun-chun et al., 2016). Biocontrol of plant diseases has become more important in addressing these concerns. Plant growth-promoting rhizobacteria (PGPR) have long been investigated by many scientists and rhizosphere treatments for biocontrol have mostly focused on them. Due to the expanding range of ways that microorganisms may be used to boost plant development and lower disease-causing pathogens, researchers have lately turned their attention to those that colonize interior tissues with laser beams (Saeed et al., 2021). Researchers have recently focused a lot of emphasis on the function of bacterial endophytes among these microorganisms in plant disease management. Endophytic bacteria were defined by Wilson (1995) as prokaryotes that seek to colonize the vascular tissues without causing any damage to the
host plant. Endophytes are "endo-symbionts" that live inside plant tissues without causing injury or illness and may be discovered using aseptic procedures, according to researchers. Previous studies showed the beneficial relations between plants and microorganisms and scientists believed that fungi that weren't often recognized for causing illnesses in agricultural plants had the power of microbial endophytes (Clay, 1988). The seeds of horticultural as well as agricultural crops might be used to isolate bacterial species (Kirchhof et al., 1997).

According to studies, endophytic bacteria can be found in plant parts. When describing the habitat of endophytes, Andrews (1992) stated that, unlike microorganisms dwelling in and above the rhizosphere, endophytes may exist in a fully isolated environment. Endophytic bacteria, according to Arnold and Lutzoni (2007), may reside in the rhizosphere, twig, leaves, petals, seeds and fruits of agricultural plants. Endophytes have a variety of benefits, according to a growing body of literature. Kang et al., (2007) described endophytes growth-increasing properties, whereas Senthilkumar et al., (2007) performed endophytes' disease-hampering properties. Bakker et al., (2007) investigated the work of endophytes in strengthening crop defense mechanisms against various plant disease. Endophytes have been shown to generate anti-herbivory compounds as well as catalyze biological nitrogen fixation in plants (Martínez et al., 2003) and improve their mineral absorption (Malinowski et al., 2000). Backman et al., (1997) conferred specific bacteria colonizing a specific crop species, changing populations as seasons change, the order in which they colonized and their capability to mobilize within cells and encourage systemic resistance as endophytes as antimicrobials against multiple plant diseases.

Endophytes
A quick description of 'Endophytes' is provided here to help you comprehend the subsequent sections of the review. Endophytes are microorganisms that be inherent asymptomatically in the plant for at least a portion of their lifespan (Solis et al., 2016). Endophytes thrive within their hosts intracellularly, systemically or locally without creating apparent infection or disease signs (Schulz et al., 2015). According to Busby et al., (2016), endophytism is characterized by "inconspicuous infections, diseased host tissues that are at least temporally symptomless and demonstrated microbial colonization inside host tissues". All plants are thought to have endophytes, and the biodiversity of these microorganisms relies on a range of factors, including the type of host plant, plant canopy, nutrient availability, the adequacy of the local environment and interactions between bacteria and fungi that are carried by the soil (Yan et al., 2015). Endophytes are potential biocontrol agents because they can change interactions with infections and pests. An endophyte called Acremonium alternatum boosts tomato resistance to the powdery mildew disease Leveillula taurica and shields beans from the moth Plutella xylostella. An isolated fungal endophyte from cotton plants called Phomopsis sp. prevented caterpillar herbivory on cotton plants. Sometimes an endophyte species can act as a biocontrol agent, and other times it might promote the growth of the host plant, which has additional benefits. Neotyphodium species promote host plant growth, fitness and stress tolerance while safeguarding it against infections and pests (Solis et al., 2016). Furthermore, pathogenic Sclerotium rolfsii was decreased and sunflower biomass output was boosted by endophytic Penicillium citrinum and Aspergillus terreus (Harman et al., 2021). How endophytes minimize diseases and pests is the next important question. We will explore how endophytes maintain their interaction with their hosts before diving into several biocontrol techniques.

Interaction between plants and endophytes
The concept of "balanced antagonism" between endophytes and their host explains why they colonize without exhibiting any symptoms (Schulz et al., 2015). Fungal virulence factors will be totally overcome by plant defence systems,
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preventing the fungus from colonising plant tissues. If fungal virulence elements could interfere with plant defence systems, a plant-pathogen connection would result in plant disease (Suryanarayanan et al., 2016). When they are impacted by internal or external conditions that make them express pathogenic factors, certain endophytes turn into pathogens (Kusari et al., 2012). Colletotrichum magna strains that are pathogenic and endophytic have been demonstrated to transform their life styles by interfering with certain genetic loci or closely related genes that cause anthracnose disease in cucurbitaceous crop (Rai and Agarkar, 2016). A non-pathogenic mutant strain of Colletotrichum magna (Path-1) produced from a pathogenic strain (CmL2.5) colonizes the roots and stems of cucurbit plants asymptotically and inhibits the virulent form of the fungus, according to experiments (Rai and Agarkar, 2016). High humidity or a shortage of nutrients may be to blame for this frequent occurrence of Colletotrichum switching lifestyles, which alters the host's vulnerability in the presence of natural circumstances (Fisher and Petrini, 1992; Rai and Agarkar, 2016).

