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Fungal Endophytes: An Eclectic Review

T. S. Suryanarayanan
Vivekananda Institute of Tropical Mycology (VINSTROM), RKM Vidyapith, Chennai-600004, India
Corresponding author Email: t_sury2002@yahoo.com

Dr. T. S. Suryanarayanan
President, Mycological Society of India
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ABSTRACT

The horizontally transmitted fungal endophytes, especially the members of *Ascomycota*, establish endosymbiotic relationship with plants of all lineages. Endophytes are universal in their occurrence and have been reported from plants from different habitats. Their ability to elaborate an array of secondary metabolites showing different desirable biological activities has resulted in studying these fungi for technological use. It is imperative that we conduct basic studies to acquire information about the biology of endophytes to harness more profitably their technological traits.

Keywords: Fungal ecology, fungus-plant interaction, biotechnology, bioactive compounds

INTRODUCTION

At the outset, I express my sincere thanks to MSI for electing me as its President for the period 2015-2016 - an honour which I cherish and accept with humility considering the eminent mycologists who have preceded me as President. I convey my appreciation to the current and erstwhile office bearers of MSI for the furtherance of mycology in India.

For my Presidential address, I choose to delve into certain relatively underexplored facets of endophyte biology with the view to enthuse young mycologists to address these issues. Another motivation for this choice is that knowledge acquired from such explorations would improve substantially the options to harness the attractive technological potential offered by endophytes. I refer here to the so called Class 3 endophytes which generally reside in the above ground tissues of plants, cause highly localized infections and are transmitted horizontally (Rodriguez *et al*., 2009). They are associated with vascular and non-vascular plants of all biomes. Ascomycetous fungi, especially members of *Sordariomycetes* and *Dothideomycetes* occur most commonly as endophytes in all these plants (Higgins *et al*., 2007).

ENDOPHYTISM-A LIFE STRATEGY

Association of fungi with plants began very early during the evolution of land plants and such association has influenced their evolution (Krings *et al*., 2012). Plants as early as those of Early Devonian period which were devoid of true root systems had endophytic mycorrhizal associations (Remy *et al*., 1994). With reference to the leaf endophytes, lack of well-preserved fossils leads to the surmise that they probably evolved later during Early Cretaceous period coinciding with the appearance and diversification of angiosperms (Krings *et al*., 2012). Such a long time association of endophytes with plants and their universal presence in all vascular and non-vascular plants of the present time confirm that endophytism is a successful life strategy among fungi. Endophytes are not benign associates of plants. It is now clear that for some fungal species, endophytic existence is only a phase in their life cycle (Suryanarayanan, 2015). The study of Kumaresan and Suryanarayanan, (2002) showed some endophytic fungi of mangrove leaves continued to survive in fallen leaves as saprotrophs and could function as litter degraders. The results of a few recent studies support this observation (Korkama-Rajala *et al*., 2008; Voříšková and Baldrian, 2013; Prakash *et al*., 2015). Molecular analyses prove that endophytes switch to a saprotrophic mode in decomposing leaf litter (Szink *et al*., 2016). To facilitate such a biphasic life, different genes are upregulated depending on whether the fungus is in an endophytic or saprotrophic phase (Zuccaro *et al*., 2011).These observations bring into focus the advantage such endophytes have over the non-endophytic saprotrophic fungi which degrade plant litter, as the endophytes in the living leaves have a ready nutritional source to exploit once the leaf falls. Thus they could perform as pioneer degraders of litter and possibly prepare the substrate for the next players in succession. It is clear that endophytes with such biphasic life strategies (endophytic in living tissue and saprotrophic in dead tissue) have evolved to exploit more than one environmental niche. It would be of interest to study the competition between biphasic endophytes and true saprotrophs in nutrient recycling by plant biomass degradation (Szink *et al*., 2016). Similarly, degradation of crop litter should be revisited considering the impact that fungicides would have on resident endophytes.

