

Plant-endophyte symbiosis, an ecological perspective

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Abstract Endophytism is the phenomenon of mutualistic association of a plant with a microorganism wherein the microbe lives within the tissues of the plant without causing any symptoms of disease. In addition to being a treasured biological resource, endophytes play diverse indispensable functions in nature for plant growth, development, stress tolerance, and adaptation. Our understanding of endophytism and its ecological aspects are overtly limited, and we have only recently started to appreciate its essence. Endophytes may impact plant biology through the production of diverse chemical entities including, but not limited to, plant growth hormones and by modulating the gene expression of defense and other secondary metabolic pathways of the host. Studies have shown differential recruitment of endophytes in endophytic populations of plants growing in the same locations, indicating host specificity and that endophytes evolve in a coordinated fashion with the host plants. Endophytic technology can be employed for the efficient production of agricultural and economically important plants and plant products. The rational application of endophytes to manipulate the microbiota, intimately asso-

ciated with plants, can help in enhancement of production of agricultural produce, increased production of key metabolites in medicinal and aromatic plants, as well as adaptation to new bio-geographic regions through tolerance to various biotic and abiotic conditions. However, the potential of endophytic biology can be judiciously harnessed only when we obtain insight into the molecular mechanism of this unique mutualistic relationship. In this paper, we present a discussion on endophytes, endophytism, their significance, and diverse functions in nature as unraveled by the latest research to understand this universal natural phenomenon.

Keywords Endophytes · Endophytism · Multitrophic interaction · Phytoremediation · Plant adaptation · Systems biology approach

Introduction

Endophytic biology is pursued in research with multitude of objectives that can be broadly classified into two categories—*bioprospecting* and *plant-microbe symbiosis* (Fig. 1). The bioprospecting aspect of endophytism has been extensively reviewed (Aly et al. 2011; Porrás-Alfaro and Bayman 2011; Mousa and Raizada 2013; Chen et al. 2014; Brader et al. 2014; Strobel 2015). However, the other aspect, i.e., plant-microbe *symbiosis*, at molecular level, has been poorly understood (Rodríguez and Roossinck 2012; Saikkonen et al. 1998; Ryan et al. 2008). Plant-microbe interactions are ubiquitous and diverse in nature (Redman et al. 2002; Kuldau and Bacon 2008; Mitter et al. 2013). In fact, each plant is a complex community, rather than a single organism, owing to its engagement in diverse heterospecific associations (Kiers and Denison 2008; Rodríguez et al. 2009; Rey and Schornack 2013). The complex interplay of diverse array of microbial communities with the host plant affects its ecophysiology such

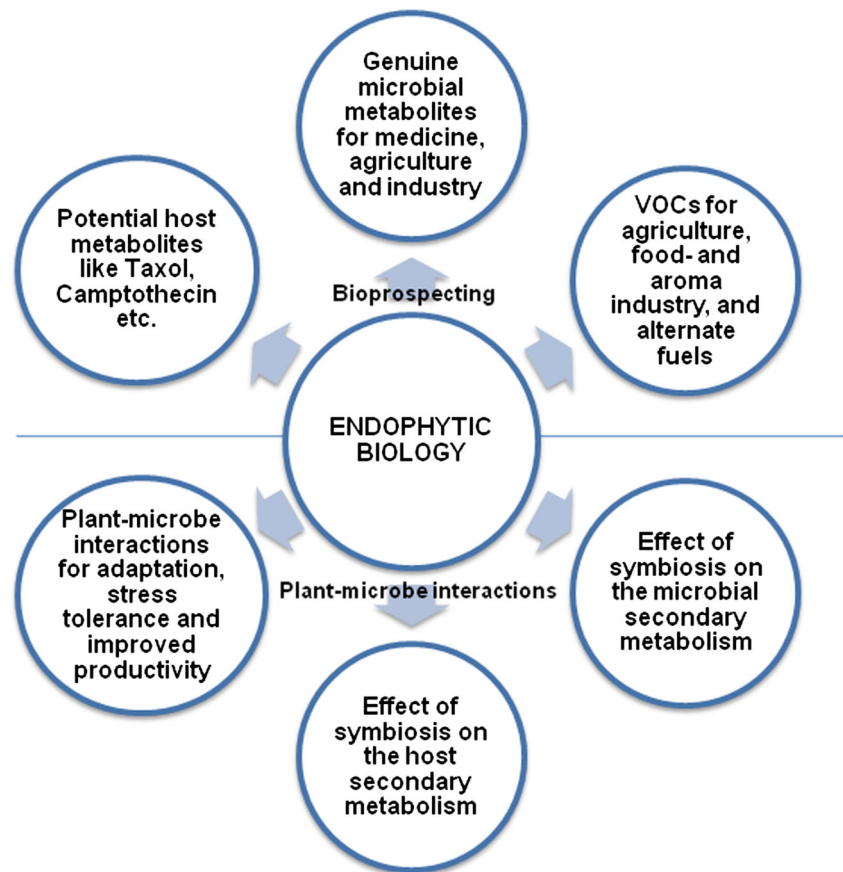
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Fig. 1 Endophytic biology is studied with the aim of bioprospecting for genuine microbial products, potential host metabolites, and industrially important volatile organic compounds (VOCs) or to understand the principles of endophytism and its consequences on the secondary metabolism of the partners as well as adaptation of the plant host to biotic and abiotic stress conditions