Some endophytes produce small quantities of antifungal and antibacterial chemicals to prevent competitors (both pathogenic and endophytic bacteria and fungi) and maintain a competitive balance (Suryanarayanan et al., 2016). The insecticidal metabolite rugulosin generated by endophytic Phialocephala species from Picea glauca (white spruce) poisons Choristoneura fumiferana (spruce bud worm). Secondary metabolites regulate the antagonistic connections between competitors, plant hosts, and endophytes (Hashem et al., 2023). Estrada et al., (2012) found that endophytic Fusarium verticillioides in maize might lower pathogenic Ustilago maydis aggressiveness while simultaneously destroying protective systems.

The compounds in the plant are effective against U. maydis. Pathogen reduction may also come through multipartite healthy relations between endophytes, competitors and host plants.

Secondary metabolites will impair their ability to develop and survive (Suryanarayanan et al., 2016). In conclusion, interactions between plants and endophytes are complex and control the balance of host defence, fungal virulence and secondary metabolites.

Metabolites and activities of endophytes
The potentiality of microbial endophytes to yield a variety of crucial compounds for pharmacology, including antiviral, antifungal, antibacterial, antitumor and anticancer medications, is well documented. Several endophytes can produce plant hormones and growth factors (Kandel et al., 2017; Chaudhary et al., 2022). Abiotic stress tolerance, siderophores, nematocidal, insecticidal and agricultural chemicals are some of their other potential products. A variety of extracellular enzymes, including the phosphatase enzyme, which transforms insoluble phosphate into soluble phosphates for easier digestion by plants, have been shown to be secreted by endophytes (Sharma et al., 2021). Endophytes create chemicals that can be employed in the production of biofuels and the degradation of sophisticated organic and inorganic pollutants that are produced during industrial operations (Burragoni and Jeon, 2021). The advantages of endophytes are listed below, along with some prospective uses for them in various industries.

Endophytes potential in agriculture
Endophytes, according to published studies, are a good source of metabolites and desirable functionalities that might benefit an organic agricultural system. Some endophytes might be employed as bio-pesticides against plant pathogens because of their antibacterial, nematocidal and insecticidal capabilities.

Biopesticidal properties of Endophytes
A systemic weed commensal fungal endophyte Epiclchoe typhina releases mycotoxic properties in extracts of Phleum pratense, a perennial grass native to much of Europe. Bacteria generated chitinase, which is known to dissolve chitin polymers, which are a key component of a fungal cell wall. Bacillus cereus strain was recognized as
bacterial endophyte, was previously perform a defense mechanism against *Rhizoctonia solani* (Pleban *et al.*, 1997). A strain of *Neotyphodium* sp. (AR601) that produces substantial amounts of alkaloids such as loline and ovaline and is injected into the turf tall fescue cultivar 'Jackal' has shown bird deterring capacity (Pennell, 2010). By generating pathogenesis-related proteins, some endophytes have been confirmed to reliably produce effective resistance in plants against common phytopathogens. Fungal endophytes isolated from the tree leaves were shown to produce chitinase and chitosanase, which may help...
Table 1. Mechanism involved in the mode of action of bacterial endophytes

