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Opinion

The Sebacinales: Elusive Enigmatic Endophyte

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The rhizosphere is the zone around a plant's roots where the most intensive interactions between plant hosts and their bacterial or fungal partners take place. Many fungal interactions are parasitic and association with an appropriate host can lead to disease, some are commensal or opportunistic endophytes, while others are mutualistic symbioses which are beneficial to host plants. The term fungal endophyte defines a fungus which spends at least a significant part of its life cycle inside of plant tissues without causing symptoms of disease. Many of these beneficial fungi are able to colonize the plant and form different types of mycorrhiza [1]. Generally speaking, endophytes from the rhizosphere can be easily distinguished from mycorrhizae by lacking external hyphal networks and mantles.

Mycorrhizas are highly evolved mutualistic associations between soil fungi and plant roots [2]. Such mutualism defines a symbiosis which is beneficial for both partners. The benefits are based on a fine-tuned balance between the demands of the invader and those of the plant host, and depend on environmental, physiological and genetic parameters. The mechanisms which ultimately determine whether a plant/fungus interaction is mutualistic or parasitic are quite complex and largely unknown. Substantial progress has been obtained in recent years for mycorrhizal interactions and many of the principles also apply to endophytic interactions [3,4,5]. The partners in these associations are members of most fungal classes (Basidiomycetes, Ascomycetes and Zygomycetes) and the large majority of vascular plant [6,7]. In the mycorrhizal literature, the term mutualism is often used to describe this symbiotic relationship where the host plant receives mineral nutrients while the fungus obtains photosynthetically-derived carbon compounds. More than 80% of plant families are associated with arbuscular mycorrhizae (AM), in comparison to only 3% that are associated with ectomycorrhizae [8]. However, in contrast to AM fungi, a large, taxonomically diverse number of fungal species form ectomycorrhizal associations, mainly belonging to the basidiomycetes and ascomycetes.

The Sebacinales belong to a taxonomically, ecologically, and physiologically diverse group of fungi in the Basidiomycota [9,10]. While historically recognized as orchid mycorrhizae, more recent culture-independent efforts utilizing sequence-based classification have demonstrated both their pandemic distribution and the broad spectrum of mycorrhizal types they form [11,12,13].

The Sebacinales have a worldwide distribution and an unparalleled interactive spectrum with land plants. Molecular ecology studies, based on rDNA sequences, have revealed that Sebacinales are common mycorrhizal associates with many plant species all over the world. Original reports come from India [14,15], Australia [16], South American (Argentina, Ecuador), Canada, and Europe (France, Germany and Estonia) [17]. They form ectomycorrhiza, orchid, ericoid, jungermannioid and cavendishoid mycorrhiza. Their presence is documented in field specimens of bryophytes (moss), pteridophytes (fern) and all families of herbaceous angiosperms (flowering plants) from diverse agro-climatic regions. These natural host plants include, among others, liverworts, wheat, maize and *Arabidopsis thaliana*, a genetic model plant traditionally viewed as non-mycorrhizal [18-20].

The two most studied species of the order Sebacinales are (a) *Sebacina vermifera*, and (b)*Piriformospora indica*. *Sebacina vermifera* was isolated from the Australian orchid *Cyrtostylis reniformis* [16], and *Piriformospora indica* was isolated from the rhizosphere of *Prosopis juliflora* and *Zizyphus nummularia* from Rajasthan, India [14]. The beneficial effects of *Piriformospora indica* and *Sebacina vermifera* mycobionts on experimental host plants, comprising increased growth, seed and metabolite yield, stimulation of systemic defense against parasites, and improved resistance towards abiotic and biotic stresses, are well documented [10,21]. Several additional properties of these fungi lead us to believe they can be a very valuable tool in efforts to facilitate low-input agriculture. Firstly, they are culturable and can be manipulated fairly easily in the lab. Secondly, perhaps most importantly, there has been no evidence of host specificity to date.

While studies with Sebacinales fungi are relatively few, particularly regarding agricultural applications, the future seems bright for this previously hidden group of symbionts. However, considering their proven beneficial influence on plant growth and their apparent ubiquity, Sebacinales fungi should be considered as a previously hidden, but amenable and effective microbial tool for enhancing plant productivity and stress tolerance [22]. In this day and age, the application of inorganic fertilizers has proven to be both unsustainable and ecologically damaging. With the world's natural resources being depleted daily, the race is on to find the technologies that satisfy the triple bottom line requirements of economic, social and environmental sustainability. Together with improving cultural practices such as precision pesticide and fertilizer application, continued improvements in breeding efforts led by high-throughput SNP genotyping, and genetic modification that is deemed safe and effective, harnessing the potential of the plant microbiome can play an important role in promoting low-input agriculture and making the second green revolution a reality.

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