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Role of Endophytes in Plant Disease Management

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SUMMARY

Plants are attacked by a wide spectrum of pathogens, being the targets of viruses, bacteria, fungi, protozoa, nematodes and insects. Attacked plants have developed numerous defence mechanisms including the chemical and physical barriers that are constitutive elements of plant cell responses locally and/or systemically. Several effective pesticides have been recommended for use against these pathogens, they are not considered to be long-term solutions due to concerns of expense, exposure risks, fungicide residues, toxicity to non-target organisms and other health and environmental hazards. Therefore, efforts are being focused on developing eco-friendly safe, long lasting and effective measures against many plant pathogens for the management of plant diseases. Among the various strategies, use of Endophytes against plant pathogens is an emerging strategy as they might interact more closely with the host plant and therefore, could be more effective bio control agents in sustainable crop production and offer unique opportunity for crop protection and biological control.

INTRODUCTION

Plants interact with diverse microbial communities and share complex relationships with each other. Endophytes are heterogeneous groups of microbes that live inside the host tissue without showing any apparent sign of infection. Symbiotic relationship between the plant host and an endophyte is a bipartite beneficial event. Furthermore, endophytes can be transmitted to new host plants either horizontally or vertically. Apart from nitrogen fixation and phosphate solubilization, they play a major role in production of essential phytohormones such as indole acetic acid (IAA), abscisic acid, cytokinin, etc. Their role in enhancing resistance/tolerance of the plant host to biotic stresses and abiotic stress is noteworthy. So also, they function as an antagonist against plant pathogens by producing antibiotics, pathogen cell wall degrading enzymes, hydrolytic enzymes, volatile compounds and siderophores. Along with mycoparasitism and competition they also trigger induced systemic resistance (ISR) and systemic acquired resistance (SAR) in plants (Vandana *et al.*, 2021).

Classification of fungal endophytes

Based on evolutionary origin, endophytes are classified under two categories: clavicipitaceous endophytes (C-endophytes) and non-clavicipitaceous endophytes (Non endophytes).