<table>
<thead>
<tr>
<th>Broad mode of action</th>
<th>Mechanism involved</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Root colonization through competition</td>
<td>Various growth stages, the capability to adhere to roots and circulate around without inhibition, and the efficient utilization of the organic acids released from root exudates, the generation of a range of chemicals, together with amino acids, and the type III secretion system are all characteristics of this species.</td>
<td>Lugtenberg and Kamilova, 2009</td>
</tr>
<tr>
<td>Antibiosis and antibiotics suppressing pathogens</td>
<td>Pharmaceuticals such as phenazines, pyoluteorin, pyrrolnitrin, and the volatile HCN are produced. There is the production of D-gluconic acid, 2-hexyl-5-propyl resorcinol, and the volatiles 2,3-butanediol, 6-pentyl—pyrone, and DMDS. Lipopeptides with disease-controlling abilities include surfactin, fengycin, polymyxin, bacitracin, and the iturin group. Pyrrolnitrin, pyrrologlucinol, phenols, and volatile organic compounds such benzothiazole, pyrazine (2,5-dimethyl), and phenolic derivatives are produced.</td>
<td>Pierson and Pierson, 2010; Dandurishvili et al., 2011; Henry et al., 2011; Savadogo et al., 2011; Ramkumar et al., 2013; Zhang et al., 2013; Torres et al., 2016</td>
</tr>
<tr>
<td>Signal interference</td>
<td>Exo-enzyme synthesis requires the deactivation of AHL molecules.</td>
<td>Dandurishvili et al., 2011</td>
</tr>
<tr>
<td>Ferric iron ion competition</td>
<td>Siderophores are synthesized in order to trap ferric ion.</td>
<td>Whipp, 2001</td>
</tr>
<tr>
<td>Competition for nutrients and niches (CNN)</td>
<td>CNN follows the same method as competitive root colonization.</td>
<td>Malfanova, 2013</td>
</tr>
<tr>
<td>Detoxification and degradation of virulence factors</td>
<td>Fusaric acid detoxifies toxins released by pathogens. By destroying autoinducer signals, which prevent the expression of several virulence genes, the ability to sense quorum is achieved. Resistance produced by salicylic acid, c-LPs, pyocyanins, siderophores, and other substances</td>
<td>Uroz et al., 2003</td>
</tr>
</tbody>
</table>

Host plants defend against many plant pathogens by activating host defenses and enhancing resistance (Zheng et al., 2017).

Antimicrobial properties of endophytes

Some endophyte species have been found to form antimicrobial compounds (Jha et al., 2023). For
their antibacterial properties, endophytic microbes from plants have also been taken into consideration (Wang et al., 2019; Xu et al., 2020). Phomopsichalasin was extracted from Phomopsis sp., isolate no. MF6031, which was attained from the twigs of Salix gracilostyla var. melanostachys was shown to have antibacterial action against Bacillus subtilis, Salmonella gallinarium and Staphylococcus aureus as well as antagonistic activity against Candida tropicalis (Horn et al., 1995). In one more investigation, a Colletotrichum spp. isolated from internal stem cells of Artemisia annua L. was found to exhibit antifungal, antibacterial and fungistatic activities (Lu et al., 2000).

**Direct inhibition on plant pathogens**

Several recent research has initiated that endophytes may defend the host plants from diseases or may decrease the destruction triggered by pathogenic microorganisms (Ganley et al., 2008; Meja et al., 2008). Despite the fact that certain research suggests potential endophyte mechanisms for limiting pathogen damage, our understanding of the exact control of endophyte, pathogen and plant is still in its infancy. In this part, we will talk about the processes as direct effects, indirect effects by increasing plant defence and ecological effects. During direct influence, endophytes actively conquer plant diseases by generating antibiotics and lytic enzymes (Fadiji and Babalola, 2020). Conversely, direct interactions amongst bacterial endophytes and biotic plant diseases can be challenging and hostile depending on the species involved (Afzal et al. 2019).

**Indirect effects of on host plant resistance**

In reaction to severe environmental circumstances such as drought, cold, salt stress or during biotic infections, plants generate a number of defence mechanisms. In response to diverse stimuli, rapid structural and biochemical changes occur, such as cellular necrosis, hypersensitive response and phytoalexin synthesis. Over time, two forms of innate resistance develop to withstand pathogen infestation: non-specific (generic) resistance and particular resistance (Kira'ly et al., 2007). The previous one is efficient compared to a wide range of pathogenic microbial species, whereas the latter can tolerate infection by a few pathogenic strains. In fact, resistance improvement and secondary metabolite synthesis boost plant defence against endophytes.

**Plant Disease Management**

Endophytic bacteria have arisen as an attractive, promising and ecologically friendly biological control technique because they can efficaciously decrease biotic disease incidence and severity by blocking the vascular development of the target pathogen (Constantin et al. 2019; de Lamo et al. 2018). These endophytes infiltrate plant portions without causing harm. On a variety of hosts, they either directly or indirectly promote plant growth and/or also act as biocontrol agents by inducing resistance (Constantin et al. 2019).

