

Microbial Endophytes: Ecology and Biological Interactions

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Abstract – Microbial endophytes are plant associated microbes that colonize living internal tissues of plants without causing any visible symptoms. Virtually all plants are hosts to endophytic microorganisms and may usually be Fungi, Bacteria and Actinomycetes. In last two decades, good deal of information relating endophytic associations has been accumulated. In this review, we focus endophytic microorganisms concerning to their unique ecological niche and their interactions with host. The information about endophytic evolution, transmission, nature, ecological significance, role and their benefits have been elaborated. Study of microbial endophyte ecology and interactions holds a great promise and use of endophytes may offer an innovative, economical, novel and environmentally sound strategies for plant health, productivity and sustainable environment management in near future.

Keywords – Balanced Antagonism, Ecological Fitness, Balanced Antagonism, Ecological Fitness, Endophytes, Plant–Microbe Interaction.

I. INTRODUCTION

An endophyte is an endosymbiont often a bacterium, fungus or actinomycete, that lives within a plant for all or at least part of their life, apparently without inflicting negative effects or without causing any visible symptoms of their presence (Pham Quang Hung *et al.*, 2004; Bandara *et al.*, 2006; Hasegawa *et al.*, 2006; El-Tarabily *et al.*, 2008). Endophyte (Gr. *endon*, within; *phyton*, plant) in simple sense refers to location (Fig 1), relating to the organisms that live within plants (Wilson, 1995).

de Bery, (1866) first introduced the term “endophytes” for those fungi that living inside the plant tissue. Virtually all plants are hosts to endophytic microorganisms. Endophytes were discovered in Darnel, Germany in 1904 (Tan and Zou, 2001). One of the earliest publications on endophytes was that of an endophytic fungus by Freeman in 1904. Freeman found the endophytic fungus in Persian darnel (annual grass). Grasses with high endophyte content are often resistant to attack by certain insects. Since then endophytes have been found in other grasses and plants.

Each of the nearly 300,000 species of land plant on earth is likely to host to one or more endophyte species. They inhabit majority of healthy and symptomless plants, in various tissues, seeds, roots, stems and leaves (Johri, 2006). Despite this anticipated diversity, relatively few of these organisms have been characterized (Smith *et al.*, 2008). Endophytes have been considered ubiquitous among terrestrial plants and in habitats ranging from

coastal mangroves to north-temperate evergreen forests, temperate pastures and grasslands, semiarid regions of the southwestern U.S.A., and tropical forests (Arnold and Herre, 2003).

Many plant endophytes are cryptic since they induce no symptoms and escape detection using current histochemical, microscopic, isolation and cultural methods (Barrow *et al.*, 2008). Many endophytes have been shown to be novel species or strains. Thus, research on microbial endophytes holds great promise and is alluring for discovering a myriad of undescribed species, creating an enormous biodiversity: a rich source of novel natural products and an unknown genetic background of all the interdependencies thus implied (Ningthoujam, 2010; Hyde and Soyong, 2008).

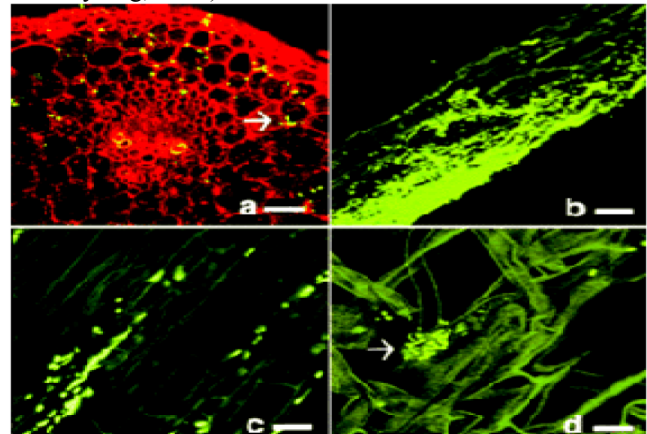


Fig.1. Endophytic microorganisms : Microbes residing in the plant tissue. (Maize stem (a) and root (b to d) colonization by GFP-labeled *K. pneumoniae* strain 2028 (a and b) or 342 (c and d)) Image Courtesy: Chelius & Triplett, (2000).

