Role of endophytes in Plant diseases resistance

Nayana K M, M. Anilkumar

¹Cell culture Lab, Research department of Botany, Union Christian collge, Aluva, Eranakulam, Pin – 683102, Kerala, India

Email: nayanakm88@gmail.com

² Cell culture Lab, Research department of Botany, Union Christian collge, Aluva, Eranakulam, Pin – 683102, Kerala, India

Email: drmakumar@gmail.com

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Abstract

For both effectiveness and commercialization, a thorough knowledge of the mechanism used by endophytes to defend the plant from diseases is still important. Even though the main purpose of the bioactive substances from endophytes is to make the host plants resistant to various diseases, endophytes present themselves as a storehouse of many bioactive metabolites such as phenolic acids, alkaloids, quinones, steroids, saponins, tannins, and terpenoids, making them a promising candidate for anticancer, antimalarial, antituberculosis, antiviral, antidiabetic, anti-inflammatory. The majority of plant diseases are caused by microorganisms, with fungi, bacteria, and viruses coming in second and third. Applying agrochemicals is currently the primary strategy for controlling plant diseases. However, this approach has hazardous effects on both people and animals. The use of biology, which includes the use of bacterial endophytes in the biocontrol of a wide range of plant pathogens, offers an alternative to chemical pest control. Endophytic bacteria are a subclass of endosymbiotic microbes, which are common in plants and establish themselves in the spaces between and within all of the sections of the plant without harming the plant. In plants, endophytes symbolise a universal and fantastical universe. It has been discovered that almost all plant species investigated by various researchers possess one or more endophytes, which defend

host plants from pathogen invasion and harmful environmental conditions. In addition to directly inhibiting pathogen growth, they can also support the growth and development of the host plants by producing a variety of metabolites. With the most recent research data, we want to clarify the contribution and important functions of endophytes and their metabolites in this field in this review, which focuses on the biological management of plant diseases. The use of endophyte metabolites to promote plant resistance is highly promising. Endophytes produce metabolites that are used to regulate plant disease.

INTRODUCTION

Agricultural pests and pathogens are one of the major threats to food security. Plant diseases caused by these pests and pathogens result in heavy crop loss. Agrochemicals are one of the major efficiently used tools in plant disease management. But overuse of chemical fertilizers adversely impacts the ecosystem and human beings, leading to environmental pollution, pathogen resistance, and imbalance of the ecological system (Hasan et al, 2013). There are beneficial microorganisms and their products, metabolites help as an eco-friendly bio-control agent (Vinale et al, 2008). To favor a sustainable ecosystem we have to reduce or avoid the overuse of chemical fertilizers and pesticides. The reason why microorganisms and their products became one of the most popular research topics is that they are the best alternative for a sustainable ecosystem (Cardoso 2019; Omomowo et al., 2019). The presence of bacterial and fungal endophytes is often beneficial for the host plant as they are present everywhere in the plant tissues without any adverse effect. These endophytes can promote tolerance to abiotic stresses, enhances growth, and play important role in modulating plant immunity and suppressing the colonization process of pathogens (Dini-Andreote. 2020). Endophytic bacteria and fungi can cover the same niche as that of fungal and bacterial phytopathogens colonizing inside the plant, so they can be used as proper biological control agents as an alternative to pesticides (Compant, et al 2013). Endophytic microbial resources are crucial in the agro-food system because of their multiple roles. Endophytes are used to improve the quality of agro-food systems which is nowadays scientific ferments trying to analyze their roles in plant-microbe interactions and plant-pathogen interaction as well (Morelli, et al 2020).

Without any immediate signs of diseases endophytes including bacteria, fungi, and actinomycetes can inhabit different parts of a plant, tissues, and intercellular space (Wilson 1995; Jia et al., 2016). There is a mutually beneficial relationship between endophytes and plants during the co-evolution time, plants produce nutrients for the endophytes, and in return, endophytes maintain the health of the plant through various mechanisms (Khare et al., 2018; Yan et al., 2019). Endophytes create a special ecological niche inside the plant that direct more positive roles and impacts on plants compared to soil microorganisms. There are research pieces of evidence showing endophytes' direct roles in plant growth promotion, reducing stress and disease resistance in host plants (khan et al., 2009; Ali et al., 2012; Ullah, et al 2019; Gao et al., 2021). Endophytes perform various mechanisms against phytopathogens. They compete for food and niche against the Phyto pathogens, also they secrete various bioactive metabolites and induce plant growth (Benhamou et al., 1996; Dubey et al., 2020; Martines et al., 2020). The bioactive metabolites produced by endophytes maintain plant health by directly or indirectly helping the host plants against several abiotic and biotic stresses. Antimicrobial compounds produced by the endophytes in plant tissues can strongly inhibit phytopathogens. The cell wall of phytopathogens can be degraded by hydrolases produced by the secretion of some endophytic bacteria and phytohormones released by endophytes have a key role in promoting plant development and stress response (Singh et al, 2017; Sturz et al., 2000). Bacillus, Burkholderia, Enterobacter, Pseudomonas, and Streptomyces are certain groups of useful endophytes that are used in the formulation against various phytopathogens (Jacob et al, 2020). Endophytes can produce different types of metabolites having various biological actions. Metabolites like alkaloids, polypeptides, polyketides, terpenoids, etc produced by endophytes have a significant role in both the agricultural and pharmaceutical industries (Dubey et al., 2020; Kusari et al., 2014; Joseph et al., 2011). These metabolites are used to serve as antibiotics, insecticidal agents, natural antioxidants, antitumor agents, and antidiabetic products (Gouda et al., 2016; Singh et al., 2021). Plant growth-promoting microbes (PGPM) are a group of microorganisms producing antimicrobials and volatile organic compounds that act as elicitors of prime systemic resistance in plants and thereby protect the host plant's health against stress (Enbe et al., 2018). We have to research more about the application of metabolites from endophytes as biological control agents in plant disease resistance for a better future to improve quality crops and yield to develop a sustainable ecosystem with a reduced negative impact on humans and the environment (Xia 2020).