**Wilt-Causing Pathogens by Bacterial Endophytes**

Wilt is a widespread disease caused by fungal and bacterial strains that can cause major financial losses for farmers. Fusarium and Verticillium are two significant fungal species that produce wilt, and they are difficult to treat since they are soilborne diseases. The pathogenic agent's soilborne origin and capability to infiltrate the vascular system of infected plants, as well as the rise of new and vigorous pathogen physiological races, make disease treatment difficult. Chemical wilt treatments are generally unsuccessful due to the pathogen's extensive host range and ability to live in soil for lengthy periods of time. As a result, biological wilt management has become more significant, encouraging many scientists to do research on discovering appropriate endophytic bacteria to control wilt infections. Endophytic microorganisms may constitute a potentially appealing and ecologically safe option for wilt pathogen biocontrol because endophytes may better restrict disease occurrence and severity by inhibiting systemic fungal progress (Aydi-Ben-Abdallah et al., 2020). Endophytic bacteria by their diverse mode of action have been revealed in
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Managing Root Rot by Endophytic Bacteria

Pathogens that cause root rot are particularly challenging to control because they may persist in the plant debris/soil up to many years until the environmental conditions are conducive for them and a susceptible host plant can be produced (Conner et al., 2014). The primary method for controlling these infections still involves the use of agrochemicals, but this method has repeatedly led to the emergence of resistance and had a negative impact on the environment. Although frequently employed to address root rots, seed coating with fungicides has had little impact on the pathogens’ control (Xu and Kim, 2014). Endophytic bacteria have been praised to manage root rot pathogens because they share a niche with the disease, secrete antifungal metabolites, and aid flora in acquiring nutrients and preparing for plant defence (Muthukumar and Bhaskaran, 2007). Root tissues are colonized by endophytic bacteria, which can defend their host plants from invasion by soilborne pathogens (Mercado-Blanco et al., 2004; Rybakova et al., 2016) because endophytes are initially seen in root hairs during the initial stages of their colonization, and afterwards move in the root cortex (Prieto et al., 2011; Castanheira et al., 2017; Rangjaroen et al., 2017). Plants benefit from endophytic bacteria invading interior plant tissue in many different ways, with the production of plant growth regulators, osmoprotectants (Beneduzi et al., 2012), exopolysaccharides (Berg et al., 2013), antifungal metabolites (Gond et al., 2015) and regulation of plant physio-biochemical components (Hashem et al., 2016). Regardless of how crucial the endophyte-plant interaction is, little is known about how pathogens, endophytes, and legumes interact in adverse environmental conditions. Management of various rot causing pathogens by endophytic bacteria is summarized in Table 3 mentioned below.

However, only a few endophytic biological control agents have been approved for practice in sustainable agriculture and are currently commercially accessible. This calls for greater research on the exploration and expansion of biocontrol organisms, particularly the utilization of endophytes.

Bacterial Endophytes for storage pest

Latest findings have documented the antagonistic behaviors of a wide variety of bacterial endophytes that are found on the outer most layer of fruits and vegetables. On the surface of the fruit, several bacterial species and actinomycetes can influence the development of postharvest diseases (Huang et al., 2021). Three primary bacterial phyla—Proteobacteria, Actinobacteria and Bacteroidetes—dominate the various microbial communities found within or on the host plant surface (Hacquard et al., 2015). The most common biocontrol bacteria discovered on fruit surfaces include Bacillus spp., Burkholderia, Citrobacter, Pseudomonas and Paenibacillus, (Huang et al., 2021). By displaying antibiosis, Pantoea dispersa prevented sweet potato from developing black rot (Jiang et al., 2019). Streptomyces species, a Gram-positive bacterium was recently discovered to be able to stop the infection caused by various bacteria and fungi, including Burkholderia glumae, a bacterial rice pathogen (Degrassi and Carpentieri-Pipolo 2020).

Notably important tasks are screening microbial antagonists against diverse phytopathogens (Kumari et al., 2022). For BCA screening, bacterial strains that may produce antibiotic or volatile chemicals as well as enzymes that can disrupt or lessen the pathogen virulence factors are favored (Zimand et al., 1996; Kapat et al., 1998; Kumari et al., 2022). Table 4 enlists the endophyte-produced bioactive compounds that may be employed to combat biotic infections after harvest.

Endophytic in nematodes management

Since the middle of the 1990s, bacterial endophytes have been revealed to be antagonistic to phytopathogenic nematode (Hallmann et al., 1997; Siddiqui and Mahmood, 1999; Bhat et al., 2023). Plant pathogens are opposed by the greater number of Gram-negative endophytic bacteria and by only few species of Gram-positive bacterial
endophyte (Kobayashi and Palumbo, 2000). Gram-negative endophytes include *Burkholderia cepacia, P. fluorescens* and *Agrobacterium radiobacter*, whereas Gram-positive endophytes include *Bacillus* spp. *Achromobacter, Acinetobacter, Agrobacterium, Bacillus,* Brevibacterium, Microbacterium, Pseudomonas, Xanthomonas and other species have also been discovered to have the capacity to suppress phytopathogenic nematodes (Yadav *et al.*, 2017; Harni *et al.*, 2023).