II. NATURE OF ENDOPHYTES

Endophytes traditionally have been considered plant mutualists, however, even in these obligate symbioses; endophytes are often neutral or even pathogenic to the host, depending on endophyte and plant genotype and environmental conditions (Stanley and Fateh, 2002). Endophytes bear symbiotic or mutualistic relationship with their host; as evident from their symptomless nature, but sometimes they may turn to aggressive saprophytes or opportunistic pathogens (Perotti, 1926; Hallmann *et al.*, 1997; Azevedo *et al.*, 2000). The interactions between host plants and endophytes are not fixed in either ecological or

evolutionary time, or geographically and range from mutualistic to antagonistic (Stanley and Fateh, 2002). Mutualism, being of foremost ecological and evolutionary importance, it is necessary to have a range of adjustments to establish a balanced mechanism among endophyte and its host, for example, the endophyte and host reproduction conflicts, energetic costs of harboring the endophyte, the nutrient demand of the endophyte, the suppression of the host immune systems that not only allow the endophyte to subsist but also might increase the susceptibility to other fungal pathogens, and host control of endophyte growth within the plant (Saikkonen *et al.*, 2004). Therefore, this mutualistic relationship has been evolved during the great physical proximity between the interacting cells as a finely tuned balance of antagonisms with a great expenditure of energy to maintain a stable state that disadvantages neither partner (Margareth, 2006).

Symbiotic relationships may be either obligate, i.e. necessary for the survival of at least one of the organisms involved, or facultative, where the relationship is beneficial but not essential for the survival of the interacting organisms (Sapp, 1994). An endosymbiotic association, in which one organism lives within the tissues of another, is often obligate in nature (Sapp, 1994). Ecological theory predicts that an obligate symbiont, without the capacity for horizontal transmission, will be lost from the host population if the net effect of the symbiont is detrimental to the host (Fine, 1975; Lipsitch *et al.*, 1995; Frank, 1997). Thus, the evolution of obligate endosymbiosis has been closely linked with mutualism.

Although, endophyte associations are commonly referred to as mutualistic, this is not entirely accurate. In some *Epichloe sp.* the onset of host flowering induces the fungal sexual cycle, which causes these fungi to switch from a mutualistic asexual lifecycle to an antagonistic pathogenic sexual lifecycle (Eaton *et al.*, 2011). During the vegetative cycle of the plant host, endophytic fungal hyphae asymptotically colonize the intercellular space of plant tissues/organs, such as leaf sheaths and blades. When the reproductive cycle of the host plant commences, the outcome of the grass-endophyte interaction can be asymptomatic or antagonistic, depending on the grass and endophytic fungal species involved (Faeth and Sullivan, 2003; Zabalgozcoa *et al.*, 2003).

The molecular and biochemical basis for the switch from endophytic to parasitic lifestyle are characterized by an imbalance in nutrient exchange that can explain why colonization of different hosts can cause a fungus to adopt contrasting lifestyles. As a result of these long-held interactions, it is feasible to arouse that some endophytic microbes may have devised genetic systems allowing for transfer of information between themselves and the host plant. As a consequence, the associated microorganisms can learn as much as teach biochemical pathways in order to produce substances common to their hosts or *vice versa* that may have application outside the host plant in which they normally reside (Strobel, 2002). Endophytes may become plant pathogens, depending on the developmental stage of host and endophyte, environmental factors, and host defense responses (Schulz and Boyle, 2005).

Endophytic “pathogens” have coevolved with their hosts and are thus not highly virulent. These pathogens must at some time sporulate, when leaves senesce or the plants are stressed or when the plants produce fruit that will eventually rot (Sieber, 2007).

The different outcomes of host-endophyte interactions are attributed to the different life history of the individual symbiont, patterns of endophytic infection, genotypic variation and ecological factors (Wei *et al.*, 2007).