I. The concept and types of endophytes

De Bary (1866) defined endophytes as "any organisms that grow in plant tissues" and can be distinguished from epiphytes that live on the surface of plants (Bary et al., 1866). Emphasizing the mutualistic relationship between plants and endophytes later Carroll (1986) proposed another definition for endophytes as organisms that inhabit the aerial parts and living tissues of plants without causing visible infection or diseases; pathogenic and mycorrhizal fungi were excluded (Carroll et al., 1986). Carroll's definition was later expanded by Petrini (1991) as all organisms that colonize within plant tissues for some of their lifecycles and not causing symptomatic infections to the host plants (Petrini et al., 1991). Endophytes are defined in different ways (Wilson 1995; Stone et al., 2000). There were controversies regarding the concepts of endophytes but majorities of the studies commonly use Petrini's definition (Xia et al., 2022). Ascomycota, Zygomycota, and Basidiomycota are the common groups of fungal endophytes. There are groups of fungal endophytes according to the life history traits and evolutionary relatedness, namely clavicipitaceous endophytes and non-clavicipitaceous endophytes. Clavicipitaceous endophytes are found colonizing within some grasses and another group is found in asymptomatic tissues of nonvascular plants, conifers, ferns, and angiosperms (Rodriguez et al., 2009; Terhonen et al., 2019). Fungal endophytic bioactive are mainly used for anti-inflammatory, antioxidant, anti-fibrosis, and antivirus drug development. Isopestacin produced from fungal endophyte Pestalotiopsis microspore has antioxidant properties (Strobel et al., 2002). Taxomyces andreanae is an important fungal endophyte from which the anticancerous drug taxol is extracted (Prakash et al., 2016). Podophyllotoxin, synthesized from Alternaria tenuissima shows excellent antitumor activity (Liang et al., 2016).

There are different species of endophytic bacteria from gram-positive bacteria to gram-negative bacteria such as *Bacillus, Agrobacterium, Brevibacterium, Pseudomonas*, etc (Sun et al., 2013). One of the recent studies by Liu et al reveals there are many endophytes in wild-variety of rice among which dominant endophytic bacterias are *Proteobacteria, Bacteroidetes*, and *Firmicutes* (Liu et al., 2021). Environment growth-related factors like plant growth stages, geographical location, climatic conditions, and the host plant directly affect the endophytic bacterial diversity in plants (Afzal et al., 2019). Endophytic actinomycetes are isolated from different plants from which particularly those found in mangroves and tropical rainforest medicinal plants (Qin et al., 2010). Other than any parts roots are the major parts where endophytic actinomycetes are found in plants. *Streptomyces* and *Micromonospora* genera are regarded as the major source of bioactive metabolites and antibiotics. For example products like Munumbicin D isolated from *Streptomyces* NRRL 30562 and coronamycin from *Streptomyces* sp.

MSU-2110 (Zin et al., 2017). Numerous species of endophytic microbes still need to be explored and identified. Many more endophytes are to be identified and to be studied (Xia et al., 2022).

II. Multi-functions of endophytes and their metabolites in Plant Disease Management.

Endophytes serve as promising biological disease controllers in plants by producing various metabolites that can directly or indirectly improve the tolerance of the host against stresses, hence making the host plant beneficial and controlling plant illnesses. An extensively studied fungal pathogen Pyricularia oryzae Cav., in rice blast may be effectively controlled by the application of endophytic microbes (Widiantini et al., 2017). The fungal endophytes of Populus alba improve the host's tolerance to the pathogen Venturia tremulae (Martínez et al., 2018). Romeralo et al., isolated several endophytes and proved their ability to guard Aleppo pine (Pinus halepensis) in against Gremmeniella abietina (Romeralo et al., 2015; Romeralo et al., 2015). The plant European ash (Fraxinus excelsior) affected the infection and colonization by the pathogen Hymenoscyphus fraxineus can be affected with help of endophytic microbes through toxin secretion and /or activation of the host defense reaction (Schlegel et al., 2016). Endophytes are a diverse group of bacteria that asymptomatically colonize inside plant tissues. According to numerous studies, endophytes directly produce bioactive secondary metabolites that protect their host plants against herbivores and pathogenic microorganisms, improving the fitness of their host plants. Additionally, it is becoming more and more clear that endophytes are able to biosynthesize medicinally significant "phytochemicals," which is exclusively produced by their host plants (Ancheeva et al., 2020).

Researchers are increasingly inquisitive about this area, and the biocontrol roles of endophytes and their metabolites against plant diseases have been mentioned and said in the literature every so often. Important mechanisms of endophytes in plants are discussed below they are, (1) competing with pathogens for niche and nutrition (2) Producing antimicrobial compounds, (3) secreting lytic enzymes, (4) inducing systemic resistance in host plants, and (5) producing plant hormones and plant growth-promoting regulators. There are nevertheless more problems to be outline of the main capabilities, future potentialities, solved. an and challenges in using endophytes and their metabolites in disease management (Xia et al., 2022).

2.1 Competition with Pathogens for Niche and Nutrition

One of the fundamental characteristics of endophytes is colonization in plant tissues (Latz et al., 2018). Similar to how pathogenic bacteria attack plants, endophytes often enter the host plant as thalli or spores through epidermal penetration or stomata entry. These useful "micro-guests" may selectively occupy the invasion sites of pathogens in plants and utilize nutrients, thereby limiting pathogen invasion (Rodriguez et al., 2009). Using the bacterial endophyte Bacillus subtilis (Ehrenberg) Cohn, Bacon et al. (Bacon et al., 2001) created a control system that showed significant potential for lowering Fusarium moniliforme invasion and mycotoxin accumulation. Because these two bacteria shared a similar biological niche in maize (Bacon et al., 2001). Furthermore, endophytes and pathogenic microorganisms compete with one another for nutrients, which leads to the lowering of growth rates of pathogens. A strong indicator of nutrient competition is the release of high-affinity iron molecules such as siderophores and peptides. Some Pseudomonas species adopted this tactic to biocontrol the Fusarium oxysporum f. sp. dianthi (Fod)-caused carnation fusarium wilt (Duijff et al., 1993). When beneficial microbes of host plants are inhabiting the same ecological niche as that of pathogens they are capable of competing for nutrients and

resources(Xia et al., 2022). It was demonstrated that competition for iron was the cause of the rice endophyte Streptomyces sporocinereus OsiSh-2's significant antagonistic activity toward Magnaporthe oryzae (Zeng et al., 2018).