HOST PREFERENCE-THE CASE OF COSMOPOLITAN ENDOPHYTES

Although endophyte diversity is high in neotropical forests (Arnold and Lutzoni, 2007), it is now established that in many plant ecosystems such as the dry tropical forests, their diversity is not exceptionally high (Murali *et al*., 2007). For instance, in our ten-year study on75 dicotyledonous tree hosts belonging to 33 families of montane evergreen, dry thorn and dry deciduous forest trees in the Nilgiri Biosphere Reserve, Western Ghats, we observed the following. Species accumulation curves for foliar endophytes fail to ascend continuously with increasing sampling effort. This is due to sharing of endophyte species by taxonomically unrelated tree species although individual tree species support rich endophyte diversity (Suryanarayanan *et al*., 2011a). Even during the rainfall seasons which favour endophyte infection, the leaves recruit more of the same endophytes such that only the endophyte frequency in a leaf increases but not its diversity (Murali *et al*., 2007). This situation is due to the presence of multi-host endophytes such as *Colletotrichum*, *Pestalotiopsis*, *Phomopsis, Phyllosticta* and *Xylaria.* These fungi occur as endophytes in a wide range of plant hosts and in different geographic locations and mostly dominate the endophyte assemblage of the plant tissue such as leaf so that the overall endophyte diversity in the given ecosystem is depressed (Pandey *et al*., 2003; Murali *et al*., 2006; Sakalidis *et al*., 2011; Suryanarayanan *et al*.,2011a; Govinda Rajulu *et al*., 2013; Sudhakara Reddy *et al*., 2016). With this group of endophytes not being transmitted vertically, the recruitment of a core group of fungi (representing the multi host endophytes) by all plants needs exploration. Suryanarayanan (2011) opines that because of the cosmopolitan occurrence and wide geographic distribution of some endophytes, the ratio of generalists and specialists (host specific) endophytes have to be considered while using endophytes as an indicator group for global fungal diversity. Indeed the loose host affiliation of these endophytes has prompted us to urge a reconsideration of the notion that endophytes are hyperdiverse in the tropics (Suryanarayanan *et al*., 2002, 2003, 2009b, 2011a; Pandey *et al*., 2003; Murali *et al*., 2007). Such a wide occurrence of some endophytes crossing host taxonomic and geographic barriers has not been satisfactorily explained. Suryanarayanan (2011) has recourse to the observations of May (1988, 1991) to explain such a loose host affiliation of some endophytes. According to May (1988, 1991), host specificity among plant associated organisms (insects, fungi) would be less in tropical forests owing to the high diversity of the plants (hosts). This is because a high diversity decreases their density (contiguity) and reduces the possibility of the plant-associated species to find a specific host - a situation which might lead to the evolution of organisms with ability to infect a wide range of plants (Basset *et al*., 1996; Novotny *et al*., 2006). In consonance with this is the fact that many plant- associated fungal guilds such as wood rotting fungi (Parfitt *et al*., 2010), ectomycorrhizal fungi (Tedersoo *et al*., 2010) and arbuscular mycorrhizal fungi (Zhao *et al*., 2003) do not exhibit host specificity. Endophytes could evolve and accumulate traits which enhance their ecological fitness leading to an expansion of their host range. This is explained by our studies in fire prone forests of the Western Ghats. Some of the multi-host endophytes in these forests which experience periodic forest fires produce thermotolerant spores (Suryanarayanan *et al*., 2011b) and utilize toxic furaldehydes (the most common and most abundant organic volatiles released during biomass burning) as carbon source (Govinda Rajulu *et al*., 2014). They also switch to a litter degrading saprotrophic phase and elaborate plant cell wall degrading enzymes to enable their survival as litter degraders (Prakash *et al*., 2015). Such traits aid in the widening of the ecological amplitude for these endophytes with reference to their host range. Cophylogenetic analyses of multi-host endophytes and their different plant hosts are necessary to determine their rates of evolution as has been done for *Xylaria* and its mycoparasites (Herrera *et al*., 2016). As some phytopathogenic fungi also reside as endophytes in the form of latent pathogens in plant tissues (Photita *et al*., 2004; Suryanarayanan and Murali, 2006), a comparative genomics approach would help in identifying the main evolutionary pressures associated with endophytes and provide clues about the evolution of endophytism as a life strategy among fungi. While cogitating on the effect of multi-host endophytes in depressing global fungal diversity, it should be stressed that molecular methods are needed to account for the unculturable endophytes (Arnold *et al*., 2007) and correcting errors arising due to host based recognition of fungal species (Photita *et al*., 2004) to assess the real contribution of endophytes to fungal diversity.