III. EVOLUTION OF ENDOPHYTES

Evolution of the endophytic lifestyle involve multiple levels of causation, the whole network of species that interact with host plant directly or indirectly (multispecies interaction), biotic and abiotic environmental conditions, genetic factors, and have traits related to mutual exploitation (Saikkonen *et al.*, 2004). The endophyte host interaction can vary in a seamless manner from mutualism to parasitism, based on a fine-tuned balance between the demands of the invader and the plant response (Kogel *et al.*, 2006). According to Schulz and Boyle, (2005), ‘Balanced Antagonism’ hypothesis, (Fig 2) which can be stated as equilibrium, under environmental, physiological and genetic control, that results in fitness benefits for both partners. On one hand, the theory depicts fungal endophytes as ‘masters of phenotypic plasticity’, able to infect as endosymbionts, to colonize cryptically, and finally to sporulate as pathogens or saprophytes. This creative endophyte’s variability implies evolutionary potential.

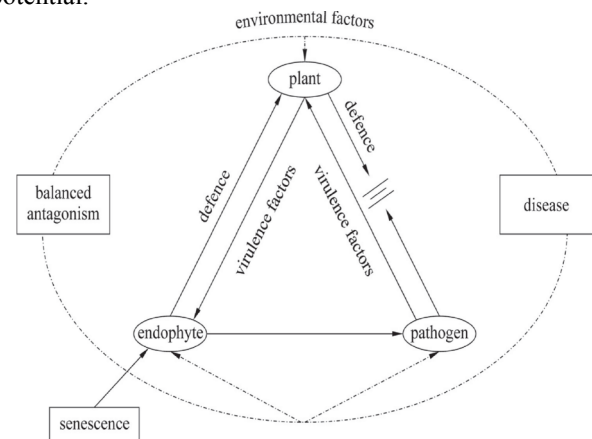


Fig.2. Balanced antagonism hypothesis (Schulz and Boyle, 2005)

Endophyte infection as driven only by the relative fitness of infected and non-infected plants predicts that an endophyte reducing the fitness of its host would tend to go extinct (Clay, 1993). However, if host fitness enhancement is the only criteria for determination of endophyte infection, it seems to be contradictory. As evident from, relatively high infection frequencies have been observed in natural grass populations exhibiting little or no evidence that the fungus confers a reproductive advantage to its host (Saikkonen *et al.*, 1998; Faeth and Hamilton, 2006) positive effect of endophytes on the fitness of their hosts has not been consistent (Cheplick *et*



al., 1989; Saikkonen *et al.*, 1998; Faeth, 2002; Faeth and Sullivan, 2003; Cheplick, 2004; Lewis, 2004; Faeth and Hamilton, 2006). As a result of metapopulation dynamics (Saikkonen *et al.*, 2002) local persistence of endophyte infection should be possible in the absence of such mutualistic effects. Second, natural populations often exhibit intermediate infection levels in contrast to modelling results showing that the frequency of infected plants in a population should equilibrate at 100 per cent if the only driver was host fitness enhancement (Clay, 1993; Ravel *et al.*, 1997). These discrepancies between the observed infection levels and the relative advantage of infected plants might be accounted for by endophyte transmission failures between plant generations or by non-equilibrium dynamics (Clay, 1993; Ravel *et al.*, 1997; Saikkonen *et al.*, 1998).

IV. TRANSMISSION OF ENDOPHYTES

Endophytes on the basis of their mode of transmission can be divided into two groups; systemic endophytes are transmitted vertically (directly from parent to offspring) via the seeds, while non-systemic endophytes are transmitted horizontally (from individual to unrelated individual) with host colonization arising from the surrounding environment (Saikkonen *et al.*, 1998; Faeth, 2002). Many grasses in the subfamily *Pooideae* are infected by asexual (anamorphic), vertically transmitted endophytic fungi, *Neotyphodium* Glenn, or their sexual (teleomorphic) counterparts of genus *Epichloe* (Fr.), which can be transmitted either vertically or horizontally (Wei *et al.*, 2007).