A useful direction for the use of endophytes in the prevention of plant disease is the competition with harmful microbes for niche and nutrition or niche exclusion (Liarzi et al., 2013). Even so, there can be limits, and it might not function if there are numerous infections present, as was clearly supported by the study of Lahlali (Lahlali et al., 2013). This issue can be resolved by inoculating host plants with endophytes in advance and in large quantities using a variety of techniques, such as seed coating, soil drenching, root dipping, and foliar spray application, and combining suitable endophytes or microbes rather than using just one type (O'Callaghan et al., 2016; Griffin 2014). Table 1 provides other illustrations of endophytes utilized in biological plant disease prevention.

2.2 Induction of Plant Disease Resistance

Induced systemic resistance (ISR) and systemic acquired resistance (SAR) are the two critical plant responses to attacks of parasites or pathogens. Induced systemic resistance (ISR) is generally dependent on jasmonic acid (JA) and ethylene (ET) signaling and systemic acquired resistance (SAR) is commonly dependent on salicylic acid (SA) signaling. While the SA system mediates resistance to biotrophic pathogens, the JA/ET pathway primarily regulates resistance to necrotrophic pathogens (Robert-Seilaniantz et al., 2011; Ghorbel et al., 2021; Van der Ent et al., 2009). ISR mediated by some endophytes may be dependent on the SA pathway rather than the JA or ET pathways, as stated by Kloepper and Ryu, and the signaling crosstalk between these pathways suggests that ISR and SAR are not entirely distinct from one another (Kloepper et al., 2006). The plant defence system also involves other plant hormones such as methyl jasmonate (MeJA) and brassinosteroids (BRs) (Robert-Seilaniantz et al., 2011; Soler et al., 2013).

Endophytes control plant diseases by promoting plant resistance, and this has gained a lot of interest and attention. Compared to uninfected plants, endophyte-inoculated plants typically have better resistance to diseases. Pathogens are infected in various sections of the host using endophytes in a specific area of the plant significantly lowers the disease index. Through the SA and JA signalling networks, the fungal endophytes Penicillium citrinum LWL4 and Aspergillus terreus LWL5 of the sunflower family (*Helianthus annuus* L.) massively increased host resistance to stem rot brought on by Sclerotium rolfsii (Waqas et al., 2015). Bacterial endophyte *Azospirillum* sp. B510 endophye isolated from rice (*Oryza sativa* cv. Nipponbare) can induce host systemic resistance to bacterial blight and rice blast disease (Kusajima et al., 2018). Similar to this, Bacillus's strain YC7010T, which was isolated from rice, was created as a new BCA against rice bacterial blight (Chung et al., 2015).

Endophytes play a critical role in the prevention and management of plant diseases because they can upregulate the expression of defense-related genes like pathogenesis-related genes like PR1, PR2, and PR3, phenylpropanoid pathway genes like chalcone synthase CHS and phenylalanine ammonia-lyase gene PAL involved in phytoalexin biosynthesis, etc. Also, they alter plant cell walls (callose deposition, stomata closure, etc) and an increased level of defense-related antioxidant enzymes helps the plants to be protected from diseases (Howlader et al., 2020; Kavroulakis et al., 2007; Boava et al., 2011). When tomato plants are treated with two endophytic strains observed high levels of polyphenol oxidase (PPO), peroxidase, and phenylalanine ammonia-lyase (PAL) were found in

these plants. These compounds activated systemic responses in the host plants against pathogens (Akram et al., 2011). ZhiNengCong (ZNC), extracted from endophytic fungi *Paecilomyces Variotii* SJ1, has been proven to be an ultrahigh activity immune inducer in tobacco in a recent study (Peng et al., 2020).

More metabolites from endophytes are yet to be exploited as elicitors, and these bioactive components could provide a promising alternative resource for plant disease management. Attention has already been given to the secondary metabolites of certain non-endophytic microbes, since they have been confirmed as elicitors of plant resistance. For example, *Bacillus amyloliquefaciens* SQR9 isolated from cucumber rhizosphere produced secondary metabolites, such as fengycin, surfactin, and 2,3-butanediol, and could elicit systemic resistance in *Arabidopsis* through different signaling pathways (Wu et al., 2018). C15 surfactin A, the main secondary metabolite of Bacillus velezensis HN-2 isolated from soil has excellent antibacterial action against Xanthomonas oryzae pv. Oryzae (Xoo), in addition successfully started rice resistance to pathogens (Jin et al., 2020). Another notable research world example is the synthesis of the glycoprotein GP-1 by the soil-isolated Streptomyces sp. ZX01, which led to the early induction of plant immune responses in tobacco (Han et al., 2020). These results are crucial for the use of endophyte metabolites in promoting plant resistance (Xia et al., 2022).

2.3 Antimicrobial Properties of Metabolites from Endophytes

It is well known that endophytes have the ability to produce a significant number of secondary metabolites with antifungal and antibacterial characteristics that can directly reduce infections (Gunatilaka 2006). The discovery that an endophytic fungus from the Pacific yew, Taxus brevifolia, could produce the same chemical as its host. This study stimulated scientists to look for biologically active compounds in plant endophytes (Stierle et al., 1993). Lasiodiplodia rubropurpurea and L. theobromae's growth was suppressed by the lipopeptide antibacterial components found in the fermentation broth of the Chinese medicinal Ginkgo biloba endophytic bacterium Bacillus amyloliquefaciens CGMCC 5569 (Yuan et al., 2012). The findings of Mousa et al., showed because of the production of antifungal chemicals by an endophytic fungus, WF4, isolated from the finger millet crop, resulted in antagonist action toward F. graminearum (Mousa, W.K., et al 2015). Endophytic actinomycete strain LGMB491 (closely related to Aeromicrobium ponti) isolated from Vochysia divergens, a medicinal plant in Pantanal, Brazil produced four major compounds that have antibacterial action against Staphylococcus aureus (Gos et al., 2017). The most widespread producers of antimicrobial compounds among Gram-positive bacteria were identified as Endophytic Bacillus and Streptomyces, which have been isolated from various environments (Ek-Ramos et al., 2019). Table 1 lists the bioactive metabolites produced by endophytes create.