Another point that needs to be underscored is that currently about 93% of the estimated species of fungi are unknown to science and that most of these are expected to be present in the tropics. Manoharachary *et al.* (2005) stressed the need to study the various ecological groups of fungi of our country including the endophytes to identify new species. Only around 27,500 fungal species have been reported from India which includes 15,500 from plant litter, 327 on herbivore dung, 450 endophytic fungi (Bhat, 2010).This figure is meagre for a country of a large geographic area supporting a multitude of habitats. It is therefore imperative we earnestly strive to discover new fungal species as they could house novel genes for technological exploitation (Suryanarayanan and Hawksworth, 2005). To make this effort more productive and rapid, a crowd sourcing model for trait-based culture collections involving students, faculty, research labs and the Government has been proposed (Suryanarayanan and Venkat Gopalan, 2014; Suryanarayanan *et al*., 2015). This model envisages, apart from manpower training, a rapid build-up of fungal cultures to enhance the bioeconomy of the country. Endophyte of plants from relatively unexplored environments and habitats hold a great promise in this regard (Raghukumar, 2008). The occurrence of some fungal genera as endophytes in almost all the plants should not deter us from screening more plants for endophytes as conspecific fungal endophytes of plants of different habitats exhibit different traits. For example, we observed that the herbicidal activity of endophyte *Phyllosticta capitalensis* differed with the host from which it was isolated (Suryanarayanan *et al*., 2009b).

THE LEAF AS AN ECOLOGICAL NICHE-A PLETHORA OF INTERACTIONS

Though not all fungi that settle on a plant can infect it to survive as endophyte, it is not clear what factors determine the recruitment of certain fungal genera as endophytes.

While infection of plants by pathogenic fungi involves suppression of host defense responses by effector molecules and host tissue reprogramming, little is known about such events in endophyte infections. A selection mechanism appears to operate such that different fungi infect different tissues. Suryanarayanan (2011) commented that 'different tissues of trees rather than the same tissue from different tree species have higher β diversity of endophytes.' Girivasan and

Suryanarayanan (2004) compared the foliar endophytic and phylloplane fungal assemblages of 12 *Calamus* species. This study involved the screening of 2400 leaf segments and showed that although several fungal species were shared as endophytes by the different *Calamus* species, the sharing between endophyte and phylloplane fungal assemblages of each host was low. Very little information is available on post inflectional interactions between the host and the endophyte. The plant host restricts the growth of the endophyte but is not able to prevent or eliminate it. Schulz *et al.* (1999) proposed a balanced antagonism mechanism to explain this phenomenon. Plant-fungus interactions are intricate involving reaction and response at various levels. For instance, *Botrytis cinerea* undergoes massive programmed cell death (PCD) after penetrating the plant host and establishing a primary lesion. The PCD is induced by the host defense molecule called camalexin. The fungus in turn overcomes this defense response by a yet to be identified mechanism (Shlezinger *et al*., 2011). Thus, one method to study endophyte-host interactions would be to compare the alterations in a host immediately after infection by an endophyte species and a pathogenic fungus.

One of the first studies to report tissue preference among endophytes is that of Suryanarayanan and Vijaykrishna, (2001) who showed that the endophyte assemblage of the leaf and aerial root of *Ficus benghalensis*, although exposed the same fungal inoculum in the air due to their proximity did not overlap. Similar observations were made while comparing endophytes of petiole and propagule of *Rhizophora apiculata* (Kumaresan and Suryanarayanan, 2002) and leaf and bark of *Kandelia candel* (Pang *et al*., 2008). Tissue preference among endophytes could be a strategy to reduce interspecific competition among them and could be achieved by adaptations of the fungi to the different microenvironment prevalent in the tissues. To cite an example, endophytes from tannin-rich leaves tolerate high levels of tannin in the growth medium, compared to conspecific endophyte taxa from leaves with less tannin content (Mohandoss and Suryanarayanan, unpublished, cited in Suryanarayanan 2011). Furthermore, similar to the succession of fungi on litter or dung substrate, the endophyte assemblage in a leaf undergoes a change as the leaf ages (Suryanarayanan and Thennarasan, 2004). Certain fungi capable of establishing an endophyte association with a plant leaf do so only when the already existing endophytes in the leaf are eliminated (Mohandoss and Suryanarayanan, 2009). An endophyte from an alien plant when introduced into a crop gets eliminated over time (Suryanarayanan *et al*., 2016). These observations taken together lead to a syllogistic inference that various types of interactions are operating in a leaf harbouring endophytes. Indeed, Schulz *et al*. (2015) hypothesized that the antimicrobial substances secreted by endophytes aid in their competition with different microbes within the plant tissue.