Non-systemic endophytes in woody plants are horizontally transmitted by spores from plant to plant and appear to rarely interact mutualistically with their hosts (Saikkonen *et al.*, 1998; Faeth, 2002). However, Systemic and vertically transmitted *Epichloe* endophytes can shift from mutualistic to antagonistic symbioses when the fungus produces external stromata (providing both spermatia and female structures) surrounding some or all host inflorescences and aborting them (Chung and Schardl, 1997) or by causing energetic costs to the host, particularly in resource-limited environments (Cheplick *et al.*, 1989; Saikkonen *et al.*, 1998; Faeth, 2002; Faeth and Sullivan, 2003; Cheplick, 2004). This relationship is subjected to change and replacement by other endophytes depending on environmental conditions and host requirement (Barrow *et al.*, 2008).

Endophyte infection and mutualism are likely to arise from difficulties in detecting small mutualistic effects, variability in endophyte transmission efficiency and an apparent prevalence of non-equilibrium in the dynamics of infection. Although endophytes would ultimately persist only if the infection confers some fitness increase to the host plants, such an increase can be very small, as long as the transmission efficiency is sufficiently high. In addition, imperfect transmission limits effectively the equilibrium infection level if the infected plants exhibit small or large reproductive advantage. Under frequent natural conditions, the equilibrium infection level is very sensitive to small

changes in transmission efficiency and host reproductive advantage, while convergence to such equilibrium is slow. As a consequence, seed immigration and environmental fluctuation are likely to keep local infection levels away from equilibrium. Transient dynamics analysis suggests that, when driven by environmental fluctuation, infection frequency increases would often be larger than decreases. By contrast, when due to immigration, overrepresentation of infected individuals tends to vanish faster than equivalent overrepresentation of non-infected individuals (Gundel *et al.*, 2008).

However, as far as the mode of transmission is concerned, horizontally transmitted fungi that form restricted local latent infections in plant tissues are by far the most common type of infection and are found in all types of plants. By contrast, systemic and vertically transmitted fungi are only rarely described from woody plants (Bloomberg, 1966; Petrini, 1991). Size, morphologically complex architecture and the longer age of maturity of woody plants probably limit the window for systemic growth and successful vertical transmission of endophytic fungi. For example, fungal endophytes infecting one part of the crown of a tree are unlikely to grow systemically through highly differentiated and woody tissues to reach the branches in another part of the crown. By contrast, the relatively small size, morphology (e.g. arrangement of tillers) and the position of the meristems of grasses allow fungi to grow throughout the host. The fungus can grow rapidly from multiple growth points within host meristematic tissues, and synchronize growth with the host plant (Christensen, *et al.*, 2002). The earlier age of first reproduction in perennial grasses, compared with in woody perennials, increases opportunities for vertical transmission of the fungus (Saikkonen *et al.*, 2004).

Vertical transmission of *Neotyphodium* endophytes from an infected mother plant to its offspring depends on a close connection between grass and fungus throughout their life cycles. To infect the seeds, the endophyte must produce a massive vegetative growth of hyphae into the developing embryos (Philipson and Christey 1986). Once the endophyte reaches the seeds, it has found the way to multiply and disperse, and its persistence becomes dependent on its ability to remain alive during the seminal stage of the host. After seed germination, the endophyte has to follow the development of the plant, growing hyphae into new plant tissues as they develop to finally infect the seeds during the reproductive stage (Clay and Schardl, 2002).

Endophyte transmission failures can either occur during pre- or postzygotic stages of the host plant's life cycle. Both types of failure would be affected by environmental variation but, when they occur, infected plants produce a proportion of non-infected offspring, influencing the dynamics of infection within the population (Gundel *et al.*, 2008).

V. COLONIZATION OF ENDOPHYTES

The process of endophytic colonization of plant tissue is complex and may include host recognition, penetration

and establishment or colonization. It has been generally observed that endophytes have wide host range and does not have host specificity (Cohen, 2006). Plants belonging to different families, growing under various ecological and geographical conditions (Petrini, 1996) may harbor endophytes.