2.4 Lytic Enzyme Activity of metabolites from Endophytes

The majority of bacteria produce lytic enzymes that hydrolyze polymers (Gao et al., 2010). A total of 1,350 substances, including cellulose, hemicellulose, proteins, DNA, and chitin, can be secreted (Tripathi et al., 2008). Endophytes must produce a significant number of enzymes that support the hydrolysis of the plant cell wall in order to colonize the surface of plants. These enzymes assist in the indirect reduction of phytopathogens as well as the breakdown of fungal cell walls. There are many different kinds of enzymes, some of which include 1, 3-glucanases, chitinases, cellulases, and hemicellulases. When 1, 3-glucanase genes in a strain of Lysobacter enzymogenes were subjected to mutation, the biocontrol ability against Pythium-caused sugar beet damping-off

disease and tall fescue leafspot disease was lowered Gao et al., 2010). Streptomyces produces lytic enzymes that are quite effective at combating cocoa witches broom disease (Macagnan et al., 2008). Enzymes might not be the only thing that can operate as an antagonist, but when paired with other processes, they can strengthen antagonistic activity. It is reported that Pectinase also helps to reduce pathogenesis (Babalola, 2007).

Endophytes are mainly extracted from the host plant's seeds, roots, stems, leaves, or other tissues. Endophytes can produce different types of enzymes such as Chitinases, cellulases, β -1, 3- glucanases, pectinases, and glucanases (Gao et al., 2010; Ben 2019; Rajulu et al., 2010). These enzymes have the power to degrade the cell wall of pathogens or prevent spore germination. This is a powerful method for suppressing phytopathogens and providing the host with biotic stress resistance. Forty-five endophytic bacteria were isolated from the Ammodendron bifolium plant in the study of Zhu and She. They observed 40% of the endophytic bacteria isolated from the Ammodendron bifolium plant had significant activities for amylase and cellulose production, 13.3% of which exhibited protease activity and 53.3% of them showed lipase activity, respectively (Zhu et al., 2018). Pathogen Plectosporium tabacinum is controlled by degrading the hyphae, inducing plasmolysis, and lysing cell walls by an endophytic isolate of Actinoplanes missouriensis (El-Tarabily 2003). Numerous lytic enzymes generated by Streptomyces served as antagonistic agents against M. perniciosa in cocoa Witches' broom disease (Macagnan et al., 2008). Table 1 lists more instances of endophytic microorganisms that have been shown to produce lytic enzymes.

To increase host disease resistance in plants, the chitinase genes of several biocontrol bacteria have been cloned and introduced into host plants (Cook 1993). In order to facilitate colonisation in host plants, endophyte Bacillus cereus XB177R from the eggplant (*Solanum melongena* L.) producing endoglucanase and pectinase enzymes (Achari et al., 2018). Because of their capacity to produce metabolites with lytic enzyme activity, many endophytes have been isolated and identified for increasing host resistance against phytopathogens. However, it is still unknown whether the lytic enzymes function as elicitors of plant systemic resistance in controlling pathogens. When these enzymes are integrated with other mechanisms, they typically exhibit substantially stronger antagonistic actions. Endophytic metabolites are good alternative sources for many extracellular hydrolytic enzymes and microbial production of enzymes, and microbial synthesis of enzymes is an attractive promise for developing sustainable agricultural systems (Khan et al., 2017).

2.5 Promotion of Plant Growth by Metabolites from Endophytes

Enhancing plant growth is one of the methods used by plants in response to pathogen attacks to increase their resistance to various stresses plant (Kuldau et al., 2008). Endophytes and their metabolites are well known for promoting plant growth. On the one hand, endophytes significantly increase plants' ability to absorb and use nutrients including nitrogen (N), phosphorus (P), and potassium (K). Particularly, endophytic diazotrophic bacteria associated with gramineous plants convert atmospheric nitrogen into ammonia by nitrogen fixation, which promotes host growth and disease resistance. According to studies, Paenibacillus polymyxa P2b-2R from lodgepole pine seedlings helped corn seedlings obtain 30% of their foliar nitrogen from the atmosphere and grow 52% longer (Puri et al., 2016). Endophytes, on the other hand, have also been found to stimulate the growth of plants by secreting hormones like auxin, ethylene, gibberellin, and cytokinin. The growth and development of host plants can be regulated and facilitated by the secondary metabolites released by endophytic bacterias

such as Staphylococcus, Azotobacter, and Azospirillum (Hallmann et al., 2016). From tissue samples of 15 different tea cultivars, Shan et al. (Shan et al., 2018) extracted 46 actinomycetes, the majority of which were able to generate IAA. Different plants have been discovered to have more growth-promoting endophytes (Eid et al., 2021; Krause et al., 2006; Tian et al., 2017; Borah et al., 2020). Therefore, it is suggested that endophytes' support of plant growth can indirectly shield host plants from diseases (Xia et al., 2022).

Growth regulators and phytohormones are generally chemically manufactured or derived from plants in the agricultural sectors. Microbial fermentation has been regarded as a more practical and effective strategy to boost productivity and reduce to manufacturing expenses plant metabolites. Few products have been mass produced commercially even after several publications demonstrating success in the manufacture of plant metabolites by endophytes in vitro. The question of whether host plants or endophytes produce bioactive metabolites must also be considered. Plant-endophyte interaction processes are not fully understood. The native plant-endophyte network is likewise disturbed when endophytes are isolated and cultivated in vitro apart from the host. Further research is required to clarify the proportional contributions of the "host plants" and the "micro-guests" in the synthesis of particular metabolites. (Xia et al., 2022).

III. Why do endophytes help plants?

The endophyte-directed mechanisms of plant growth promotion are not fully understood (Hardoim et al., 2008). Plant growth is promoted by endophytes either directly or indirectly. It is assumed that endophytes may retain their characteristics inside the plant because they begin their journey as rhizosphere bacteria. Because the majority of endophytes can be cultivated and can live outside of hosts in the rhizosphere, their processes of benefit appear connected to rhizosphere bacteria (Yadav et al., 2017). Let's discuss direct mechanism (endophytes-pathogens interactions) and indirect mechanism (enhanced plant defense) (Arnold et al., 2003).

