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**ABSTRACT**

Many fungi belonging to mostly Ascomycota inhabit living tissues of plants of all major lineages without causing any visible symptoms. Termed horizontally transmitted endophytes, they have been investigated mostly for their capacity to produce bioactive secondary metabolites. However, many questions regarding the interactions between endophytes and their plant hosts, phytophagous insects and other fungi remain unanswered. This review highlights some of these areas of endophyte biology about which very little or no knowledge exists. Information garnered' using modern methodologies' on these grey areas of 'endophytism' (endophytic mode of lifestyle) would help immensely in understanding the evolution of endophytes of aerial plant tissues and in exploiting endophytes in various fields of biotechnology.

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**Introduction**

Many ascomycetes infect aerial tissues of plants of all major lineages without causing any apparent disease symptoms. Called endophytes, these fungi have been studied mainly for two reasons: (1) as an ecological group expected to harbour many of the hitherto unknown fungal species (Petrini, 1991; Suryanarayanan et al., 1998; Arnold and Lutzoni, 2007; Hyde and Soytong, 2008; Rodriguez et al., 2009); and (2) as a source of novel bioactive compounds (Krohn et al., 2008; Suryanarayanan et al., 2009a; Shweta et al., 2010; Kharwar et al., 2011) and secondary metabolites of their host plants

(Stierle et al., 1993; Puri et al., 2005; Kusari et al., 2012; Sachin et al., 2013; Heinig et al., 2013). While endophytes are recognized as sources of novel metabolites (Debbab et al., 2011; Rösenberg et al., 2013), industrial enzymes (Govinda Rajulu et al., 2011; Thirunavukkarasu et al., 2011; Suryanarayanan et al., 2012) and as agents that enhance the abiotic (Saikkonen et al., 2010; Vesterlund et al., 2011) or biotic (Arnold et al., 2003; Vega, 2008; Rocha et al., 2011) stress tolerance of their plant hosts, information regarding many facets of their biology are incomplete. This review highlights some of the gaps in our knowledge regarding endophyte biology which need immediate attention.

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## Endophyte–plant host interaction

Endophyte–plant interaction covers the entire gamut of fungus–plant interactions since endophyte species can be latent pathogens, mutualists, commensals, temporary residents or latent saprotrophs (Davis and Shaw, 2008). Thus, strategies and counter-strategies evolved by both the partners in sustaining or avoiding endophytic association need to be investigated to understand these various shades of endophytism. Identification of genes expressed during different phases of endophytism such as pre-penetration, plant tissue penetration and plant colonization would shed light on the evolution of plant tissues as niches for endophytes. For instance, genome and transcriptome analysis of the fungal root endosymbiont *Piriformospora indica* showed that this fungus possesses genes coding for many enzymes needed for a saprotrophic lifestyle and that different and appropriate genes were upregulated during the endophytic or saprotrophic stage of the fungus (Zuccaro et al., 2011). Similar experiments could prove conclusively lifestyle shifts in certain foliar endophytes which appear to operate in a saprotrophic mode when living outside their plant hosts. Significant strides have been made in recent years in the understanding of fungal pathogen–plant host interactions. These studies could serve as models for unravelling aspects of endophytism. For instance, comparative proteomics of secreted proteins of plant pathogens in culture and *in planta* has revealed proteins critical for a fungus to establish a pathogenic association (Paper et al., 2007). Such investigations for endophytes could identify proteins necessary for an endophytic mode of life.

Precise species identification is essential for estimating endophyte diversity in diverse plant communities like tropical forests. Here, the advantage of molecular methods in the proper identification of ubiquitous endophyte species is clearly borne out by the study of Wikee et al. (2013). Making recourse to a multigene phylogenetic analysis, they showed that the multi-host and common endophyte *Phyllosticta capitensis* is not a pathogen although it is often identified erroneously as one. Similarly, chemotaxonomy of endophytes needs attention since endophytes are known to produce a wide range of secondary metabolites (Gunatilaka, 2006). Whalley and Edwards (1995) attempted the classification of Xylaria based on secondary metabolites. In a similar vein, the secondary metabolite spectrum of multi-host endophytes with fuzzy species characteristics (such as *Colletotrichum*, *Pestalotiopsis*, *Phomopsis*, and *Phyllosticta*) should be studied to evaluate their fidelity in determining species. It is pertinent to mention here that chemotaxonomy based on secondary metabolites has been used for many ascomycete fungi (Frisvad et al., 2008).