A. Portal of entry

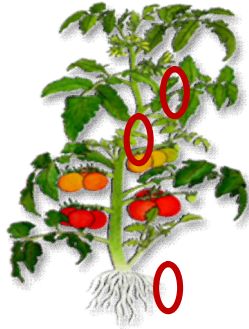


Fig.3. Portal of entry

It is apparent that endophytes penetrate their host through natural openings or wounds (Fig 3). Endophytes enter plant tissue primarily through the root zone; however, aerial portions of plants, such as flowers, stems, and cotyledons, may also be used for entry. Specifically, the bacteria enter tissues via germinating radicles, secondary roots, stomates, or as a result of foliar damage. Endophytes inside a plant may either become localized at the point of entry or spread throughout the plant (Zinniel *et al.*, 2002). These microorganisms can reside within cells, in the intercellular spaces, or in the vascular system. Vascular tissues, for instance, protoxylem and metaxylem vessels, and epidermal cells are important sites for infection and for survival of endophytes (Patriquin and Dobereiner, 1978; Dobereiner *et al.*, 1995), as well as intercellular spaces of mesophyll cells (You *et al.*, 1990). Presence of bacteria in xylem vessels is suggestive that these are means of transporting bacteria to others parts of the plant, particularly the shoot. James *et al.*, (1994); Baldani *et al.*, (1992) and Olivares *et al.*, (1995) have reported colonization of xylem by endophytic diazotrophs. Significant variations in the populations of both indigenous and introduced endophytes have been reported. These variations are attributed to plant source, plant age, tissue type, time of sampling, and environment. Generally, bacterial populations are larger in roots and decrease in the stems and leaves (Zinniel *et al.*, 2002).

There are limited numbers of studies on the endophytic population in their natural host. Infection frequencies of *Neotyphodium* in natural (wild) grass populations are much more variable than those in domesticated grasses, ranging from 0 to 100 per cent, even among populations of the same grass species (Wei *et al.*, 2007). Endophyte species composition and infection frequency vary with habitat and that infection density in woody plants tends to increase with leaf age appear consistent with horizontal transmission. Under this scenario, fungal endophytes of woody plants travel among hosts as spores, germinating epiphytically and penetrating leaf cuticles to grow intercellularly within healthy tissues (Arnold and Herre,

2003). Successful colonization of host tissues by foliar endophytes likely is correlated with factors influencing local abundance of aerial and epiphytic propagules, and with diverse aspects of host plant suitability, including host genotype and leaf characteristics (Arnold and Herre, 2003).

VI. ENDOPHYTIC MICROORGANISMS

A. Bacterial Endophytes

Endophytic bacteria are those that can be isolated from surface disinfected plant tissue or extracted from within the plant and that do not visibly harm them (Khush and Bennett, 1992; Hallmann *et al.*, 1997; Elvazhagan *et al.*, 2009). In most plant species, endophytic bacteria are ubiquitous, colonizing locally as well as systemically, and influencing plant health by suppression of disease, degradation of contaminants, and promotion of plant growth (Sturz *et al.*, 2000). Endophytic bacteria are originally evolved from epiphytic bacterial communities in rhizosphere, phylloplane. The total number present at any time being controlled by the plant and environment (Hallmann *et al.*, 1997). Endophytic bacteria occur at lower population densities than rhizospheric bacteria or bacterial pathogens (Hallmann *et al.*, 1997; Rosenblueth and Martinez-Romero, 2006). The population density of endophytes is highly variable, depending mainly on the bacterial species and host genotypes but also in the host developmental stage, inoculum density, and environmental conditions (Pillay and Nowak, 1997; Tan *et al.*, 2003). From a phylogenetic view, endophytic bacteria are between saprophytic bacteria and plant pathogens. Overall, both biotic and abiotic effects influence the dynamic patterns of bacterial endophytes, the influences come especially from the host plants (Rosenblueth and Martinez-Romero, 2006).