3.1 Directly Beneficial Mechanism

By supplying antibacterial metabolites, insecticidal byproducts, iron chelators, phosphate solubilizing chemicals, and nitrogen-fixing abilities, endophytes can significantly assist plants (Yadav et al., 2017). Additionally, endophytes have an impact on plant growth by synthesizing phytohormones, and siderophores, generating systemic tolerance by the formation of 1-aminocyclopropane-1-carboxylase deaminase and inducing systemic resistance and antagonism. Additionally, a number of sulfur-oxidizing endophytes are known to convert elemental sulfur into sulfate, which is then utilized by plants (Knoth 2014). Furthermore, endophytes are abundant sources of phytochemicals that prevent plant diseases from spreading. Endophytes play a role in the formation of plant metabolites and are a strong source of physiologically active secondary metabolites. There are mainly two types of mechanisms Direct and Indirect mechanisms discussed below benefit the host plant (Chen 2011; Benhamou et al., 1998; Brader 2014; Schulz et al., 2002)

Studies on endophytes have found they can improve the host's ability to fight against diseases and lower the damage caused by harmful pathogens (Ganley et al., 2008; Mejia et al., 2008). These researchers used strategies such as comparing the rate of survival of plants inoculated with controls or using in vitro direct plate antagonistic reaction to pathogens. However new methods employed by endophytes to lessen the impacts of infections have been described in certain research, and endophytes, pathogens, and plant regulators are still poorly understood at

this time (Ganley et al., 2008). Endophytes directly produce antibiotics that assist in inhibiting infections in the direct mechanism. Direct endophyte-pathogen interactions are complicated and prone to species-specific antagonism (Arnold et al., 2003). Given below are few examples of direct mechanisms used by endophytes.

Phytohormones production: The mechanism of phytohormone production by endophytes is widely accepted for promoting plant development and morphological and structural changes in the plant. Endophytes are used in agricultural systems for sustainable agriculture because of these advantages (Yadav et al., 2017). The process by which endophytes in host plants produce phytohormones is similar to how rhizobacteria stimulate plant growth (Sturz et al., 2000). By boosting their growth through the formation of indole acetic acid, gibberellic acid, ethylene, and auxins, they promote the growth of non-legumes (Yadav et al., 2017). Endophytes have succeeded in the field of agricultural sustainability as a result of this quality (Sturz et al., 2000). The technique utilised by rhizobacteria to promote plant growth is similar to the mechanism adopted by endophytes in the generation of phytohormones in the host plant. They aid in the growth promotion and protection of non-leguminous plants by secreting gibberellic acid (Khan et al., 2014), auxins (Dutta et al., 2014), indole acetic acid (Khan et al., 2014; Patel 2014), and ethylene (Babalola 2010; Kang et al., 2012).

Phytohormone indole acetic acid (IAA) stimulates plant cell division, differentiation, and extension; seed and tuber germination; root and xylem development; lateral initiation; rate of vegetative growth; adventitious root formation; along with pigment and metabolite biosynthesis; responses to gravity, light, and fluorescence; photosynthesis; and tolerance to extreme temperatures (Gao et al., 2010). The physiological processes mentioned above can occasionally be slowed down by IAA released by bacteria that promote plant growth by altering the amount of auxin secreted by the plant. Additionally, IAA made by endophytic bacteria has the power to increase the surface area of roots, allowing plants to more easily acquire nutrients from the soil. IAA synthesis also boosts the size of bacterial cell walls and exudate secretion while delivering additional nutrients to encourage the growth of other beneficial bacteria in the rhizosphere. Thus IAA released by endophytic bacteria acknowledges as the the primary effector molecule in phytostimulation, pathogenesis, and plant-microbe interaction (Gao &Tao 2012). Number of studies have shown that endophytic actinomycetes generate substances that promote plant growth, such as IAA, which is known to enhance the formation and lengthening of adventitious roots in plants (de Oliveira et al., 2010; Shimizu 2011).

Nitrogen Fixation: The most limiting nutritional factor for plant growth is the availability of nitrogen. Because plants are unable to reduce atmospheric N, they need a constant external supply of N. The potential for biological N fixation as a solution for chemical fertilizers is significant. Agriculture may benefit from a number of symbiotic prokaryotic endophytes that can fix atmospheric nitrogen. Nitrogen can be delivered to plants directly by diazotrophic endophytes. Free-living, nitrogen-fixing endophytic bacteria have been the subject of study for the past few seasons (Yadav et al 2017). The most well-known and researched legume-Rhizobium symbiosis is still the focus of international research that aims to increase the efficiency of N2 fixation through plant and genome manipulation (Reis 2004).

Production of siderophores: Some endophytes create siderophores, which are tiny molecules that act as iron chelating agents to plants and deprive pathogens of iron (Compant S,2005). Catacholate, hydroxymate, and/or

phenolate kinds are among the siderophores made by endophytes that have biocontrolling qualities (Rajkumar et al.,2010). Moreover, siderophores specifically support iron defficideficient plants with in fixing nitrogen since diazotrophs need Fe++ and Mo components for the synthesis and operation of nitrogenase (Kraepiel 2009). There is a great deal of research that validates endophytes' capacity to eradicate insects (Azevedo et al., 2000). Some endophytes thicken the endodermal cell wall to prevent pests from penetrating the stele (Gao et al., 2010). Others produce secondary metabolites that destroy insects. Although some harmful metabolites can be linked to endophytes such as pyrrolizidine, alkaloids, pyrrolopyrazine alkaloid, peramine ergot alkaloid, and ergovaline (Wilkinson et al., 2000). In the case of bacteria that promote plant growth, Fe2+ is converted into Fe3+ siderophore complex in the bacterial membrane, which is then brought into the cell by endophytes through a gating mechanism (Gao et al., 2010). When siderophores bind to the metal surface, the concentration of soluble metals rises (Rajkumar et al., 2010). After the level of heavy metal contamination is reduced, plants use a variety of processes to absorb iron from bacterial siderophores, such as ligand exchange or the direct absorption of siderophore-Fe complexes with the help of iron chelates (Schmidt, 1999). Pseudomonas strain GRP3 a siderophore-generating endophyte was tested on the Vigna radiate for iron nutrition. After 45 days, the plants showed a decrease in iron and chlorotic symptoms and an increase in the content of chlorophyll a and chlorophyll b when the plant was inoculated with strain GRP3 when compared to the control (Sharma et al., 2003). Few endophytic actinomyces have been found to produce siderophores, including Streptomyces sp. GMKU 3100, Streptomyces sp. mhcr0816, Streptomyces sp. UKCW/B, and Nocardia sp (Singh & Dubey 2018). Similar to this, S. acidiscabies E13 was also observed as an excellent producer of siderophore that promotes Vigna unguiculata growth when nickel stress is present (Sessitsch et al., 2013).