Endophyte diversity is expected to be high in tropical forests as they support a high diversity of plant hosts (see Hyde and Soytong, 2008; Zimmerman and Vitousek, 2012). This generalization has exceptions; the dry tropical forests of southern India accumulate a lot of litter and experience prolonged dry periods as well as periodic ground fires (Kodandapani et al., 2008). The spores of litter fungi in these fire prone forests are heat tolerant and some of these fungi also exist as endophytes in leaves of taxonomically unrelated

trees thus depressing overall endophyte diversity (Suryanarayanan et al., 2011a). Culture and molecular studies suggest that adaptations in a few fungal species to the local conditions lead to the occurrence of generalist endophytes in these forests (Pandey et al., 2003; Murali et al., 2006; Suryanarayanan et al., 2011a; Govinda Rajulu et al., 2013). Thus, environment rather than the host traits could be the determinant of endophyte communities in certain geographical locations (Davis and Shaw, 2008). Apart from conventional culture studies, methods such as next-generation sequencing (Jumpponen and Jones, 2009) and barcoded amplicon pyrosequencing (Zimmerman and Vitousek, 2012) have to be used for studying endophyte diversity in diverse geographical locations and plant communities to get a more complete picture of global endophyte diversity.

One approach to understanding strategies of endophytism is to study endophyte distribution in plant tissues rich in defence chemicals. Endophytes with higher tolerance to such chemicals dominate in the tissues producing these compounds (Saunders and Kohn, 2009). Maize tissues are rich in antifungal benzoxazinoids but harbour endophytes which are tolerant to these compounds (Saunders and Kohn, 2009). Given this scenario, it would be worthwhile to determine if host defence metabolites exert a selection pressure in the evolution of endophytism. A comparison of the endophyte diversity of varieties of plant species differing in their anti-fungal compounds composition (such as sorghum – Mueller-Harvey and Dohana, 1991) and their tolerance to such chemicals would be of heuristic value. It is well known that plants produce defence chemicals such as phytoalexins as a response to fungal infections (Hammerschmidt, 1999). It is not clear though how plants respond to endophyte infection with reference to such post-formed defence chemicals. Here, the model plant *Arabidopsis thaliana* and its various mutants (such as the phytoalexin-deficient *pad* mutant), which have been employed for studying fungal pathogen–plant interactions (Oliver and Ipcho, 2004; Nawrath and Métraux, 1999), could be used to gain insights into endophyte associations. Many classes of secondary metabolites, including benzylisoquinoline alkaloids and iridoids, are specific to certain families of angiosperm plants such that they are used as taxonomic characters (Gershenzon and Mabry, 1983). The secondary metabolism of conspecific endophytes from plant hosts differing significantly in the chemistry of their secondary metabolites could be studied to understand host influence on the secondary metabolite spectrum of endophytes. Again, only recent studies have dispelled the popular notion that horizontal gene transfer events from plant hosts to endophytes are responsible for the heightened biosynthetic ability of endophytes (Heinig et al., 2013; Sachin et al., 2013). This emphasizes how little we know about endophytes.