B. Fungal Endophytes

Endophytic fungi are taxonomically and biologically diverse but all share the character of colonizing internal plant tissues without causing apparent harm to their host (Wilson, 1995). They are distinguished from mycorrhizal fungi on the basis of their presence in the above ground plant parts as well as lack of external hyphae and mantle (Saikkonen *et al.*, 1998). The distinction is not firm, because endophytes may also inhabit root tissues. Endophytic fungi have been identified in woody plants, trees, shrubs, ferns and grasses (Saikkonen *et al.*, 1998). Every plant species is found to be at least host one fungal endophytes, but usually asymptomatic and sometimes systemically (Faeth and Fagan, 2002). It has been estimated that there may be more than one million species of endophytic fungi (Hawksworth, 1991; Clay, 1992). Each plant species is thought to develop a highly specific endophytic community (Petrini, 1996). They include Ascomycetes, Basidiomycetes, and Deuteromycetes, as well as Oomycetes (Sinclair and Cerkauskas, 1996; Arnold *et al.*, 2000).

Historically, two endophytic groups (Clavicipitaceous (C/class 1) and nonclavicipitaceous (NC/class 2) have been discriminated based on phylogeny and life history

traits. NC-endophytes can be differentiated into three functional classes based on host colonization patterns, mechanism of transmission between host generations, *in planta* biodiversity levels, and ecological function. Although all three classes have broad host ranges, Class 2 endophytes may grow in both above- and below-ground tissues. By contrast, Class 3 and 4 endophytes are restricted to above-ground tissues and roots, respectively. Colonization of host tissues also differs: Class 3 endophytes form highly localized infections, while Class 2 and 4 endophytes are capable of extensive tissue colonization (Rodriguez *et al.*, 2009).

C. Actinomycetal Endophytes

Endophytic actinomycetes have been defined as that can be isolated from the disinfected surfaces of plant tissues or that can be extracted from within the plant that do not cause visible harm to the host (Sharma *et al.*, 2011). A variety of actinomycetes inhabit a wide range of plants as symbionts, parasites or saprophytes (Matsukuma *et al.*, 1994, Okazaki *et al.*, 1995; Matsumoto *et al.*, 1998). These enter the root system either through a root hair or directly through the epidermis. Once inside it invades the cortical tissues, passing from cell to cell, sometimes invading the plant cell walls.

Almost all vascular plants examined to date were found to harbor several endophytic actinomycetes. Hasegawa *et al.*, (2006) reviewed endophytic actinomycetes. A variety of actinomycetes inhabit a wide range of plants as symbionts, parasites or saprophytes, most of them belong to the genera, *Streptomyces* and *Microbispora*. Coombs and Franco, (2004) isolated 38 strains belonging to *Streptomyces*, *Microbispora*, *Micromonospora* and *Nocardia* from surface-sterilized root tissues of healthy wheat plants. Likewise Okazaki *et al.*, (1995) reported a total of 246 strains of actinomycetes of plant origin: belonged to *Streptomyces*, *Microbispora*, *Nocardia*, *Micromonospora*, *Actinomadura* and several others. Similarly, Takahashi and Omura (2003) successfully isolated 32 strains of *Streptomyces*, 33 *Microbispora* and 10 other rare actinomycetes from fallen leaves of 9 genera of higher plants. Rosenblueth and Martinez-Romero, (2006) listed 8 genera of plant-associated actinomycetes including *Arthrobacter*, *Curtobacterium*, *Kocuria*, *Nocardia*, *Streptomyces*.

D. Factors affecting endophytic community

The plant-associated habitat is a dynamic environment in which many factors, such plant tissues, soil type, and interaction with other microorganisms, may affect the structure and species composition of the endophytes (Kuklinsky-Sobral, 2005).

The presence of the endophytic communities depend on the nutrient supplied by host plants, plant genotype, plant age (developmental stages), environmental conditions. Physical factors, such as temperature, rainfall, edaphic factors and UV radiation will affect endophytic communities indirectly. Those factors that influences the microorganisms from rhizosphere and phylloplane in a similar way may also affect the endophytic community for ex. consistent nutrient flow, pH, moisture, etc. In addition, soil physical and chemical factors also have an indirect

effect on the endophytic communities. The factors, including pH, salinity and soil texture can alter the saprophytic bacteria in rhizosphere, resulting in preselecting the endophytic source (Microbewiki).