1-Aminocyclopropane-1-Carboxylate (ACC) Utlization: Ethylene is often a crucial metabolite for the healthy growth and development of plants (Khalid et al., 2006). Almost all plants emit this crucial hormone, which is recognized for promoting plant growth. It is influenced by many abiotic and biotic processes in the soil, which enhance physiological changes in most plants. Extreme environmental factors like disease, drought, salinity, and heavy metals raise the level of ethylene, which has negative impacts on plant growth and can change cellular processes and cause defoliation, which reduces agricultural output (Bhattacharyya & Jha 2012). In genera including *Achromobacter, Agrobacterium, Acinetobacter, Bacillus, Enterobacter, Pseudomonas, Serratia, Ralstonia, Rhizobium, Alcaligenes, Burkholderia*, etc., numerous endophytic bacterial species that may manufacture ACC deaminase (Kang et al., 2012). The ethylene precursor of ACC is largely trapped by bacterial endophytes, which convert it to ammonia and 2-oxobutanoate (Arshad et al., 2007). According to Lugtenberg and Kamilova, plants that can produce ACC deaminase can withstand some stresses like radiation, heavy metals, flooding resistance due to stress from polyaromatic hydrocarbons, high light intensity, wounds, high salt concentration, insect predation, drought, and extreme temperature (Lugten B and Kamilova, 2009).

Competition with pathogen: Endophytes exploit competition as a potent barrier against pathogen colonization of the host tissue (Martinuz et al., 2012). Endophytes can colonise within plant tissues either systemically or locally (Latz et al., 2018). They act by colonizing, hiding nutrients, and occupying space where pathogens can carry out their activities (Rodriguez et al., 2009). Mohandoss and Suryanarayanan (2009) found that the destruction of endophytes in mango leaves by the use of fungicides in their treatment permits other fungi, particularly pathogenic fungi, to occupy the niche. Most endophytes have a mechanism for competition, although this mechanism

generally operates in connection with other mechanisms rather than operating on its own. Endophytes frequently use localised control strategies, thus they will need to deliberately colonise the areas of the host where pathogens are most likely to attack. Heteroconium chaetospira endophyte colonization of the oilseed rape root was unsuccessful in preventing clubroot symptoms (Lahlali et al., 2014). The outcome thus highlights the potential drawbacks of competition as a biocontrol strategy since it may become inactive in situations when there are a lot of pathogenic bacteria present. Competition is one method by which disease is suppressed in plants. Phytophthora sp. symptoms were successfully decreased when treated with a foliar treatment with mixes of endophytes from cacao tree leaves. However, it was shown that some of the strains also produced additional active metabolites, suggesting that competition may not be the only mechanism employed to manage the disease (Arnold et al., 2003).

Antibiotics by endophytes

Endophytes have been found to generate secondary metabolites, of which some have been shown to have antibacterial and antifungal effects, preventing the growth of phytopathogenic microbes (Gunatilaka, 2006). There are different kinds of stustudiesdy being carried out to identify endophyte metabolites that might have a commercial purpose. Numerous phytopathogens have been researcpreventhed because of their potential to prevent various phytopathogens by bioactive substances (Suryanarayanan, 2013; Daguerre et al., 2016). Several endophyte metabolites have been found to have antimicrobial effects; some of them including flavonoids, peptides, quinones, alkaloids, phenols, steroids, terpenoids, and polyketides (Mousa and Raizada, 2013; Lugtenberg et al., 2016). The presence of different microbial species in a single plant encourages the secretion of metabolites by endophytes or the host to prevent the establishment of dangerous microorganisms (Kusari et al., 2012). In some cases, the host plant and the endophytes employ alternate paths to increase the synthesis of metabolites; in other cases, they use induced metabolism to help metabolize one another's products (Kusari et al., 2012; Ludwig-Müller, 2015). Later from many studies concluded that many endophytic strains cannot independently generate the compounds (Heinig et al., 2013). Phomopis cassia, which is an endophyte isolated from the Cassia spectabilis. This endophyte can produce five derivatives which are effective antifungal metabolite against Cladosporium cladsporioides and Cladosporium sphaerospermum and shows similarity with compunds 3,11,12-trihydroxycadalene and cadinane sesquiterpenes (Silva et al., 2006). Alkaloids have been shown to be highly effective at preventing the growth of germs. For example, altersetin, a new alkaloid that was isolated from the endophyte Alternaria spp., shown a powerful antibacterial action against numerous pathogenic gram-positive bacteria (Hellwig et al., 2002). A volatile oil is another metabolite that demonstrated antibiosis. Likewise, Artemisia annua fungal endophytes isolated in vitro can inhibit the growth of the majority of phytopathogenic organisms by producing antifungal substances such n-butanol and ethylacetate (Liu et al., 2001). The effectiveness of the anti-fungal protein generated by Epichlo festucae in suppressing Sclerotinia homoeocarpa in Festuca rubra was studied (Tian et al., 2017). The outcome highlighted this characteristic of fescues as one of its special qualities. Mechanism of plant defence used by Paraconiothyrium strain SSM001 associated with the generation of taxol from yew tree (Taxus spp.) against harmful wood-decaying fungus (Rafiqi et al. 2013;Soliman et al. 2015) Table 1 summarises relevant studies on the antibacterial abilities of endophytes.

When it comes to preventing the spread of above-ground fungal infections, the emission of volatile chemicals by bacteria associated with plants has come to the fore in some instances (Köberl et al., 2013; Bailly and Weisskopf, 2017; Garbeva and Weisskopf, 2020). Bacillus subtilis and Bacillus cereus strains were found in the grapevine

leaf microbiome and it is thought that these strains are able to limit the growth of Phytophthora infestans by releasing volatile chemicals such as pyrazines, chalconoids, and tryptophan derivatives. Endophytes isolated from Salvia abrotanoides stimulate the synthesis of the bioactive diterpenoid cryptotanshinone in plants. At the same producing the same molecule independent of the host. Findings reveal that endophytes can hijack host's metabolic setup and create an interesting basis for the agriculture and pharmaceutical industry by utilizing medicinal plant's ability to produce bioactive metabolites (Morelli M et al.,2020).

3.3 Indirect Mechanisms

Plants are able to adapt to a variety of harmful biotic and environmental challenges, such as pathogenesis, hypersaline conditions, cold, and drought. Endophytes provide indirect processes that facilitate plants in overcoming such challenges. The mechanism of induced systemic resistance (ISR) states some of the endophytes that may have descended from plant infections are capable of inducing similar plant defence like pathogens. Below, some of the recognised mechanisms are discussed (Yadav A and Yadav K.2017). In order to survive in harsh environments like drought, salt stress, and cold, plants use a variety of strategies. The formation of phytoalexins, cellular necrosis, and the hypersensitive response are a few of the quickly apparent biochemical and morphological alterations that have been reported. Innate resistance generated for pathogen resistance in long-term evolution includes both non-specific (generic) and particular resistance.One or a few infections can be prevented by those with specific resistance, whereas many pathogens can be prevented by those with non-specific resistance, whereas many pathogens can be prevented by those with non-specific resistance. Endophytes produce secondary metabolites and have improved resistance, which strengthen the plant's defence system (Fadiji AE, Babalola OO.2020).