Almost all studies relating to endophytes of different plant species are based on a one time sampling of the plant tissue (mainly, the leaf) resulting in a snapshot record of its endophyte community. Although useful for comparing endophyte assemblages of plants of different lineages or geographic locations, such single screenings do not reveal the dynamics of endophyte communities. Suryanarayanan and Thennarasan (2004) showed that the species composition of the foliar endophyte assemblage of a tropical tree changes

significantly with time. Colonization by foliar endophytes in *Fraxinus excelsior* is heavily dependent on microclimatic factors and leaf characteristics resulting in highly variable spatial and temporal distribution patterns of them in an individual tree (Scholtysik et al., 2013). Thus, periodic sampling is essential to obtain complete information on the endophyte community status of a plant. Such a within-tissue succession of endophytes may have other consequences; some endophytes produce phytohormones (Stone and Petrini, 1997; Nassar et al., 2005) and thus may influence leaf senescence and leaf fall in some cases. Changes in the leaf chemistry with time may be a crucial factor in determining foliar endophyte assemblages (see Sanchez-Azofeifa et al., 2012). Since colonization by endophytes can also alter leaf chemistry (Estrada et al., 2013), investigations on the reciprocal influence of leaf chemistry and endophytes would throw more light on plant–endophyte association. Here, it is desirable to use a tractable model host such as *Arabidopsis* to test the various hypotheses of endophytism (Garcia et al., 2013). With the available knowledge on functional genomics of *Arabidopsis*, using this plant host and metaproteomics would be ideal to understand endophytism better. Metaproteomics has helped in defining the functional roles of different microbes in complex, multi-microbe communities such as soil (Wang et al., 2011), ground water (Benndorf et al., 2007), leaf surface (Delmotte et al., 2009) and plant litter (Schneider et al., 2012). This technique could go a long way to aid understanding endophyte–plant host associations and provide greater insight than the usual method of merely documenting endophytes (based on culture or molecular characters), which gives only a partial image of endophytism and ignores functional aspects of the association.

Most of the studies on the horizontally transmitted endophytes are with reference to those harboured by the leaf. Since a few studies (e.g. Huang et al., 2008; Suryanarayanan et al., 2009b) indicate tissue preference among endophytes, different tissues of plants have to be sampled. This is well illustrated by the study of Gazis et al. (2012) who describe a new class of fungi (Xylonomycetes) from the sapwood of rubber trees. It is also essential to elucidate the life cycle of endophytes and to establish their anamorph–teleomorph connections in order to understand their survival outside their hosts, dispersal and diversity. Since most of these endophytes are anamorphs, confirming anamorph–teleomorph relationships could also facilitate proper identification of the fungus and better bioprospecting in cases where the teleomorph is free living (Bills et al., 2012).

Another unsettled question concerns multi-host endophyte genera. Species of these endophytes transgress taxonomic barriers of host plants and colonize phylogenetically distant hosts even in disjointed geographical locations (Pandey et al., 2003; Jeewon et al., 2004; Murali et al., 2006; Wei et al., 2007; Davis and Shaw 2008; Tejesvi et al., 2009). There are no studies on the adaptations of these generalist endophytes which lead to such a wide host range, though this phenomenon points to fungal adaptations allowing them to counter a variety of host defence mechanisms.

There are only a few reports on costs and benefits to the host plant due to endophyte association. An endophyte association could enhance the tolerance of the plant to fungal

pathogens (Arnold et al., 2003), herbivores (Jallow et al., 2004), and abiotic stress (Rodriguez et al., 2008; White and Torres, 2010). As far as the cost to the host, one inconclusive study (Arnold and Engelbrecht, 2007) indicates that water loss under dry conditions is more rapid in plants with endophytes than in those without them. Experiments under controlled conditions are needed to study this facet of endophyte–plant interactions particularly with reference to photosynthesis. Sanchez-Azofeifa et al. (2012) found a correlation between foliar endophyte richness and diversity and leaf properties, including spectral vegetation indices of chlorophyll content. Endophytes could affect photosynthesis by elaborating toxins which interfere with electron transport in the thylakoid membranes or by reducing the chlorophyll content (Pinto et al., 2000). The influence of such high densities of endophyte infection in plants of the wet tropical forests (Lodge et al., 1996; Arnold and Herre, 2003) on photosynthesis is unknown. Although it is expected that the plants would suffer a cost in terms of photosynthates supplied to the colonizers, it is not known if the concentration of respiratory CO<sub>2</sub> of the endophytes would be high enough to create islands of low photorespiration in the leaf tissue. It should be emphasized here that even the limited quantities of CO<sub>2</sub> released by leaf mitochondrial respiration provides for photosynthesis (Pinelli and Loreto, 2003). Studies along this line could help identify the truly mutual partners in endophyte associations and ultimately lead to artificial infection of plants with select endophyte species to increase photosynthetic efficiency through reduction of photorespiration. Furthermore, some basic information regarding endophyte status in homobaric and heterobaric leaves which differ in their physiology and mechanical functions (Kenzo et al., 2007) may throw light on endophytism as a survival strategy among fungi.