The interaction between phytophagous insects and endophyte-laden plant tissue is another dimension of endophytsim that has not been studied in detail. It is reported that the density of endophyte infection is directly correlated with insect visitations of the plants (Suryanarayanan *et al*., 2011c). Endophyte infection (Petrini, 1991) and dissemination (Devarajan and Suryanarayanan, 2006) could be facilitated by phytophagous insects. According to David *et al.* (2016), insect herbivory influences the structuring of endophyte communities in plants. They quantified the associations between endophytes of an invasive plant (*Lythrum salicaria*) and leaf-chewing beetles (*Galerucella pusilla* and *G. calmariensis*) which were introduced in USA as biocontrol agents of *Lythrum salicaria.* They observed a positive correlation between insect damage of plants and endophyte isolation frequency and suggest that quantifying the associations between heterotrophic organisms may give clearer picture of their interactions with plants. It is also known that endophyte infection alters the leaf chemistry in some Neotropical plants such that leaf-cutting ants are warded off (Estrada *et al*., 2013). Suryanarayanan *et al.* (2016) speculate on the possible interactions between plant hosts and endophytes, among endophytes and between endophytes and other leaf inhabiting microbes and suggest that a clearer understanding of these would help in better utilizing endophytes as biocontrol agents. Fungus-plant interaction influences plant-feeding insects in complex ways and hence, with the present knowledge, it is impossible to generate a unifying model on the interrelationships among the interacting insects, plants, and fungi (Raman and Suryanarayanan, 2017).

Another aspect of endophyte biology is the cost and benefit for the host plant for housing endophytes. A few studies indicate that supporting endophytes is beneficial to the host plant. Endophytes increase the tolerance of plants to pathogens (Arnold *et al*., 2003) and abiotic stress (Redman *et al*., 2002). Leaf-cutting ants avoid feeding on leaves with high loads of endophytes (Estrada *et al*., 2015), diamondback moth larvae feed significantly more on control leaves than on endophyte-inoculated leaves (Suryanarayanan *et al*., 2016), and coffee plants are protected from coffee berry borers when they support entomopathogenic fungi as endophytes (Vega *et al*., 2008; see also Vidal and Jaber, 2015). *Fusarium verticillioides*, an endophyte of maize decreases the damage caused to the crop by its smut pathogen *Ustilago maydis*; however, the endophyte also metabolizes the defense compounds produced by the host to protect it from *U. maydis*. This indicates that an endophyte could be both a defensive mutualist and a parasite in the host plant (Rodriguez Estrada *et al*., 2012). A leaf supports numerous discrete infection foci of endophytes. Although the fungi are highly localized without exhibiting any intracellular growth, their presence in such high densities should cause a drain on the plant nutrients. On the other hand, the possibility of the respiratory CO_2 released by such highly localized endophytes reducing the photorespiration has to be discerned (Suryanarayanan, 2013). Such a situation would offset to an extent the cost for the plant bearing a heavy endophyte load. As the plant microbiome is complex involving interactions between different forms of life, it requires, apart from other methodologies, a community ecology approach to understand endophytism.