as plant nutrition, growth rate, resistance to biotic and abiotic stress conditions, as well as plant survival and distribution (Reinhold-Hurek and Hurek 2011; Singh et al. 2011; Iqbal et al. 2013). Owing to the fact that the association of plants with microbes dates back to more than 400 million years ago, along with the modern scientific reports of these associations, it can be stated with certainty that the presence of symbiotic microorganisms inside the plant tissues “must be considered to be the rule, rather than the exception” (Strobel et al. 2004; Albrechtsen et al. 2010; Partida-Martínez and Heil 2011).

Endophytism as a natural phenomenon is a question of history, and its origin probably dates back to the existence of plants on the planet earth (Redecker et al. 2000), but its advancement as a discipline of science began in 1886 when De Barry put forth the concept of “endophyte.” However, this discipline of science did not receive much attention until the recent recognition of their pharmaceutical and ecological significance (Gunatilaka 2006). Since then, endophytes have created immense scientific curiosity pertaining to their biology, evolution, ecology, and applications. The aim of this paper is to present a general description of endophytes in the light of recent scientific reports with an emphasis on its general classification, interaction with plants, communication between endophytes and host plants, and differential recruitment of endophytes. Furthermore, the importance of endophyte

technology is also discussed with examples of their potential application in agriculture, drug discovery, and bioremediation.

Classification of endophytes

Previously, fungal endophytes were categorized into two general groups viz. clavicipitaceous and non-clavicipitaceous based on their taxonomy, host specificity, evolution, and ecological functions. However, Rodriguez et al. (2009) described four distinct functional groups based on six criteria viz., host range, tissue(s) colonized, in planta colonization pattern, in planta biodiversity levels, mechanism of transmission between host generations, and ecological functions. Clavicipitaceous endophytes are referred to as class 1, and non-clavicipitaceous endophytes are further classified into three distinct functional groups as class 2, class 3, and class 4 (Rodriguez et al. 2009).

However, endophytes comprise different groups of microorganisms, and there is a wide diversity of nonfungal endophytes associated with almost every plant. The endophytic microorganisms can be bacteria, fungi, actinomycetes, or viruses (Stepniewska and Kuzniar 2013; Bao and Roossinck 2013) while they express a variety of symbiotic lifestyle ranging from parasitism to mutualism (Redman et al. 2001; Schulz

and Boyle 2005) depending on the plant host genotype and/or environmental conditions. Endophytes are classified into two general categories, systemic/true endophytes and transient/nonsystemic endophytes, based on their taxonomy, functional diversity, biology, and mode of transmission (Table 1).