### 'Endophytism' as a phase in the life cycle of some fungi

It is likely that the suite of endophytes of a given plant species is an assembly of different ecological groups of fungi. For instance, it is envisaged that at least some of the endophytes continue to survive in the dead leaf tissue as leaf litter decomposers. Kumaresan and Suryanarayanan (2002) reported that some of the foliar endophytes of the mangrove *Rhizophora apiculata* continue to grow in fallen leaves and also produce extracellular enzymes which act on wall polymers of plant cells. Several recent investigations confirm that some endophyte species are also litter decomposers (Promputtha et al., 2010; Chaverri and Gazis, 2011; Purahong and Hyde, 2011; Sun et al., 2011; Hirose et al., 2013). Given their potential to elaborate many plant polymer destructuring enzymes (Suryanarayanan et al., 2012; Govinda Rajulu et al., 2011) and their ability to continue to exist as saprotrophs in fallen leaves (Unterseher et al., 2013), it is likely that endophytism represents a stage in the life cycle of fungi which alternates between a saprotrophic and an endophytic lifestyle. Spores of such biphasic fungi in forests experiencing periodic ground fires exhibit constitutive heat tolerance lending credence to this hypothesis (Suryanarayanan et al., 2011b). Expression of specific genes during endophytic and saprotrophic phases has

been observed for a root endophyte (Zuccaro et al., 2011). Similar genomic studies are needed to answer the question of whether multi-host endophytes which were not subjected to host-guided specialization have also evolved an endophyte–saprotroph (litter degrader) biphasic lifestyle governed by expressions of specific genes. While it is conceivable that litter decomposition is more rapid in leaves harbouring such biphasic endophytes, some endophytes affect litter decomposition in a negative way; for instance, colonization of *Acer macrophyllum* by the endophyte *Rhytisma punctatum* retards its litter decomposition (Le Roy et al., 2011). Hence, the role of endophytes in nutrient cycling in plant communities needs to be addressed.

### **Endophyte, host and insect interactions**

Even the limited studies on insect–endophyte interactions show that such interactions could be varied (Gange et al., 2012). For instance, while grasshoppers feed equally on heavily and moderately endophyte-infected leaves (Devarajan and Suryanarayanan, 2006), leaf-cutter ants avoid leaves with high densities of endophytes (Estrada et al., 2013). Thus, supporting more endophytes could be advantageous to plants in the Neotropics where leaf-cutter ants are one of the major defoliators (Van Bael et al., 2012). Other insect interactions include dispersal of endophyte propagules by phytophagous insects. Grasshoppers could disperse endophyte inoculum as endophytes pass undigested through their guts (Devarajan and Suryanarayanan, 2006). Tissues of Bt cotton plants which have restricted insect visitations have significantly lower endophyte infection frequencies indicating an insect-dependant endophyte infection process (Suryanarayanan et al., 2011c). Pažoutová et al. (2013), while elucidating the life cycle of a new insect-associated, endophytic anamorph species of *Daldinia*, opine that more studies are needed to unravel the relationship between plant host-specific insects and xylariaceous endophytes. In another recent study, Behie et al. (2013) show that the insect-parasite *Metarrhizium robertsii* upon establishing an endophytic association transfers nitrogen directly to its plant host from the insect which it parasitizes. These few investigations suggest that endophyte–plant–insect interaction is an important component of endophytism requiring more intense inquiry.