Table 2. Role of bacterial endophytes in wilt disease management

<table>
<thead>
<tr>
<th>Sr No.</th>
<th>Pathogens causing wilt</th>
<th>Endophytic bacteria have been shown to reduce wilt incidence</th>
<th>Mode of action</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Verticillium dahliae</em> F. oxysporum f. Sp. lycopersici F. oxysporum f. Sp. radicislycopersici</td>
<td><em>Pseudomonas</em> sp. strain PsJN <em>P. fluorescens</em> WCS417r B. pumilus SE-34 <em>Bacillus amyloliquefaciens</em> BO7 B. amyloliquefaciens RWL-1</td>
<td>Endophytic bacteria colonize tomato plants and thicken their cortical cell walls as structural barrier. Siderophores and plant defence hormones like jasmonic acid, and salicylic acid are generated, enhancing ISR.</td>
<td>Vitullo <em>et al.</em>, 2012; Shahzad <em>et al.</em>, 2017</td>
</tr>
<tr>
<td>2</td>
<td><em>F. oxysporum</em> f. Sp. vasinfectum <em>Verticillium dahliae</em></td>
<td><em>Aureobacterium saperae,</em> <em>Bacillus pumilus,</em> <em>Burkholderia solanacearum,</em> <em>Phyllobacterium rubiacearum,</em> <em>Pseudomonas putida,</em> <em>Bacillus subtilis</em> KDRE01, <em>Bacillus megaterium</em> KDRE25</td>
<td>Antibiosis is performed by producing antibiotic components. Cotton wilt induced by mycelial growth inhibition and toxin production.</td>
<td>Lin <em>et al.</em>, 2013</td>
</tr>
<tr>
<td>3</td>
<td><em>F. oxysporum</em> f. sp. cubense race 4 <em>Fusarium oxysporum</em> f. sp. cubense</td>
<td><em>Burkholderia cepacia</em> is a kind of bacteria. Strains 84 and 48B of <em>Pseudomonas putida</em>. Strains of <em>Bacillus cereus,</em> <em>Acromobacter</em> spp., strains of <em>Bacillus flexus</em> Rhizobium spp., W19 <em>Bacillus amyloliquefaciens</em></td>
<td>Colonize the hyphae and macrospores of the fungal pathogens by inducing mycelial deformities. It has been demonstrated that siderophores and secondary metabolites like surfactin, iturin, and bacillomycin D produce a thick biological layer that prevents pathogen development.</td>
<td>Smith <em>et al.</em>, 2003; Thangavelu and Gopi, 2015</td>
</tr>
<tr>
<td>4</td>
<td><em>Fusarium oxysporum</em></td>
<td>BECS7, BECS4 and BECL5 <em>Pseudomonas fluorescens</em> (Pfl) <em>Bacillus subtilis</em> (EPCO16 and EPC5), <em>Pseudomonas</em> spp.</td>
<td>Pathogen suppression by hydrolytic enzyme synthesis</td>
<td>Amaresan <em>et al.</em>, 2014</td>
</tr>
<tr>
<td>5</td>
<td><em>F. Avenaciarum</em> F. sambucinum F. oxysporum</td>
<td><em>Bacillus</em> spp.</td>
<td><em>In vitro</em> antibiosis</td>
<td>Sturz <em>et al.</em>, 1999</td>
</tr>
<tr>
<td>6</td>
<td><em>C. fagacearum</em></td>
<td><em>Pseudomonas denitrificans</em> and <em>P. putida</em></td>
<td><em>In vitro</em> antagonism and competitive colonization of microbes</td>
<td>Brooks <em>et al.</em>, 1994</td>
</tr>
<tr>
<td>Endophytic Bacteria</td>
<td>Isolated from</td>
<td>Disease</td>
<td>Pathogen</td>
<td>Reference</td>
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<td><em>Actinoplanes issouriensis</em></td>
<td>Lupin roots</td>
<td>Root rot of lupin</td>
<td><em>Plectosporium tabacinum</em></td>
<td>El-Tarabily, 2003</td>
</tr>
<tr>
<td><em>Bacillus amyloliquefaciens</em></td>
<td>Stems, leaves, and roots of the <em>Eleusine indica</em> (weed)</td>
<td>Stem end rot of pitaya</td>
<td><em>Alternaria alternata</em></td>
<td>Trung <em>et al.</em>, 2021</td>
</tr>
<tr>
<td><em>Bacillus subtilis</em> subsp. <em>subtilis</em> and <em>B. amyloliquefaciens</em></td>
<td>Soybean roots</td>
<td>Charcoal rot of soybean</td>
<td><em>Macrophomina phaseolina</em></td>
<td>Torres <em>et al.</em>, 2016</td>
</tr>
<tr>
<td><em>Bacillus megaterium</em> and <em>Enterobacter hormaechei</em> subsp. <em>xiangfangensis</em></td>
<td>Mangroves and other vascular shrubs</td>
<td>Root rot of bean</td>
<td><em>Fusarium solani</em></td>
<td>Mutungi <em>et al.</em>, 2022</td>
</tr>
<tr>
<td><em>Bacillus subtilis</em> and <em>Mesorhizobium cicer</em></td>
<td>Nodules of chickpea</td>
<td>Root rot of chickpea</td>
<td><em>Fusarium solani</em></td>
<td>Egamberdieva <em>et al.</em>, 2017</td>
</tr>
<tr>
<td><em>Bacillus cereus</em> and <em>Pseudomonas aeruginosa</em></td>
<td>Rhizome of turmeric</td>
<td>Rhizome rot of turmeric</td>
<td><em>Pythium aphanidermatum</em></td>
<td>Vinayarani and Prakash, 2018</td>
</tr>
<tr>
<td><em>Bacillus mycoides</em> isolates BP24 from</td>
<td>Sugar beet leaves</td>
<td>Black pod rot of cacao</td>
<td><em>Phytophthora capsica</em></td>
<td>Bargabus <em>et al.</em>, 2002; Bargabus <em>et al.</em>, 2004; Melnick <em>et al.</em>, 2008</td>
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<tr>
<td><em>Bacillus pumilis</em></td>
<td>Germinating sugar beet seeds</td>
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<td><em>Bacillus cereus</em></td>
<td>Potato and tomato plants</td>
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<tr>
<td><em>Burkholderia gladioli</em></td>
<td>Healthy corm of saffron</td>
<td>Corm rot of saffron</td>
<td><em>Fusarium oxysporum</em></td>
<td>Ahmad <em>et al.</em>, 2021</td>
</tr>
<tr>
<td><em>Bacillus</em>, <em>Lysinibacillus</em>, and <em>Stenotrophomonas</em></td>
<td>Tomato plants</td>
<td>Root rot of tomato</td>
<td><em>Rhizoctonia solani</em></td>
<td>Sahu <em>et al.</em>, 2019</td>
</tr>
<tr>
<td><em>Bacillus</em></td>
<td>Tomato plants</td>
<td>Collar rot of tomato</td>
<td>Sclerotium rolfsii</td>
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<tr>
<td><em>Pseudomonas viridiflava</em></td>
<td>Apoplastic fluids attained from canola leaves</td>
<td>Black rot of canola</td>
<td><em>Xanthomonas campestris</em> pv. <em>Campestris</em></td>
<td>Romero <em>et al.</em>, 2019</td>
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<tr>
<td><em>Burkholderia cepacia</em> and <em>Pseudomonas aeruginosa</em></td>
<td>Symptomless oil palm root tissues</td>
<td>Basal stem rot of oil palm</td>
<td><em>Ganoderma boninense</em></td>
<td>Sapak <em>et al.</em>, 2008</td>
</tr>
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<td><em>Paenibacillus polymyxa</em></td>
<td>Spermosphere of the Styrian oil pumpkin</td>
<td>Fruit rot of Styrian oil pumpkins</td>
<td><em>Didymella bryoniae</em></td>
<td>Fürnkranz <em>et al.</em>, 2012</td>
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Table 4. Role of bioactive compounds secreted by endophytic bacteria against post-harvest diseases