ENDOHYPHAL BACTERIA/VIRUSES-THE INSIDE STORY

The hyphae of endophytes may harbour bacteria or viruses. Hoffman and Arnold (2010) reported for the first time the existence of such endohyphal bacteria in endophytic fungi isolated from cupressaceous trees. A majority of these bacteria belonged to the Proteobacteria. Although facultative, (unlike the endohyphal bacteria of *Glomeromycota*), such endohyphal associates could affect the interactions between the endophyte and its plant host, endophyte and other plant associates and the plant and its environment. For instance, the endohyphal bacteria of the endophytes of *Cupressus sempervirens* exhibit activity against other endophytes and pathogens of the host plant thereby possibly increasing host fitness (Pakvaz and Soltani, 2016). Hoffman *et al.* (2013) demonstrated that the endohyphal bacteria of endophytes could enhance phytohormone production thus probably influencing the growth of the host. Endophytes also carry endohyphal viruses which play an important role in the mutualism exhibited by a plant and its fungal endophyte. The endophyte *Curvularia protuberata* provides thermotolerance to its host plant *Dichanthelium lanuginosum* (panic grass) (Rodriguez *et al*., 2008). Now it is known that the ability for both the endophyte and the plant to survive in geothermal soils is dependent on the presence of a double-stranded RNA mycovirus in the hypha of the endophyte (Morsy *et al*., 2010). Feldman *et al.* (2012) found that the mycovirus types in the endophytes of *Ambrosia psilostachya* and its parasite *Cuscuta cuspidata* were shared between different fungi indicating that these mycoviruses are not specific to a fungal taxon. Contrary to this, De Wet *et al.* (2011) showed that the endohyphal viruses of two closely related endophytes of Pine, *Diplodia scrobiculata* and *D. pinea* are not related. The diversity of endohyphal bacteria and viruses, their influence on the physiology of their fungal hosts, and their effect on the ecological fitness of the plant which are colonized by endophytes housing them are yet to be understood.

ENDOPHYTES-PROLIFIC PRODUCERS OF BIOACTIVE COMPOUNDS

The main reason for endophytes being the current focus of mycology is because of their ability to produce an array of secondary metabolites exhibiting different bioactivities. Many studies endorse the potential of endophytes to elaborate chemicals of different molecular make up (Aly *et al*., 2008; Krohn *et al*., 2008; Kusari *et al*., 2009; Shweta *et al*., 2010; Kharwar *et al*., 2011; Mohana Kumara *et al*., 2012; Zhang *et al*., 2012). The bioactivities of these metabolites include antibacterial, antifungal, anticancer (Suryanarayanan *et al*., 2009a), antimalarial (Kaushik *et al*., 2014) cytokine suppressing (Kaur *et al*., 2016), and weedicidal (Suryanarayanan *et al*., 2016) activities. Endophytes as an ecological group produce more novel metabolites than soil fungi (Nisa *et al*., 2015). It is possible that the multiple interactions that endophytes experience in the host tissue (with the host plant, with other competing endophytes and the pest and pathogens of the host plant) have guided the evolution of these fungi to elaborate many novel metabolites (Schulz *et al*., 2015). It is not clear how far the host chemistry and metabolism influences the metabolic profile of endophyte. It is not known if the metabolite profile of an endophyte differs with (i) the age of the plant tissue hosting it, (ii) the taxonomy of the host plant, and (iii) in the presence and absence of co-occurring endophytes. While it is known that endophyte infection upregulates many genes of the plant host (Mejia *et al*., 2014), the effect of host plant milieu on endophyte gene expressions are not clear. Genomic and transcriptomic analysis of the endophytic fungus *Pestalotiopsis fici* showed that it has a significant expansion of pectinase genes and gene clusters for secondary metabolite synthesis thus identifying it as a potential candidate for technological use (Wang *et al*., 2015). In this regard, I have highlighted in my earlier review some facets of endophyte ecology that need to be addressed (Suryanarayanan, 2013).

Some endophytes produce the metabolites of their host plants, a situation lending itself for straight forward technological exploitation in the production of plant based drugs. Examples include the production of plant metabolites such as taxol, camptothecin, podophyllotoxin, vinblastine, vincristine, hypericin, diosgenin, rohitukine, and azadirachtin (Sachin *et al*., 2013; Nicoletti and Fiorentino, 2015). Although this has given a new impetus to natural products based drug discovery, no endophyte has so far been used as an alternative source of plant metabolites as their production by the fungi rapidly dwindles under *in vitro* conditions. While horizontal gene transfer between the host plant and the endophyte is generally invoked to explain the fungal origin of plant metabolites (Tan and Zou, 2001), the work of Heinig *et al*. (2013) convincingly negates such a possibility at least with reference to taxol. Furthermore, fungi seem to lack the gene coding for strictosidine synthase (STR) which is a crucial enzyme in the pathway leading to the synthesis of strictosidine from which numerous terpenoid indole alkaloids (TIA) including camptothecin are synthesized by plants (Sachin *et al*., 2013). In the absence of STR and other downstream genes in TIA synthesis pathway, other possibilities have to be explored to explain the synthesis of TIA by fungi. Sachin *et al*. (2013) proposed the following possibilities to explain this. It is likely that the function of STR is carried out by a different enzyme and if so the attenuation of secondary metabolite production in culture could be due to gene silencing or gene methylation. Alternatively, since fungal hyphae are known to carry plasmids and endohyphal bacteria, the STR gene could be located in the free plasmid or in that carried by the bacterium. Loss from fungi of endohyphal plasmids and bacteria is common with subculturing and would explain attenuation of metabolite production. Studying the interaction between endophytes and plant hosts and endophyte and co-occurring microbes at various levels would aid in sustained production of plant metabolites by endophytes thereby relieving the dependence on plants for such bioactive compounds (Kusari and Spiteller, 2012; Vasanthakumari *et al*., 2015; Wang *et al*., 2016).