The concept of systemic/true endophytes was put forth by Mostert et al. (2000). Systemic endophytes can be defined as the organisms that inhabit the plant organization, share a symbiotic relationship with the host, and do not produce any visible symptoms of disease at any stage. However, the widely accepted definition of Petrini (1991) with a minor modification is valid for the transient endophytes, as the organisms that live within the plant tissues at least for part of their life cycle without producing any apparent disease symptoms in plants under normal conditions but turn pathogenic when host plant is stressed or resource-limited. Systemic endophytes are cocladogenetic, i.e., in different environmental conditions, a given host possesses phylogenetically same endophytes, while as transient endophytes vary both in diversity and abundance with change in environment (Botella and Diez 2011; Higgins et al. 2014). These endophytes, because of coevolutionary selection process, share the metabolic and genetic makeup of the host and are resistant to host metabolites and/or defense mechanism (Christensen et al. 2008; Soliman et al. 2013). Systemic endophytes share a symbiotic relationship with the host plant and when grown under axenic conditions may lose their vitality after subculturing. For example, recently, it was found that a camptothecin-producing endophyte, *F. solani* isolated from *C. acuminata* (Kusari et al. 2009), could indigenously produce the precursors of camptothecin. However, a host plant enzyme absent in the fungus, strictosidine synthase, was employed in planta for the key step in producing camptothecin (Kusari et al. 2012). This was the main reason for substantial reduction of camptothecin production on subculturing under axenic conditions. The possible reason for this molecular and metabolic cross talk may be horizontal gene transfer between endophyte and the host plant (Kusari and Spiteller 2012). However, the

association of transient endophytes is short lived and seasonal; therefore, they share only physiological cues, and their diversity varies with change in the host's physiological parameters in relation to varying environmental conditions (Botella and Diez 2011). As systemic endophytes are symbiotically associated with the host plant, their transmission to next generation would be usually vertical, i.e., by means of seeds and/or vegetative propagules, while as the transient endophytes are horizontally transmitted, via spores (Scharidl et al. 1991; Saikkonen et al. 1998; Moricca and Ragazzi 2008).

Endophytism: a unique interaction between the microbe (endophyte) and the plant

According to the theory of “balanced antagonism” the endophyte-host interactions (endophytism) exhibit great phenotypic plasticity from mutualism to antagonism depending on the biocommunication between endophytes and host plant and environmental conditions (Schulz and Boyle 2005). In widely studied epichloe endophyte association, it has been reported that in some *Epichloe* spp., the onset of flowering in the host plant induces the fungal endophyte to switch from mutualistic asexual life cycle to antagonistic sexual life cycle (Scharidl et al. 2004). Prevailing views contend that fungal endophytes are presumably thought to have evolved from plant pathogenic fungi, as evidenced by some root endophytic fungi that require host cell death for proliferation during the formation of mutualistic symbiosis with the host plants; they remain asymptomatic for many years and only become parasitic when their hosts are stressed (Deshmukh et al. 2006; Kogel et al. 2006). In general, a variety of microbes may enter and become transient endophytes, and those consistently found inside the host tissues for long periods of time and eventually share the physiological and genetic makeup of the host are candidate symbionts or true endophytes (Moricca and Ragazzi 2008; Conn et al. 2008). Recently, it has been reported that the establishment of biotrophic lifestyle

Table 1 Criteria for classification of endophytes into systemic and nonsystemic endophytes

Criteria	Systemic endophytes	Nonsystemic endophytes
1. Taxonomy	Cocladogenetic species	Varies spatially and temporally
2. Mode of transmission	Usually vertical but in some cases horizontal as well	Horizontal only
3. Life style	Mutualistic	Changes from mutualism to parasitism with change in environment
4. Host defense response	Lack host defense response	Host defense response is active
5. Ecological functions	Beneficial	Beneficial or detrimental depending on the environment, age of the plant, etc.
6. Evolutionary pattern	Coevolved with the host plant	Association with the host is transient and short lived
7. Diversity	Rare	Rich

of endophytes during the colonization of host plants is an important feature of the host endophyte interactions, as it implies a strong genetic and metabolic relief to both the interacting partners. However, the response of long-term association of an endophyte may be mutualistic or antagonistic depending on nutrient availability to the endophytes and metabolic status of the host plant (Eaton et al. 2011; Lahrman et al. 2013). Also, some endophytes produce signals like reactive oxygen species (ROS), which result in switching of endophytism to either antagonism or mutualism in response to some environmental cues (White and Torres 2010). Thus, endophytes, in the earlier stage, are detected as minor pathogens which over a period of time evolve with the host into a benign or mutualistic symbiont with varying degrees of dependence, depending on the cost-benefit analysis of the host-endophyte association (Fig. 2) (Freeman and Rodriguez 1993; Schulz and Boyle 2005; Conn et al. 2008).