<table>
<thead>
<tr>
<th>Endophytic bacteria</th>
<th>Secretion of bioactive compound</th>
<th>Role against post-harvest pathogens</th>
<th>References</th>
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<tr>
<td><em>Bacillus subtilis</em></td>
<td>Iturin A, lipopolysaccharide</td>
<td>Antifungal activity</td>
<td>Ek-Ramos <em>et al.</em>, 2019</td>
</tr>
<tr>
<td><em>Bacillus sp.</em></td>
<td>Surfactin, fengycin</td>
<td>Used against bacterial diseases</td>
<td>Jasim <em>et al.</em>, 2016</td>
</tr>
<tr>
<td><em>Bacillus amyloliquefaciens CEIZ-11</em></td>
<td>Lipopolysaccharide</td>
<td>Antifungal activity</td>
<td>Zouari <em>et al.</em>, 2016</td>
</tr>
<tr>
<td><em>Bacillus strains and Enterobacter</em></td>
<td>3-Methylbutan-1-ol</td>
<td>Manage postharvest infection of <em>Botrytis cinerea</em> on tomato fruit, as well as control grey mold during storage and transit</td>
<td>Chaouachi <em>et al.</em>, 2021</td>
</tr>
<tr>
<td><em>Bacillus sp. and Exiguobacterium acetylicum</em></td>
<td>α-Farnesene</td>
<td>Reduces the postharvest infection of litchi fruit caused by <em>Peronosphythora litchii</em></td>
<td>Zheng <em>et al.</em>, 2019</td>
</tr>
<tr>
<td><em>Bacillus pumilus TM-R</em></td>
<td>Ethanol</td>
<td>Antifungal activity against post-harvest pathogens</td>
<td>Morita <em>et al.</em>, 2019</td>
</tr>
<tr>
<td><em>Pseudomonas aeruginosa</em></td>
<td>Phenyltetradeca-2,5-dienoate</td>
<td>Antibacterial activity</td>
<td>Pratiwi <em>et al.</em>, 2017</td>
</tr>
<tr>
<td><em>Pseudomonas donghuensis P482</em></td>
<td>Dimethyl sulphide, S-methyl thioacetate, methyl thiocyanate, dimethyl trisulphide, 1-undecan and HCN</td>
<td>Against post-harvest losses caused by <em>Rhizoctonia solani</em></td>
<td>Ossowicki <em>et al.</em>, 2017</td>
</tr>
<tr>
<td><em>Pseudomonas fluorescens</em> strain WR-1</td>
<td>Volatile organic compounds (VOCs)</td>
<td>Both antibacterial and antifungal activity</td>
<td>Raza <em>et al.</em>, 2016</td>
</tr>
<tr>
<td><em>Pseudomonas putida</em> BP25</td>
<td>Volatile organic compounds (VOCs)</td>
<td>Antifungal activities against <em>Phytophthora capsici</em></td>
<td>Sheoran <em>et al.</em>, 2015</td>
</tr>
<tr>
<td><em>Streptomyces lavendulae SPS-33</em></td>
<td>2-Methyl-butanol and 3-methyl-1-butanol</td>
<td>Check the infection of <em>Ceratocystis fimbriata</em> causes postharvest losses in sweet potato</td>
<td>Li <em>et al.</em>, 2020</td>
</tr>
</tbody>
</table>
Table 5. Effect of endophytic bacteria against phytopathogenic nematodes (PPN)