Induction of Plant resistance

Numerous research have focused on the approach that plants react to attacks from parasites and diseases using various levels. The two resistance patterns that have garnered the most interest from researchers are induced systemic resistance (ISR) and systemic acquired resistance (SAR). ISR is controlled by ethylene or jasmonic acid, which cannot be connected to the accumulation of pathogenesis-related (PR) proteins and is generated by some non-pathogenic rhizobacteria. Salicylic acid mediates SAR, which is brought on by infections from pathogens and connected to the development of PR proteins (Tripathi et al., 2008). Invading cells are directly lysed by these enzymes, such as 1, 3-glucanases and chitinases produced by PR proteins which also strengthen cell wall borders and increase resistance to infection and cell death (Gao et al., 2010). ISR generated by endophytes has also been linked to an increased expression of genes involved in pathogenesis. Fusarium solani, a significant endophyte found in tomato roots, induces ISR against Septoria lycopersici, the pathogen responsible for tomato foliar infections, and activates PR genes, PR7, and PR5 activity in the roots (Kavroulakis et al., 2007). According to Redman et al. (1999), inoculating Cucumis sativus and Citrullus lanatus with a non-pathogenic mutant strain of Colletotrichum magna resulted in the production of large amounts of peroxidase, lignin deposition, and phenylalanine ammonialyase, all of which assist in defending the plant against disease caused by Fusarium oxysporum and Colletotrichum orbiculare. Neotyphodium lolii reduced lesions on leaves with their ability to attack four different pathogens resulted. This endophytes increased peroxidase and superoxide dismutase activities of host plant (Tian et al., 2008).

Plant secondary metabolite stimulation

Secondary metabolites from plants are that have limited purposes during the plant's life cycle but are crucial for the adaptation of the plant to various environments (Bourgaud et al., 2001). Phytoalexins, a class of lowmolecular-weight antibacterial molecules, stand out among all the secondary compounds produced by plants. It contains a variety of ingredients, including flavonoids and terpenoids among many others. In response to a fungus attack Orchis morio and Loroglossum hircinum were the first to produce phytoalexins. However, results of subsequent studies revealed that phytoalexins can now be produced through some abiotic stress factors such as heavy metal ions, salt stress, and UV light (Gao et al., 2010). Studies have focused on how pathogens cause the development of phytoalexins (Pedras et al., 2008). A relatively unexplored area of study is the formation of plant secondary metabolism controlled by endophytes. The elicitors of Fusarium E5 were found to be able to increase the production of triterpene and dipertene in E. pekinensis cell suspensions. I n Taxus cuspidate culture suspensions endophyte culture supernatants led to higher paclitaxel synthesis as compared to the control (Li Y.-C., Tao W.-Y. 2009). Co-culturing with elicitor endophytes is thought to be a viable strategy for enhancing plant resistance and secondary metabolite production in plants. Endophytic colonisation caused plant cells to produce hydrolase, which inhibited the growth of fungi and allowed endophytes to function as elicitors by producing hydroxylation. Glycoprotein, polysaccharides, and lipopolysaccharides are examples of elicitors that activate plant defence mechanisms and boost the secretion of secondary metabolites from plants, thereby reducing pathogen attack. There is, unfortunately, little data on how endophytes persist in the host plant when significant amounts of secondary metabolites are produced (Gao et al., 2010)

Promotion of Plant growth and Physiology

By taking control of the plant's physiology, endophytes can often aid the host plant's defensive mechanism against plant pathogenic bacteria (Gimenez et al., 2007). When plant grows, it accumulates strength and tolerance to various biotic and abiotic stimuli; this is one of the techniques the plant employs to defend itself against diseases (Kuldau and Bacon, 2008). S tudies have demonstrated that plants inoculated with endophytes experienced an increase in growth, drought resistance (Gao et al., 2010), and soil tolerance (Malinowski et al., 2004). Several chemicals can help plants grow, and one endophyte, Colletotrichum sp., isolated from A. annua, makes an ingredient called indole acetic acid (IAA), which aids in controlling plant physiology. According to studies, Fusarium sp. E5 extracts produced auxin. The release of phytohormones can be thought of as another mechanism used by endophytes (Dai et al., 2008). Therefore, we can assume that endophytic stimulation of plant development will indirectly protect the plant from infections.

Hyper parasites and Predation

Another method by which endophytes defend their host ecologically is through hyperparasites. This technique involves endophytes attacking known diseases or their propagules directly (Tripathi et al., 2008). Endophytic fungi trap the pathogens by twisting and penetrating their hyphae and by producing lyase, which breaks down the pathogen's cell wall. For instance, the well-known plant pathogen Rhizoctonia solani's hyphae were capable of being captured and penetrated by Trichoderma sp. This discovery was connected to biocontrol efforts (Grosch et al., 2006). The reduction of plant pathogens through microbial predation is another technique. The majority of

endophytes show their predatory traits in nutrient-poor environments. Trichoderma sp., for instance, produces a number of enzymes that directly destroy the cell wall of fungal infections.

IV. A cross talk with plants Defense pathways

One of the most difficult findings from the study on the use of endophytes, and particularly of plant growthpromoting bacteria (PGPB), is that some strains can activate plant defence mechanisms (Ma, 2017). PGPBinduced systemic resistance (ISR) connected to the up-regulation of genes involved in the pathways of ethylene and jasmonic acid (Pangesti et al., 2016). ISR is frequently accompanied by biochemical reactions including an increase in the production of reactive oxygen species (ROS) and phenolic compounds as well as morphological changes like the deposition of callose and lignin in endophyte-colonized tissues (Benhamou, 1996; Constantin et al., 2019). Certain Paenibacillus strains (i.e. PB2), when used to control Mycosphaerella graminicola, induced upregulation of genes, such as pathogenesis-related proteins (PR1) and chitinases, typically considered as markers of SAR (systemic acquired resistance) (Van Loon L et al., 1998; Samain E et al., 2017). This study demonstrated the complicated distinction between ISR and the pathogen-induced systemic acquired resistance (SAR). The distinctive induced resistance that gives wheat a long-lasting resistance is fascinating since it may be a more common phenomena that has been seen in other PGPB taxa, such as Bacillus and Pseudomonas (Park and Kloepper, 2000; Trotel-Aziz et al., 2008; Samain et al., 2017). There is a need to address its method of action, which appears to be strongly influenced by the pathogen strain, the plant growth period, and its genotype (Morelli M et al, 2020).