The existence of entomopathogenic fungi such as species of *Acremonium*, *Beauveria*, *Clonostachys* and *Paecilomyces* as endophytes in some plants has nurtured the concept of using them as biocontrol agents for managing insect pests of crops. Vega et al. (2008) reported that two endophytic entomopathogenic fungi, *Beauveria bassiana* and *Clonostachys rosea* of coffee were effective against coffee berry borer insect. When a suitable endophytic entomopathogen is identified, it has to be artificially inoculated in to plants to optimum levels to function as an effective biocontrol agent. In such a case, the interaction between an introduced (alien) endophyte and the native endophytes supported by a plant host has to be understood for successful biocontrol. Our preliminary study on this aspect suggests that an alien endophyte is not permanently integrated into the endophyte community of the plant host (Suryanarayanan, Govindarajalu & Vidal –

unpublished). We isolated an endophytic *Trichoderma* sp. from a marine alga which was effective against *Helicoverpa armigera*, a common insect pest of many crops. A spore suspension ( $10^7$  spores ml<sup>-1</sup>) of this fungus was sprayed on several vegetable crops and its survival as a foliar endophyte in these plants was studied by re-isolating it from surface sterilized leaves at regular intervals. In all plants, while the initial recovery of this alien endophyte was high 7 d after spraying (ca. 90%), it declined to 30–40% by 28 d after spraying. It has been observed that interactions between endophytes in the leaf could influence insect deterring properties of the plant (Gange et al., 2012). In the case of the vertically transmitted grass endophytes, they even trigger the evolution of specialist insects capable of detoxifying insect-deterrant chemicals of the endophytes (Faeth and Saari, 2012). Thus, specific studies on the tritrophic interactions between plants, their endophytes and their insect herbivores are essential to effectively utilize endophytes in biocontrol programs.

Endophytes appear to be admirably suited for biocontrol programmes considering their capacity to cause disease-free infections in a wide variety of plant species. It is easy to visualize genetically transformed endophytes carrying agronomically desirable genes to be incorporated in plant hosts. One caveat though in using endophytes as biocontrol agents emerges from our study (Thirumalai et al., 2013). *Fusarium pallidoroseum* (a non-endophyte) is used to control the fresh water weed *Eichhornia crassipes* (Naseema et al., 2004) and also as a biofertilizer to enhance the growth of crops (Srivastava et al., 2011). We discovered that this fungus survives as an endophyte in the leaves of *Piper betle* and that its colonization frequency increases in the leaf during storage. We also observed that the fungus produces mycotoxins. Considering the health hazards posed by mycotoxins, this fungus (and related species) is unsuitable for biocontrol.

### **Interaction of endophytes with other fungi**

The interactions among endophytes as well as endophytes and other fungi are little understood (Saunders et al., 2010). They may include competition among endophyte species in the host tissue mediated by production of antifungal compounds and detoxification of such inhibitors by endophytes. Circumstantial evidence for this comes from the study of Mohandoss and Suryanarayanan (2009); they showed that a systemic fungicide (hexaconazole) treatment eliminates certain native endophytes in the leaves of *Mangifera indica* with the attendant competitive release enabling alien endophyte species to colonize the leaf. Since endophytes produce in vitro a variety of antifungal compounds including alkaloids, terpenoids, and phenolics (Kumar and Kaushik, 2012), it needs to be unravelled if production of antifungal compounds and their detoxification by endophytes in vivo determine the final endophyte community in a plant tissue. If this were true, a situation akin to antibiosis prevailing in the soil can be expected in the endophyte-host milieu. Such interactions occurring in plant tissues could be visualized by Desorption Electrospray Ionization Mass Spectrometry (DESI-MS) imaging (Lane et al., 2009). Other types of imaging mass spectrometry (IMS) employing suitable scanning probes may also help

unravel interactions between endophytes in plant tissues, as has been done for studying interactions between bacterial species (Watrous and Dorrestein, 2011).