<table>
<thead>
<tr>
<th>Endophytic Bacteria</th>
<th>Crop</th>
<th>Plant Pathogenic Nematode (PPN)</th>
<th>Effect of Endophyte on PPN</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pantoe agglomerans</em>, <em>Cedecea davisea</em>, <em>Enterobacter intermedius</em>, <em>Pseudomonas putida</em> and <em>Pseudomonas Fluorescens</em></td>
<td>Tomato</td>
<td><em>Meloidogyne incognita</em></td>
<td>As a seed treatment, it reduces nematode infestation.</td>
<td>Munif et al., 2000</td>
</tr>
<tr>
<td><em>Agrobacterium radiobacter</em>, <em>Bacillus pumilus</em>, <em>B. brevis</em>, <em>B. megaterium</em>, <em>B. mycoides</em>, <em>B. licheniformis</em>, <em>Chryseobacterium balustinum</em>, <em>Cedecea davisea</em>, <em>Cytophaga johnsonae</em>, <em>Lactobacillus paracasei</em>, <em>Micrococcus luteus</em>, <em>Micrococcus halobius</em>, <em>Pseudomonas syringae</em> and <em>Stenotrophomonas maltophilia</em></td>
<td>Tomato</td>
<td><em>Meloidogyne incognita</em></td>
<td>Number of galls and egg masses were reduced.</td>
<td>Mekete et al., 2009</td>
</tr>
<tr>
<td><em>Pseudomonas</em> spp., <em>Bacillus</em> spp., <em>Methlobacterium</em> spp.</td>
<td>Okra</td>
<td><em>Meloidogyne incognita</em></td>
<td>The quantity of adult females, egg masses, eggs per egg mass, and root gall index were all reduced.</td>
<td>Vetrivelkalai et al., 2010</td>
</tr>
<tr>
<td><em>Rhizobium etli</em></td>
<td>Tomato</td>
<td><em>Meloidogyne incognita</em></td>
<td>35 days after nematode inoculation, the quantity of eggs per female was reduced.</td>
<td>Martinuz et al., 2013</td>
</tr>
<tr>
<td><em>Pantoea agglomerans</em>, <em>Cedecea davisea</em>, <em>Enterobacter</em> spp., <em>Pseudomonas putida</em></td>
<td>Tomato</td>
<td><em>Meloidogyne incognita</em></td>
<td>When used as a root dip and soil drench, it reduced early root penetration by second stage juvenile along with the reduction in gall formation.</td>
<td>Munif et al., 2013</td>
</tr>
<tr>
<td><strong>Bacillus cereus, Methylobacterium sp., Pseudomonas sp.</strong></td>
<td><strong>Tomato</strong></td>
<td><strong>Meloidogyne incognita</strong></td>
<td>Adult female population, egg masses, eggs per egg mass were all reduced.</td>
<td><strong>Hu et al., 2017; Vetrivelkalai, 2019</strong></td>
</tr>
<tr>
<td>---</td>
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</tr>
<tr>
<td><strong>Bacillus subtilis (Talc based)</strong></td>
<td><strong>Banana</strong></td>
<td><strong>Meloidogyne incognita, Pratylenchus coffeae, Radopholus similis, Helicotylenchus multicinctus</strong></td>
<td>Reduced nematode population</td>
<td><strong>Jonathan and Unamaheswari, 2006</strong></td>
</tr>
<tr>
<td><strong>Streptomyces sp.</strong></td>
<td><strong>Banana</strong></td>
<td><strong>Meloidogyne javanica</strong></td>
<td>J2s inhibition</td>
<td><strong>Su et al., 2017</strong></td>
</tr>
<tr>
<td><strong>Rhizobium etli</strong></td>
<td><strong>Potato</strong></td>
<td><strong>Meloidogyne incognita</strong></td>
<td>Reduced number of galls on roots.</td>
<td><strong>Hallmann et al., 2001</strong></td>
</tr>
<tr>
<td><strong>Pseudomonas fluorescens, P. putida, P. syxantha, and P. aurantiacea</strong></td>
<td><strong>Potato</strong></td>
<td><strong>Globodera rostochiensis</strong></td>
<td>Growth and multiplication of nematode population was reduced.</td>
<td><strong>Trifonova et al., 2014</strong></td>
</tr>
<tr>
<td><strong>Bacillus carotarum, B. cereus, and Pseudomonas pseudoalcaligenes</strong></td>
<td><strong>Potato</strong></td>
<td><strong>Globodera rostochiensis</strong></td>
<td>J2 mortality increased by 67-97%; Reduces the amount of cysts by 51-65% and J2s by 48-76%</td>
<td><strong>Istifadah et al., 2018</strong></td>
</tr>
</tbody>
</table>