The other unique aspect of endophytism is the multitrophic association between different endophytic groups and the host plants. The variegated cross talks between endophytic fungi, endophytic bacteria, endophytic viruses and between these endophytes and the host plants under different biotic and abiotic selection pressures shape the outcome of this cross-kingdom symbiosis (Kusari et al. 2012; Rodriguez and Roossinck 2012). As in case of *Dichanthelium lanuginosum* (host plant) and *Curvularia protuberata* (fungal endophyte) association, the thermotolerance ability in the host plant provided by the endophytic fungal symbiont was because of a double-stranded virus harbored by the fungal endophyte (Márquez et al. 2007; Rodriguez and Roossinck 2012). Therefore, in order to understand the complexity of endophytism, future endophyte research should focus on multitrophic association models with cost-benefit analysis of communications between different interacting partners in a systems biology approach.

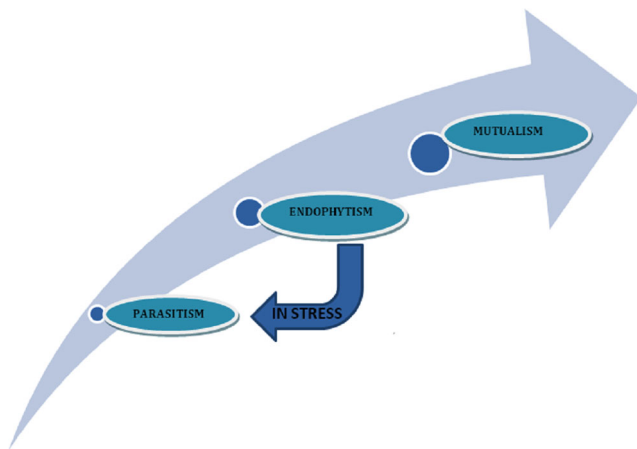


Fig. 2 Evolutionary progression of the host-endophyte relationship

Mechanism of action of endophytes in the host plant

Researchers have endeavored to elucidate the molecular mechanisms underlying the establishment of plant-endophyte association and their responses, but very limited data is available as of now (Sherameti et al. 2005; Mathys et al. 2012; Straub et al. 2013). There are two main reasons for it, one is the complex relationship between the host and the endophyte and the other is that it is not easy to imitate living condition of endophytes in vitro as well as studying the mechanisms in planta. It is generally believed that the endophytic response in plants is largely primed by the plant genotype, endophyte species, and endophyte strain (Gundel et al. 2012; Qawasmeh et al. 2012). Broadly, there are two basic mechanisms, through which endophytes affect their responses in host plants:

1. By producing diverse chemical entities (reactive oxygen species (ROS), phytoalexins, phytohormones, volatile organic compounds (VOCs), toxicants, antibiotics, peptaibols, etc.) (Schirmbock et al. 1994; Griffin et al. 2010; Khan et al. 2012), it has been reported that in some plant lines inoculated with endophytes, there was more growth in the roots, and by far, the most common mechanism that endophytes use to stimulate root growth is through secretion of phytohormones within the plant (Khan et al. 2012; Waqas et al. 2014). Also, endophytic interactions with the host generate reactive oxygen species stimulating antioxidant production in their host plants, which in turn are responsible for protecting the hosts from oxidative stress (Tanaka et al. 2006; White and Torres 2010). Recently, it was reported in *Lolium perenne* that colonization with the endophyte, *Neotyphodium lolii* significantly influenced the phenolic content and antioxidant activity. However, the effect was found to be dependent on the endophytic strain (Qawasmeh et al. 2012). In addition to this, some endophytes manipulate the host plant metabolism by changing the nutrient uptake and nutrient homeostasis (Sherameti et al. 2005; Singh et al. 2013).
2. By altering/inducing gene expression of plants' defense and metabolic pathways (Rosenblueth and Martínez-Romero 2006; Sherameti et al. 2008; Mathys et al. 2012), it is well established that the interaction of microbes with plants can induce both local and systemic alterations in the host (Heil and Bostock 2002; Glazebrook 2005; Ownley et al. 2010). Studies of plant gene expression in response to endophytic colonization reveal that genes for C and N metabolism, and plant growth and plant defense are induced (Elvira-Recuenco and Van Vuurde 2000). Plants can detect the presence of molecules from endophytes through chemoperception systems (Boller 1995). Recognition of endophytes by