VII. BIOLOGICAL RECIPROcity OF ENDOPHYTES

The endophytic population associated with phytosystems is diverse in nature, but still the fundamental aspects about their interactions with host are not very clear. It is evident from the literature cited that the endophytes confer the fitness benefits to it's host and in turn gains shelter, protection and nutrition from their host. The endophytic population at a particular growth stages is not constant and may change in terms of diversity and density, as directed by the prevailing conditions.

The inner space of plants represents an unique ecological niche (Fig 4), in the endosphere, mutualistic endophytes are in protected environments that give them a competitive advantage over organisms of the rhizosphere and phyllosphere consistent nutrient flow, pH, moisture, as well as protection from high numbers and densities of competitors. Also important is the fact that the organisms occupying the endosphere are not accidentally there but most probably have been selected for this niche by the plant, because of the beneficial effects they offer their host and their abilities to resist the effects of plant defense products. The energy lost by the plant in the production of endophyte biomass is in all likelihood adequately compensated for by the improvements in plant health derived from the presence of mutualistic microorganisms, adequately compensated for by the improvements in plant health derived from the presence of mutualistic microorganisms (Backman and Sikora, 2008).

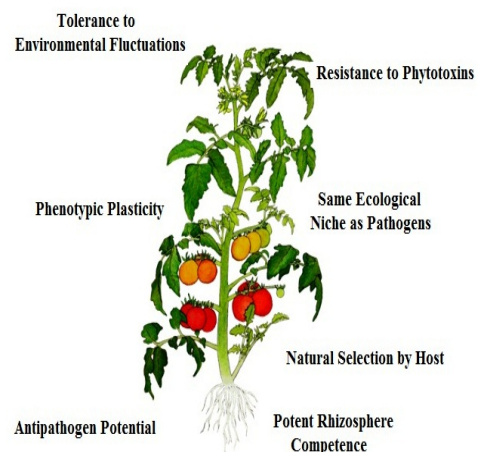


Fig.4. Propitious endophytes

VIII. ENDOPHYTE'S LEVERAGE

A. Protection

Intimate associations between endophytes and host plants can be formed without harming the plant and they have been demonstrated to improve and promote growth of host plant as well as to protect and procure resistance

from plant pathogens and/or to various environmental stresses (Hasegawa *et al.*, 2006). Endophytes may benefit host plants by preventing pathogenic organisms from colonizing them. Extensive colonization of the plant tissue by endophytes creates a "barrier effect", where the local endophytes outcompete and prevent pathogenic organisms from taking hold. Endophytes may also produce chemicals which inhibit the growth of competitors, including pathogenic organisms. The suppression of plant diseases due to the action of endophytic microorganisms has been demonstrated by several mechanisms of disease control, either directly by antibiosis, competition for nutrients, or indirectly by induction of plant resistance response (ISR) (Shiomi *et al.*, 2006) (Fig 5).

B. Growth promotion

Endophytes promote the plant growth through production of a wide range of phytohormones, such as auxins, cytokinins, gibberellins, ethylene etc. In addition, may help to enhance the nutrient ability and fix nitrogen for plants (Hornschuh *et al.*, 2002), via phosphate solubilizing activity (Wakelin *et al.*, 2004), production of siderophores (Costa and Loper, 1994). Endophytes also promote plant growth by a number of similar mechanisms (Fig. 5). Endophytic organisms can also supply essential vitamins to plants (Pirttila *et al.*, 2004). The recent areas where these plant growth promoting bacterial endophytes are being used are in the developing areas of forest regeneration and phytoremediation of contaminated soils.

C. Fitness improvement

Endophytes may have an important role in the adaptation of plants to some particular environments (Rodriguez *et al.*, 2004). Endophytes have been shown to confer fitness benefits to host plants including heat, salt, heavy metals, disease, and drought and increased below and above ground biomass. Endophytic colonization may also improve the ecological adaptability of the host by enhancing tolerance to biotic and abiotic stresses (Khan *et al.*, 2008) (Fig 5) as well as alteration in physiological properties (Azevedo *et al.*, 2000), such as mediating effects osmotic adjustment, stomatal regulation, modification of root morphology, enhanced uptake of minerals and alteration of nitrogen accumulation and metabolism (Malinowski and Belesky, 1999; Compant *et al.*, 2005).