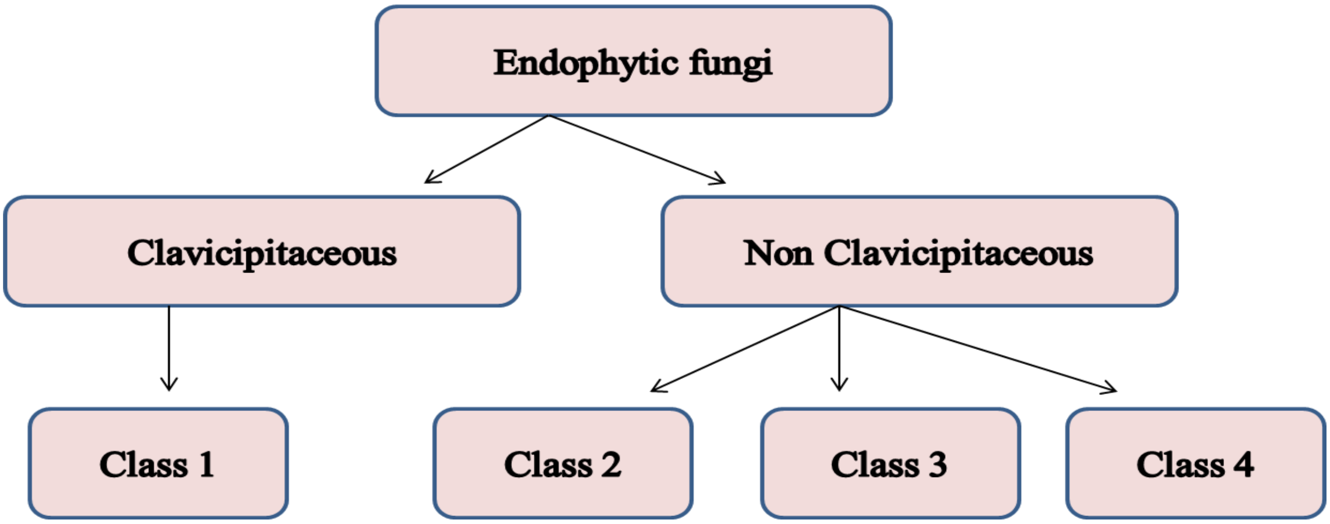


Fig 1: Classification of Fungal endophytes

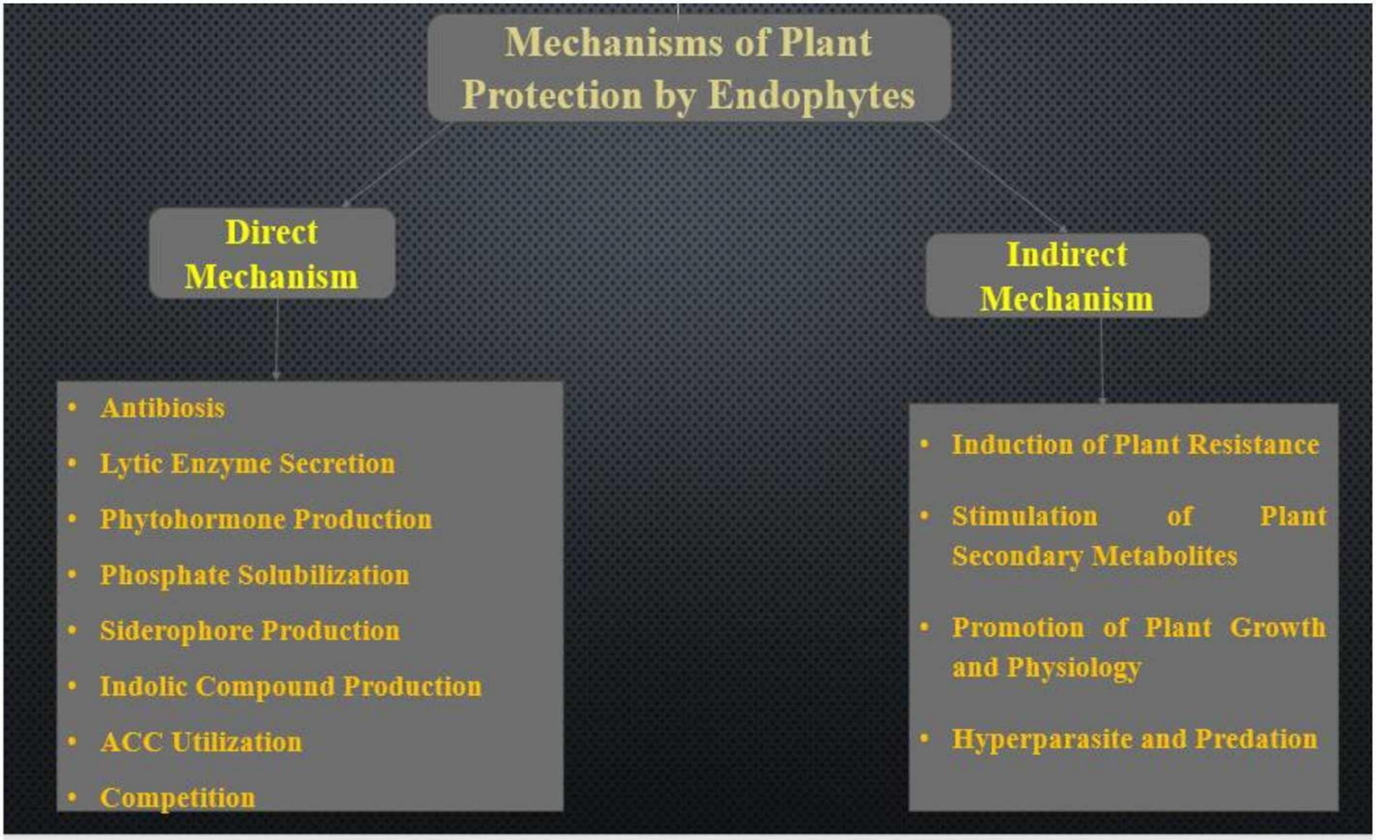
Class 1: Class 1 endophytes include symbiotic and free living species of fungi associated with grasses and sedges. They are derived phylogenetically from hypocreales family. Association of class 1 endophytes with plant tissues enhances host resistance to insect feeding. This is due to the secretion of fungal metabolites peramine that imparts protection from herbivores, insects and other parasite feeding. It was also proved the presence of anti-nematode activity.