the host plants triggers a cascade of signal transduction, which gives rise to a series of plant defense responses similar to plant pathogen interaction, thus leading to a noticeable change in plant metabolic state (Qawasmeh et al. 2012). The endophytic rhizobacteria and actinobacteria have been shown to enhance disease resistance by stimulating the systemic defense pathways (Heil and Bostock 2002; Conn et al. 2008). The systemic acquired resistance (SAR) pathway in the model plant, *Arabidopsis*, is normally activated by biotrophic pathogens either as a part of the hypersensitive response or as a symptom of disease, and the jasmonic acid/ethylene (JA/ET) pathway is triggered by infection with necrotrophic pathogens (Durrant and Dong 2004; Glazebrook 2005). However, the activation of plant defense genes in the absence of a pathogen by endophytic actinobacteria reveals that the latter are detected as “minor” pathogens which do not trigger a full resistance response on their own, because they do not have pathogenic determinants; thus, this may result in more effective priming of the defense response (Conn et al. 2008). Recently, it was reported that an endophytic bacterium *Bacillus thuringiensis* GS1 isolated from *Pteridium aquilinum* induced defense response against *Rhizoctonia solani* KACC 40111 in cucumber plants. The possible mode of action was reported to be the induction of PR proteins and defense-related enzymes by *B. thuringiensis* GS1 against *R. solani* KACC 40111 in cucumber plants (Seo et al. 2012). Though this is some of the basic work done on mechanistic aspect of endophytism, a complete comprehension of this ecological phenomenon can only be obtained by the integration of the “omics” technologies, such as metagenomics, metabolomics, or transcriptomics together with ecogenomics.

Are endophytes a metabolic drain on plants or an ecological bargain?

Symbiotic plant-fungal interactions are of widespread interest to ecological research as they influence important ecosystem processes including plant productivity, plant diversity, and plant pathogen interactions (Van der Heijden et al. 2006; Rodriguez et al. 2009; Van Bael et al. 2012), as exemplified by the association of endophytic systemic clavicipitaceous fungi with grasses exerting beneficial effects on hosts, through increased resistance to herbivores, pathogens, and drought stresses, which are of great ecological significance (Kuldau and Bacon 2008). Many environmental factors influence the plant-endophyte interactions; however, host plant response to endophyte infection is mainly mediated by the host genotype, endophytic strain, resource availability, and environmental cues (Fig. 3) (Hesse et al. 2003; Malinowski and Belesky 2006; Singh et al. 2011; Qawasmeh et al. 2012). For example, the endophyte interactions in tall fescue develop a low osmotic potential, primarily in young meristematic and elongating leaves, which enable tall fescue to remain stable during drought stress (Elmi and west 1995). Similarly, thermotolerance and salt tolerance is observed in certain plants colonized with endophytes (Redman et al. 2002; Waller et al. 2005). Fungal endophyte colonization significantly affects both primary and secondary metabolism of its host plant, clearly demonstrating the need for wider metabolic studies beyond alkaloid accumulation to understand ecosystem functions of this association (Vandenkoornhuyse et al. 2002; Rudgers et al. 2012). It has been reported that a shift in C to N ratios and in secondary metabolite production due to endophyte colonization are likely to have impacts on herbivore and plant pathogen responses to grasses infected with *Neotyphodium* sp. (Rasmussen et al. 2008). Recent studies have shown that plant