Most fungal secondary metabolites gene clusters are not expressed under *in vitro* growth conditions. Mechanisms of modulation of such silent genes have to be explored for sustained production of secondary metabolites by fungi (Lim *et al*., 2012; Brakhage, 2013). For instance, transforming *Cordyceps militaris* with *lae*A gene which regulates the secondary metabolism in most filamentous fungi increased the secondary metabolite production in this fungus (Rachmawati *et al*., 2013).

ENDOPHYTES FOR BIOCONTROL-THE FIGHT FROM WITHIN

Fungal genera such as *Acremonium, Beauveria, Isaria, Paecilomyces* and *Verticillium* which have entomopathogenic species also survive as endophytes in plants. Such endophytes which are natural enemies of insects could be used for pest management in agriculture. Vega *et al*. (2008) reported that entomopathogenic endophytes in coffee could control coffee berry borer.

According to Suryanarayanan *et al*. (2016), the prevalence of entomopathogenic fungi as endophytes in plants is very low and they suggest the screening of non entomopathogenic endophytes for insect control ability. They showed that a *Trichoderma harzianum* from a brown alga could be established as an endophyte in crop plants and it was effective in controlling *Helicoverpa armigera* (Suryanarayanan *et al*., 2016). Apart from insect control, for the first time Suryanarayanan *et al*. (2016) showed that endophytes also exhibit weedicidal properties. Basic studies regarding inoculation method and dose, interaction between the introduced and native endophytes, the cost and benefit for the crop for supporting the effective endophyte etc.are needed for using endophytes as biocontrol agents (Parsa *et al*., 2013; Vidal and Jaber, 2015).

Though endophytes have the potential to function as biocontrol agents, it should be underscored that some of them are latent pathogens and could initiate plant disease when the conditions are favourable. Many endophytic species of *Botryosphaeriaceae* are aggressive pathogens and could cause devastating disease when the host plants are stressed (Slippers and Wingfield, 2007). Many groundnut varieties carry *Leptosphaerulina crassiasca*, the causal agent of pepper spot disease of groundnut as symptomless endophyte (Suryanarayanan and Murali, 2006). Slippers and Wingfield (2007) observe that, in general, the current quarantine methods are not suitable for detecting latent pathogens in seed materials. This needs attention as fungal pathogen hiding as symptomless endophytes could spread widely and rapidly.

CONCLUSION

A plant is invariably associated with microorganisms (bacteria and fungi) which are present inside and outside. These microorganisms play a role in the nutrition and ecological fitness of the plant and hence a plant's performance and fitness is the result of both the plant and its microbial associates. Therefore, a plant can no longer be viewed as an isolated unit of life but as a holobiont together with its associated microbes (Vandenkoornhuyse *et al*., 2015). It is known that the fungal associates of plants aid in maintaining the diversity of tropical plants (Bagchi *et al*., 2014) and their functional traits govern important ecological processes (Treseder and Lennon, 2015). In this context, hardly any information is available on the ecology and the role played by endophytes in an ecosystem. The available information on endophytes is limited largely to their ability to produce bioactive and novel molecules in cultures. Studies tackling fundamental issues of endophytism such as their diversity in plants of less-studied and extreme habitats, ecology, within tissue interactions with the host and other competing microbes are the current need to understand fully the nature of plant-endophyte association.Techniques such as quantitative gene expression profiling, proteomics and metabolomics which have provided new information about phytopathogenic fungi (Tan *et al*., 2009), should help resolve many unanswered questions regarding endophytism as a mode of life among fungi. Information obtained from such investigations would vastly improve the understanding regarding the larger roles played by endophytes and the chances of utilizing their technologically important traits more profitably.

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