Class 2: This class includes majority of the ascomycota fungi with few basidiomycota fungi also. Class 2 Non C-endophytes vary from other class of Non C-endophytes as they infect roots, stems and leaves resulting in substantial infections. They are sparse in rhizosphere and are transmitted through seed coat and rhizomes. Protection against fungal pathogens through secondary metabolites are also reflected in such endophytes. Upon the exposure to pathogens, these microbes induce host defense mechanisms by producing signaling molecules such as abscisic acid (ABA), osmolytes and the generation of reactive oxygen species (ROS).

Class 3: Class 3 endophytes are also Non C-endophytes varying in their occurrence i.e., on above ground parts, localized infections and horizontal transmission. Members include largely basidiomycota group *viz.*, agaricomycotina, pucciniomycotina and ustilaginomycotina. Plants infected with such microbes exhibited no change in growth and development. However, endophytes invading inner bark is found to impart resistance against dutch elm disease. Mainly, invaded host are likely to be preferred by several herbivores and insects.

Class 4: Terrestrial plant roots are identified to possess brown to black colored fungi along with mycorrhizal fungi referred as dark septate endophytes (DSE) and are classified under class 4 endophytes. These microbes are multi-functional with their activities not only on plant growth and nutritional acquisition but in deterring pathogens by lowering carbon levels in rhizosphere. They produce secondary metabolites with high melanin levels that are toxic to herbivores.

Mechanisms of Endophytes



Hydrolytic Enzymes

Enzymes are proteins that chemically aid animals and plants to biocatalyze the substrate into a product. This also enhances the plant defense mechanisms to constrain or inhibit biotic stress. Hydrolytic enzymes have an antagonistic property that can inhibit or resist pathogens through the hyperparasite mechanism and thus have an incredible biocontrol role in crop fertility. The bacterial cell wall is protected by rigid peptidoglycan or murein, which is lysed by endophytes that produce hydrolytic enzymes such as peptidase, amylase, xylanase and carboxylase. The fungal cell wall constitutes glycoprotein as an exterior layer and chitin and β-glucans or α-glucans as an interior layer. Chitin, a chief component of the fungal cell wall, adds rigidity and a skeletal framework to thin cells. α-glucan or β-glucan provides structural rigidity and protects the fungus. Endophytic hydrolytic enzymes can degrade the cell wall of pathogenic fungi and thus protect plants during infection. For example, *Trichoderma* species degrades the pathogenic fungal cell wall by producing enzymes such as β-1,3-glucanase, chitinase, N-acetylglucosaminidase and protease.

Mycoparasitism

The fungi that exhibit parasitic effects on other fungi are mycoparasites. Mycoparasite coils around the hyphae or grows adjacent to the virulent fungi and produces the hydrolytic enzyme to degrade the cell wall of the virulent fungi. Mycoparasite interacts with pathogens either as necrotrophs or biotrophs by producing hydrolytic enzymes, antibiotics or secondary metabolites for antagonistic activity and procuring nutrition from the virulent fungi through a biotrophic interface. Example, *Trichoderma* is able to parasitize hyphae of plant pathogens, including *Rhizoctonia solani*.

Competition

Nutrients are the primary source that aids spore germination and regulates the growth of pathogens or endophytes in the host. Biotrophic and necrotrophic pathogens procure specific nutrients from the defected living or dead organisms in the environment. Endophytes occupy such niches and compete with the pathogen by acquiring the essential nutrients and space in the plant, thus preventing the infection of the host. This antagonistic action does not kill the pathogens; instead, it mitigates the pathogenic microbiomes. For example, tomato enriches *Flavobacterium* spp. to suppress pathogens.