Studies on endophytic bacteria invading plant roots and inhibiting nematode development are few. For this study, we show several instances of endophytes as biocontrol agents of phytopathogenic nematode in a range of crops and forests, despite the fact that regulatory rules may classify endophytes as bio-stimulants or soil supplements and others as biopesticides (Table 5). Endophytes are a poorly explored group of microorganisms especially bacterial endophyte which are capable of producing bioactive compounds that can be utilized to combat numerous plant pathogens. Endophytic bacteria have been sources of bioactive and volatile compounds and have proven to be useful for different group of plant pathogens. In both the pre-harvest and post-harvest stages, endophytic bacterial and actinomycete strains have been widely used as BCAs against a variety of plant diseases. Therefore, the potential colonization efficacy of endophytes is a crucial characteristic for disease management. In conclusion this review explained how plants harbor diverse endophytic bacterial strains, colonizing their parts and some of them emitting volatile organic compounds (VOCs) with antifungal and/or plant growth promotion activity. Using these natural symbionts provides a chance to increase crop production while minimizing the use of hazardous pesticides against plant diseases. Finally, given the lack of research
on endophytic diversity, there is a high likelihood of discovering novel and unique bacterial strains from unexplored wild/cultivated plants.

CONFLICT OF INTEREST
The authors declare that there is no conflict of interest

AUTHOR CONTRIBUTIONS
Conceptualization and writing of manuscript: Seweta Srivastava and Aspak; table making: Kanuri Komala Siva Katayani and Dipshikha Kaushik; reviewing and editing: Seweta Srivastava and Meenakshi Rana; Figure drawing and Grammer editing: Shubham Kumar and Raghavendra Reddy Manda; Reference setting: Manash Shukla and Vinit Pratap Singh. All authors have read and agreed to the published version of the manuscript.

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