In fact, a crucial component of management techniques is the length of the resistance effect to pathogen-induced biotic stresses that endophytes may activate.Plants primed with Rhizobium etli appear to develop a transgenerational defence memory, which is important in showcasing the skill of R. etli, a common bean symbiont, to activate strong defence responses against the pathogen Pseudomonas syringae pv. Phaseolicola (Diaz-Valle et al.,2019). According to previous research, transcription factors previously implicated in the stimulation of the PR gene expression and independent of the ethylene signalling pathway appear to be responsible for the persistence of this ability in the F1 generation (Huang et al., 2016). Associative symbioses in various helpful bacteria have been extensively researched recently (Ahemad and Kibret, 2014; Coutinho et al., 2015). Only a small number of studies have examined their effects on the transcriptional response of plants. Differences in transcriptional regulations induced by two closely related PGPB with different phylogenetic and ecological backgrounds (King et al., 2019) relying on an established model of symbiosis made up of rice and Burkholderia sensu lato (s.l.) (Cottyn et al., 2001; Mannaa et al., 2019). The jasmonic acid signalling pathway was differentially expressed by each strain, and intriguingly, these variations have been linked to various colonisation methods (King et al., 2019). In plants exposed to PGPB, biochemical changes are frequently accompanied by anatomical modifications. According to research Gluconacetobacter diazotrophicus can cause a number of structural alterations in infected Arabidopsis thaliana seedlings by depositing callose (Rodriguez et al.,). Studies revealed that sclerosis in the root, stem, and leaf tissues strengthen the plant's cell wall and helps it resist colonisation by the wilt diseasecausing Ralstonia solanacearum (Morelli M et al., 2020).

Conclusions

Research on plant-microbe interactions has greatly evolved. Endophytes are thought of as naturally occurring agents that decrease plant diseases because they colonise plant tissues. Their success is largely credited to the creation of a wide variety of metabolites. These metabolites are a prospective resource collection with a wide range of biological functions, and they are becoming more and more significant in several sectors. We discussed the numerous roles that endophytes and their metabolites play in the biocontrol of plants in this article. We outlined the significance of these bioresources for future agricultural development and presented substantial data and recent examples. As we have mentioned, one of the strategies by which endophytes defend plants is by inducing plant resistance. Additionally, a number of metabolites from non-endophytic bacteria have been recognised as plant resistance elicitors. The findings on the induction of plant resistance are comparatively rare, and the present study on endophyte metabolites in biological control is mostly focused on antibacterial, hydrolase activities, and growthpromoting value. In managing plant diseases, biological control agents are dependable, eco-friendly, and essential for sustainable agriculture. In comparison to chemical pesticides and traditional bioformulations, using endophytes and their metabolites for plant protection has many benefits. Instead of just having poisonous qualities, the metabolites of plant endophytes have a variety of bioactive components that improve the host's defence against infections. Therefore, one of the most promising methods for developing green pesticides in the future is to use one or more naturally occurring active compounds as the lead chemical. The following characteristics must meet by those endophytes present for agricultural use. They must not cause plant disease, they must be able to spread inside plant parts, they must be cultivable; and they must obligately colonise plant parts with species specificity. To increase agricultural productivity, it is imperative to find innovative entophyte strains with as many desirable traits as possible. The necessity for host-specific research will soon be replaced by newer methods of exploration, such as the search for novel endophytes or the change of endophyte genes. Instead, desirable features in novel endophytes can be screened from plants thriving in harsh setting.

Table 1

Metabolites/Compounds	Endophytic Strain
ND	Ten endophytes functionally annotated
ND	Bacillus cereus BCM2, B. cereus SZ5, B. altitudinis CCM7 etc.
ND	Pyrenochaeta cava, M. nivalis var. neglecta
ND	Burkholderia gladioli E39CS3
ZhiNengCong, ZNC	Paecilomyces Variotii SJ1
ND	Bacillus sp. 2P2

Metabolites/Compounds	Endophytic Strain
Antimicrobial compounds, cell wall degradation enzymes, etc.	Streptomyces albidoflavus OsiLf-2
Hydrolytic enzymes, protease, siderophore, IAA, etc.	Klebsiella pneumoniae HR1
Antimicrobial compounds	Pseudomonas viridiflava
Antifungal compounds	Pseudomonas aeruginosa H40, Stenotrophomonas maltophila H8, Bacillus subtilis H18
Antimicrobial compounds	Penicillium, Colletotrichum, Diaporthe, Daldinia, Alternaria, Didymella
Eugenol, myristaldehyde, lauric acid, caprylic acid	Neopestalotiopsis sp., Diaporthe sp.
Ethyl acetate, chloroform, methanol	Proteus mirabilis, Bacillus
Erythromycin, ketoconazole, fluconazole, chloramphenicol etc.	Streptomyces olivaceus BPSAC77, Streptomyces sp. BPSAC121 etc.
Volatile substances	Pseudomonas putida BP25
Antifungal compounds	Phomopis cassia
Lipases, proteases, amylases, cellulases, pectinases, xylanases	Pseudomonas, Micrococcus, Paenibacillus, Streptococcus, Curtobacterium, Chryseobacterium, Bacillus
Amylase, protease, cellulase, pectinase, lipase	Doritis pulcherrima, Dendrobiuma phyllum, Dendrobium anosmum, Ascocentrum curvifolium, Aerides falcata
Proteolytic enzymes, cellulase	Phoma putaminum, Penicillium, Myrmecridium schulzeri
Chitinase	Streptomyces sp. P4
ΙΑΑ	Staphylococcus pasteuri MBL_B3; Kocuria sp. MBL_B19 etc.
Siderophore, IAA	Ralstonia sp.

Metabolites/Compounds	Endophytic Strain
Siderophore, IAA, gibberellic acid	Streptomyces spp.
Gibberellins	Bacillus amyloliquefaciens RWL-1
Indol acetic acid	B. subtilis NA-108

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