Siderophore Productions

Siderophores are small molecular compounds which are capable of chelating iron which can be produced by endophytes and can make iron available for plant use while starving pathogens of iron. Siderophores function is to accumulate Fe in the cells and inhibit pathogenic organisms. Under Fe^{2+} limited conditions, microbial siderophores form complexes with Fe containing minerals or organic compounds, which is then taken up by microbial cells where Fe^{3+} is converted and released as Fe^{2+}. For Example, Siderophores produced by plant growth-promoting bacteria (*Pseudomonas* and *Bacillus* spp.) play a vital role in niche competition by deploying Fe in pathogens and thus mitigating the upshot of pathogens in the plants (Narayanan *et al*., 2022)

Secondary Metabolites Productions

Secondary metabolites are bioactive compounds that perform a significant role in defense signaling, ecological interactions and competition. The establishment of microbial interaction involves the synthesis of secondary metabolites during metabolic exchange, which shows a complex regulatory response. These interactions can be antagonistic, mutualistic, competitive or parasitic. Bioactive metabolites such as alkaloids, steroids, tannins, terpenoids, quinones, saponins, phenols and flavonoids produced by endophytes have a prime role in protecting the host from biotic and abiotic stresses. Secondary metabolites have antibacterial and antifungal properties, which control the growth of phytopathogens. Plants can produce secondary metabolites either independently or in association with other endophytes to cope with stress and defense responses during biotic stress. Thus, endophytic secondary metabolites are used as a biocontrol agent to protect plants and improve crop qualities. For example, *Pseudomonas* strains (*P. donghuensis* 22G5 and *P. protegens* XY2F4) secrete the tropolone compound 7-hydroxytropolone, which has potential resistance against *Verticillium dahlia*, which causes *Verticillium* wilt in cotton plants.

Systemic Acquired Resistance (SAR) and Induced Systemic Resistance (ISR)

Systemic acquired resistance (SAR) is a plant resistance response aroused by pathogens and pre-existing pathogen infections. SAR induces local resistance by triggering hypersensitive reaction (HR) via signaling molecules such as salicylic acid (SA) and associated PR proteins to the infected parts and neighboring parts of the plant, thus defending against biotrophic pathogens. SAR acquires long-term protection against a diversity of microorganisms. For example, *Bacillus subtilis* induces disease resistance via the SA-dependent signaling pathway, thus controlling *Blumeria graminis* f. sp. *tritici*, which causes powdery mildew in wheat.

ISR is mediated by beneficial microbes living in the rhizosphere. It triggers signaling molecules such as Jasmonic Acid (JA) and associated PR proteins to the infected parts and leads to plant defense against necrotrophic pathogens. The ISR mechanism does not execute direct killing or inhibit the pathogen. Instead, it augments the physical or chemical barrier of the plants. The ISR signal is unspecified due to the recruitment of varied components by diverse microbes. Generally, JA and its derivative JA-isoleucine (JA-Ile) hormone regulate signaling pathways via abscisic acid (ABA) or ethylene (necrotrophic pathogens defender). ISR and SAR often show an antagonistic effect, which regulates the cellular level signaling. Upstream and downstream signaling occurs between SA and JA during the antagonistic effect on nectro or biotrophic pathogens and vice versa.

Solubilization of Phosphate

Phosphorus (P) is the second most important element, supplemented to soil for plant growth, after nitrogen. This low accessibility of phosphorus to plants is due to its insoluble forms in soil. In contrast, plants assimilate it just in two soluble ways i.e., monobasic (H_2PO_4) and the dibasic (HPO_4) ions of phosphate. The regular use of phosphate fertilizers is not only expensive but also environmentally undesirable. The microbes, having phosphate-solubilizing activity termed phosphate-solubilizing microorganisms (PSM), may provide the accessible phosphate for the plants. There are different PGPR genera such as *Serratia, Pseudomonas, Rhizobium, Bacillus, Azotobacter, Burkholderia, Enterobacter, Bradyrhizobium, Streptomyces, Cladosporium* etc., which are the most efficient phosphate-solubilizing PGPR. PGPR employs different mechanisms to solubilize the insoluble phosphates. One of the critical mechanisms is the production of organic acids during sugar metabolism. The rhizosphere inhabiting PGPR exploits the sugars of plant root exudates and releases various organic acids. It creates an acidic condition by lowering the pH and then the organic acids act as chelating agents and release phosphates from insoluble phosphate compounds. The synthesis of phosphatases by PGPR also mineralizes phosphates from the organic phosphatic substances. Endophytes had been known to increase the availability of phosphorus to the plant through phosphorus solubilization. The release of low molecular weight acids enables the chelation of metal cation attached to phosphorus and creating easily accessible to plants. Example, genetic systems of endophytic strains that can solubilize phosphate and observed that *Pisum sativum* L. plants.