The leaf as an ecological niche for endophytes has not been fully explored. Considering differential gas concentrations inside a leaf (Pieruschka et al., 2005), it would be of interest to study the internal distribution of foliar endophytes. In a few cases, most of the endophytes are confined to the upper and lower epidermal layers of the leaf while very few are located in the mesophyll region (Suryanarayanan, 2011). A stratified distribution of different endophyte species in a leaf could minimize interspecific competition among them. Different endophyte species isolated from a leaf could be transformed with Green Fluorescent Protein (GFP) variants which fluoresce in different wavelengths and re-inoculated into the leaf to discern if there is preference among endophyte species for different microniches within a leaf.

There is hardly any information on the interactions of endophytes with other ecological groups of fungi. A study comparing the epiphyllous and endophytic fungi of 12 species of *Calamus* (Arecaceae), showed low overlap between the species composition of these two groups, suggesting that these two fungal groups are adapted to survive in different environments (Girivasan and Suryanarayanan, 2004). With reference to the *in vivo* interaction between pathogenic and endophytic fungi in the plant tissue, we again have very little information although it is known that some endophytes can control fungal pathogens (Arnold et al., 2003). One study indicates that foliar endophytes may bolster the quantitative resistance of *Populus* to *Melampsora* rust (Raghavendra and Newcombe, 2013). Wicklow et al. (2005) reported that an endophyte of maize produces antifungal compounds which inhibit fungal pathogens of this plant. Some pathogenic fungi survive as symptomless endophytes in plants (Suryanarayanan and Murali, 2006) and wait for the right set of signals to express disease symptoms (Photita et al., 2004; Junker et al., 2012); cues which activate latent pathogens harboured as endophytes to initiate disease symptoms need to be identified.

Despite the fact that conditions existing in leaves may not be ideal for fungal mutualists due to irregular availability of nutrients, drastic changes in temperature, humidity and gas concentrations (Goodman and Weisz, 2002), fungal endophyte–leaf associations are known even from as early as the Carboniferous period (Krings et al., 2012). This, and the fact that no plant screened for endophytes so far is free of them, indicates that endophytism is a successful adaptation of fungi and coevolved with plants. The different roles of the two partners in endophytism in guiding their co-evolution need to be studied in detail. Genomics of fungi differing in life strategies (saprotrophs, pathogens and mycorrhizae) have provided deep insights into substrate utilization by fungi and plant–fungal pathogen interactions (de Vries et al., 2011). A case in point is a study involving *Ustilago maydis* and its host plant maize. Simultaneous transcriptome profiling of both this pathogen and its host enabled Skibbe et al. (2010) to conclude that disease expression involves organ-specific gene expression of both organisms. Metabolic profiling of endophyte bacterium-infected and endophyte-free poplars showed that infection by the endophytic prokaryote significantly influences plant metabolite composition (Scherling et al., 2009). Such profiling of transcripts and metabolites of

both the host and fungal endophytes at different stages of endophytism is bound to unravel many unanswered questions about the evolution of this cryptic form of lifestyle among fungi. Moreover, considerable progress has been made in recent years in understanding the plant signal pathways related to pathogenesis and fungal effector molecules which manoeuvre host metabolism in favour of the pathogen (Djamei and Kahmann, 2012; Dou and Zhou, 2012; Doeblemann and Hemetsberger, 2013). Such studies could serve as a template to discover the intricacies of endophytism.

In summary, the rapid development in molecular biology and genomics in the recent past offers a lot of scope for unravelling the various facets of the ecology and phylogenetics of the horizontally transmitted endophytes. Viewing endophytes not merely as a subset of fungi, but as an integral part of the plant community, and studying the different aspects of their biology will help us to understand the evolution of endophytism among fungi. Information gained by such basic studies would go a long way towards better utilizing endophytes for technological applications.

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