Endophytes may also change nutritional quality of plants to herbivores (Smith *et al.*, 1985; Rasmussen *et al.*, 2009) or induce responses in plants that may turn the host plant less palatable or unattractive to herbivores (Clay, 1993). Increased herbivore resistance has been suggested to make infected plants competitively superior compared to endophyte-free plants which may lead to increased infection frequencies in plant communities (Cheplick and Clay, 1988; Schardl *et al.*, 2004). However, Grass endophytes may have negative indirect effects on predators at higher trophic levels, mediated through herbivores, for example, endophytes have been shown to negatively affect the fecundity, reproductive capacity and survival of invertebrate predators (de Sassi, 2006; Bultman *et al.*, 2009; Harri *et al.*, 2009).

Endophytes can influence community biodiversity. Together with mycorrhizal fungi, endophytes form an integral part of the extended phenotype or symbiotic community of a plant. The full range of ecological functions of endophytes of woody plants is poorly understood, but it likely to be correlated with their species diversity (Ganley *et al.*, 2004).

D. Bioactive Fount

Apart from the ecological benefits the endophytes, as a poorly investigated group of microorganisms they represent an abundant and dependable source of bioactive and biochemically novel metabolites. Hence, endophytes may offer enormous opportunities for discovering products and processes with potential applications in agriculture, industry, and medicine arenas. Endophytes have proved to be the promising sources of biologically active products which are of interest for wide applications. An array of natural products has been characterized from endophytes, which includes pigments, bioactive metabolites (antibacterial, antifungal, antiparasite), immune-suppressants, immune-modulators, anticancer compounds, antivirals, antidiabetic, antioxidant, antineurodegeneratives etc. (Cheng *et al.*, 2009; El-Tarabily *et al.*, 2006; Pandey *et al.*, 2008; Siciliano *et al.*, 2001). Therefore, endophytes may be "treasure trove" for new bioactives due to their wide biochemical diversity and hence they are aptly called as "chemical factories inside plants"

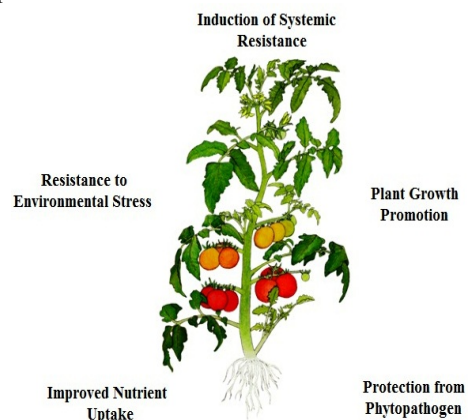


Fig.5. Benefits induced by endophytes

IX. CONCLUSION

Traditionally, endophytes have been considered as being mutualists but their relationship seems to be complex and contradictory, and may vary from, mutualistic, commensalistic and trophobiotic, elaborating positive, neutral or negative effects, depending upon the prevailing environmental conditions. Although, endophyte-host relationship holds great promise for positive interactions (e.g., plant growth promotion, protection etc.), a comprehensive understanding of detailed mechanisms related to endophyte-host relationships pertaining to selection, growth, protection, survival, population dynamics, transmission, bypassing host defense, manifestation of resistance to environmental stress conditions, synthesis of important secondary metabolites,

commanding over host genome expressions etc. is of prime importance. These interactions should not only be studied at molecular level but also at genetic level to get insight into endophyte-host relationship.

Overall review herein suggests that endophytes microbiology should be considered as a separate scientific discipline, as evident from their unique ecological niche, effects, function, biodiversity, metabolite diversity, their potential importance to industrial usage for ex., biotechnological products like enzymes, drugs, secondary metabolites, biofertilizers, biopesticides, bioinsecticides etc., as well as their role in environmental remediation, biofuel, biomass generation. Hence, endophytes may offer an innovative, economical, novel and environmentally sound strategies for plant health and productivity and sustainable environment management in near future.

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