1-Aminocyclopropane-1-carboxylate (ACC) Deaminase

Ethylene is a vital plant phytohormone that facilitates plant growth and development under non-tressed conditions. However, under stressed conditions, the level of ethylene increases and negatively regulates plant growth. It restricts the elongation of root and transport of auxin, supports aging and extirpation of organs and assists in the ripening of fruits. Ethylene plays a key role in the activation of plant defense against biotic stresses. 1-Aminocyclopropane-1-carboxylate (ACC) is the primary precursor in plants for ethylene synthesized by ACC synthase by converting S-adenosyl methionine. Under stressed conditions, the activity of ACC synthase increases and produces a high amount of ethylene. When the ACC is degraded by the ACC deaminase producing bacteria, the level of ethylene decreased, which results in the elongation of roots. A diverse group of PGPR having ACC deaminase activity has been reported as *Serratia, Pseudomonas, Bacillus, Acinetobacter, Rhizobium,* etc. This PGPR with ACC deaminase activity hydrolyses the primary precursor ACC to ketobutyrate and ammonia and reduces the ethylene level and improves plant health under stressed conditions. ACC deaminase is a stress release enzyme, as it alleviates different types of biotic and abiotic stressors such as pathogenic attacks, drought, metal, radiation, salt, heat stress, etc. Endophytic microorganisms with the ability to utilize ACC as the nitrogen source could reduce the level of ACC and ethylene that led to the prevention of ethylene mediated plant growth inhibition. Physiological and molecular characterization of endophytic bacteria such as *Enterobacter, Klebsiella* and *Pseudomonas*, with the ability to produce ACC deaminase, have been reported.

Production of phytohormone

Endophytes produce phytohormone which enhances plant growth promotion and changes the morphology and structure of the plant. The mechanism adopted by endophytes in the production of phytohormones in the host plant is related to the mechanism used by rhizobacteria in plant growth promotion. They help in growth promotion and protection of non-leguminous plants by the secretion of gibberellic acid, auxins, indole acetic acid and ethylene. Indole acetic acid (IAA) triggers plant cell division, differentiation and extension; stimulates of seed and tuber germination; increases the rate at which root and xylem develop, enhances lateral initiation, controls the rate of vegetative growth and the formation of adventitious root formation; as well as the formation of pigments and biosynthesis of metabolites, controls responses to gravity, light and fluorescence, affects photosynthesis and resistance to extreme conditions. IAA secreted by plant growth-promoting bacteria sometimes slows down the physiological processes listed above by affecting the level of auxin secretion by the plant. Also, the IAA produced by endophytic bacteria has the capacity to increase the root length and surface area, thereby giving room for the plant to have better access to nutrients from the soil.

CONCLUSION

Organic farming is one of the strategies that aid in the longer shelf life of plants; it generally depends on the natural microflora of soil and PGP microbes including endophytes, epiphytes and rhizospheric microbes. Endophytes are a promising candidate for the biological control of plant pathogenic fungi. Endophytes establish long-term or lifelong associations with their host. Fungal endophytes have attracted considerable attention for their ability to promote the growth of plants by direct or indirect mechanisms. Endophytes play an active biocontrol role in suppressing pathogens and enhancing crop yields. They protect plants by producing hydrolytic enzymes, secondary antifungal metabolites and siderophores and considerably improve the antioxidant system. They also induce plant defense via SAR and ISR mechanisms.

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