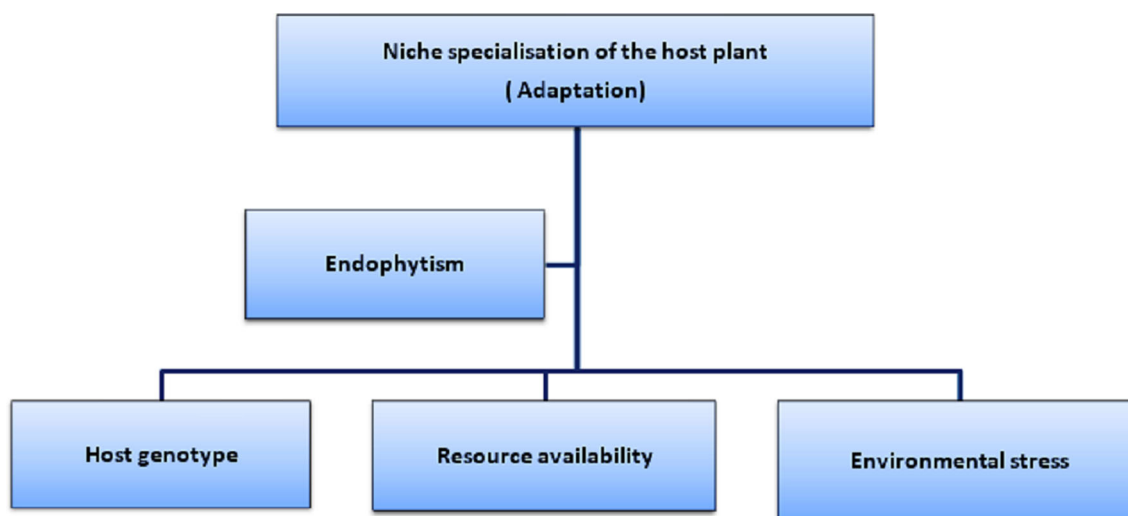


Fig. 3 Endophytism derived niche specialization of plants leading to their adaptation to varied environmental conditions and bio-geographical regions

microsymbionts may produce a range of different types of metabolites that not only play a role in defense and competition, but also take part in specific interactions and communication with the host plant (Brader et al. 2014). Further, metagenomic studies in rice found that endophytic root bacteria contain several groups of genes involved in motility, plant polymer degradation, iron acquisition (e.g., siderophores), quorum-sensing, and detoxification of reactive oxygen species, indicating that control over those pathways is important for colonization by the root microbiome (Sessitsch et al. 2012). Also, the phenotype and functional traits of most plants in nature are product of the multitrophic interactions of plants with other organisms, mainly microorganisms, sharing the same habitat and resulting in complex and transient metabolic flux across the interacting partners essential for their survival (Kusari et al. 2014). It has also been found that positive effects of the endophyte on plant performance depend on genetic variation in the host and endophyte and on nutrient availability (Cheplick 2007; Gundel et al. 2012). This link between resource availability and beneficial or neutral versus detrimental effects on plant performance suggests a metabolic cost of the endophyte to the host plant (Rasmussen et al. 2008; Lahrmann et al. 2013). Thus, fungal symbionts might be a drain (net cost) on plant metabolism or might upregulate metabolism, but endophyte hosting plants have been reported to have increased tolerance to drought, heat, metal toxicity, low pH, and high salinity, thereby invoking an ecological significance to the plants (Waller et al. 2005; Rodriguez et al. 2008; Singh et al. 2011; Nagabhyru et al. 2013).

Why is there a differential recruitment of endophytes?

Plants growing in different geographical regions are confronted with different environmental challenges (Arnold 2007). These environmental cues, in combinatorial effect with host genotype, may shape the endophytic diversity harbored by the host plants (Vega et al. 2010). The diversity of endophytes associated with the plants varies not only temporally but spatially as well (Herrera et al. 2010; Ek-Ramos et al. 2013). For instance, studies showed that endophytes may increase in incidence, diversity, and host breadth as a function of latitude (Arnold and Lutzoni 2007). Furthermore, endophyte communities from higher latitudes were characterized by relatively few fungal species representing several classes of Ascomycota, whereas tropical endophyte assemblages were dominated by a small number of classes but a very large number of different endophytic species (Arnold and Lutzoni 2007).

Also, the different plants growing in similar environmental conditions do not harbor same endophytes. It was observed that none of the endophytes isolated from cottonwood were identical to any of the endophytes of willow, even though both

tree species were growing at the same site within a meter of distance from each other (Doty et al. 2009). This differential “recruitment” of endophytes has been noted in other studies of endophytic populations from plants growing in the same location. Ulrich et al. (2008), while studying the diversity of endophytes within four clones of poplar, noted that the four poplar clones harbored four distinct endophytic populations, supporting the hypothesis that plant genotype plays a role in determining which endophyte can colonize the host (Ulrich et al. 2008). A recent metagenomic study of root-associated microbiomes of rice, using plants grown under controlled conditions as well as field cultivation, showed that the composition of the microbial consortia varies with root-associated compartments viz. endosphere (root interior), rhizoplane (root surface), and rhizosphere (soil close to the root surface). Under controlled conditions, microbiome composition varies with soil source and genotype, while as in field conditions, geographical location and cultivation practice were the factors responsible for microbiome variation. This differential recruitment of microbes across the rhizocompartments is a result of active selection of microbial consortia at different steps and each step involving molecular signals (general plant metabolites, cell wall components or membrane proteins, small molecule hormones particularly jasmonic acid, salicylic acid, and ethylene) from the plant. These results suggest that a core microbiota can be recruited from very diverse microbial surroundings, narrowing down both the most relevant community members and pointing to the host detriments controlling the mechanisms of assembly (Lebeis 2014; Edwards et al. 2014).

The above-mentioned findings suggest that the endophytic community of the plants is determined by the combinatorial effect of the host genotype and the environment consistent with a coevolutionary process whereby the endophytes may have evolved in a coordinated fashion with the host plants (Saikkonen et al. 2004; Heath 2010). There is the evidence for multiple horizontal transfers of genes between the symbionts, as an important ecological event that conferred a selective advantage on the interacting partners (Saikkonen et al. 2004). However, the interactions between plant and symbiotic microbial genomes (i.e., intergenomic epistasis, or genotype (G)×genotype (G) interactions) can have important effects on the rate and direction of coevolutionary selection (Wade 2007). Thus, it can be hypothesized that differential recruitment of endophytes in plants is a result of coevolutionary selection process determined by intergenomic interactions of both the interacting partners with environmental conditions acting as a catalyst in this evolutionary selection process. However, the genetic principles governing the differential recruitment of endophytes by a specific host and in a particular environment are poorly understood and need to be deliberated in future.

Endophytic technology and its ecological implications

The complexity of association of endophytes with its host plant is of great ecological significance owing to their compatibility, ease of reinfection, and pattern of colonization (Backman and Sikora 2008; Sikora et al. 2010). Whenever we think of a microbial infection to plants, symptoms of diseases or detrimental effects come to our mind, but this is not true in case of endophytes. However, research work in this aspect of plant-microbe interactions, with respect to the endophytes, is in infancy, and the molecular mechanism to understand this unique relationship is yet to be explored. Interests are often also dictated by more immediate socioeconomic impulses because microbes are responsible for many plant diseases that cause substantial economic losses in agriculture or have a substantial aesthetic impact. These harmful effects are often manifested directly through pathogen-mediated damage to the plants and a consequent reduction in plant vigor and yield or quality of crops. However, there is a diverse community of microorganisms (endophytes) which interact positively with plants in agricultural systems in relation to their nutrition and ability to resist biotic and abiotic stress and have the potential to be manipulated such that the benefits of their positive effects are harnessed. Endophytes can be genetically engineered, and these engineered endophytes have the potential to provide an alternative to plant transgenic technology by conferring plants a new pathway to benefit from foreign genes (Li et al. 2007). For example, an endophyte *Leifsonia xyli* subsp. *cynodontis*, a xylem inhabiting bacterium, was genetically modified with a gene from *Bacillus thuringiensis*, producing Delta-endotoxin which is active against insects in nature, especially Lepidoptera and Coleoptera. When inoculated in the plant, it secretes the toxin inside the plant tissues protecting it against attacks from the target insects (Fahey et al. 1991; Tikhonovich and Provorov 2009; Porras-Alfaro and Bayman 2011; Selim et al. 2012; Saikkonen et al. 2013). Endophytes are especially interesting for integrative pest management as innovative biological control agents (BCAs) (Scherwinski et al. 2008; Berg 2009; Li et al. 2012). An important advantage of endophytes as BCAs over the conventional BCAs is that they can be applied directly to seeds or seedlings, thereby avoiding treatment to large quantities of soil or large numbers of already established plants. Recently, an *Enterobacter* sp. has been reported as a potent biocontrol agent against *Verticillium dahliae* Kleb, which is the causative agent of verticillium wilt of cotton (Li et al. 2012). Few fungal endophytes are already being produced on large scale as commercial BCAs for example *Trichoderma harzianum*, *Paecilomyces lilacinus*, *Beauveria bassiana*, *Fusarium oxysporum* etc. (Mendoza and Sikora 2009; Sikora et al. 2010). However, so far, single microorganisms have been used as BCAs, and the use of multiple organisms in a consortium imitating the complexity of associations within the plant

system has just begun to be explored (Friesen 2012; Kiers et al. 2013). As the world becomes wary of the ecological damage done by synthetic agrochemicals, endophytes continue for the discovery of powerful, selective, and safe alternatives. The other important aspect of biotechnological implication of endophytes is in phytoremediation process either directly through degradation and/or accumulation of environmental pollutants or indirectly by promoting the growth of plants having the ability of phytoremediation (Stepniewska and Kuzniar 2013). For example, plants inoculated with genetically engineered endophytes were more tolerant to toluene, and they also reduced the transpiration of toluene to the atmosphere (Newman and Reynolds 2005). Some endophytes have been found to help the host plant in nitrogen acquisition, either by tapping atmospheric nitrogen directly (Sherameti et al. 2005) or by translocating the insect-derived nitrogen indirectly (Behie et al. 2012) and thereby may play a larger role in nitrogen cycling. One of the most potential functions of endophytes is the facilitation of nutrient uptake. Some endophytes have been observed to mobilize phosphorous uptake in plants (Yadav et al. 2010), while others have been found to impact the growth and development of the plants by producing useful phytohormones (Khan et al. 2012; Waqas et al. 2014).

Many of the fungal endophytes have been found to produce antimycotic volatile organic compounds (VOCs). VOCs produced by microorganisms are regarded important infochemicals in the biosphere which influence the dynamics of the ecosystem and vice versa (Wheatley 2002). Microbial species produce consistent and reproducible VOC profiles under standard culture conditions (Strobel et al. 2008; Mallette et al. 2012; Riyaz-Ul-Hassan et al. 2012). Several of these endophytes may find applications in agriculture, aroma industry, food processing, and as potential biofuel molecules (Ezra et al. 2004; Strobel et al. 2008; Bitas et al. 2013; Riyaz-Ul-Hassan et al. 2013). Endophytes like *Muscodor* spp. produce bioactive VOCs that inhibit or kill important plant pathogens, thus may be used for mycofumigation, postharvest preservation of agricultural produce, and decontamination of animal waste (Strobel 2006; Bitas et al. 2013). It seems reasonable that the VOC-producing microorganisms may be preferentially establishing symbiotic associations with higher plants as they contribute to the host defense mechanism by inhibiting the plant pathogens. Production of VOCs may also help them to compete with other microbes for space, nutrients, and making associations with plants.

Greater utilization of microorganisms of endophytic origin in agricultural systems could possibly allow reductions in the use of inorganic fertilizers, herbicides, and pesticides with no impact on crop vigor and yield. Thus, in future, endophyte technology holds the key for a potential gateway to sustainable agriculture development.

Conclusions

The microbiota associated with the plants shape their health, growth, and development as well as their secondary metabolism. Endophytes are most intimately associated with plants, being present inside the plant tissues; thus, they impact the development of the host significantly. Plant-endophyte interactions may be species specific, shaped by the coevolution of both the partners together to impart essential benefits to each other. Recent studies on plant-endophyte mutualism involving “-omics” coupled to the systems biology approaches have started providing insights into different facets of plant-endophyte interactions and the dynamics of multispecies mutualism network with a high level of significance. Endophytes can be explored as a bio-resource for drug discovery in pharmaceutical industries, as plant growth-promoting regulators (PGPRs), bio-control agents (BCAs) for disease and pest management in agricultural industry, and as important technology in environmental remediation. Thus, endophyte research holds a potential gateway for sustainable development provided that we harness their potential in a holistic way.

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Conflict of interest The authors report no declarations of interest.

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