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Current Opinion in Plant Biology

Broad compatibility in fungal root symbioses

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Plants associate with a wide range of beneficial fungi in their roots which facilitate plant mineral nutrient uptake in exchange for carbohydrates and other organic metabolites. These associations play a key role in shaping terrestrial ecosystems and are widely believed to have promoted the evolution of land plants. To establish compatibility with their host, root-associated fungi have evolved diverse colonization strategies with distinct morphological, functional and genomic specializations as well as different degrees of interdependence. They include obligate biotrophic arbuscular mycorrhizal (AM), and facultative biotrophic ectomycorrhizal (ECM) interactions but are not restricted to these well-characterized symbioses. There is growing evidence that root endophytic associations, which due to their inconspicuous nature have been often overlooked, can be of mutualistic nature and represent important players in natural and managed environments. Recent research into the biology and genomics of root associations revealed fascinating insight into the phenotypic and trophic plasticity of these fungi and underlined genomic traits associated with biotrophy and saprotrophy. In this review we will consider the commonalities and differences of AM and ECM associations and contrast them with root endophytes.

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Current Opinion in Plant Biology 2014, **20**:135–145

This review comes from a themed issue on **Biotic interactions 2014**

Edited by **Makoto Hayashi** and **Martin Parniske**

http://dx.doi.org/10.1016/j.pbi.2014.05.013

Introduction

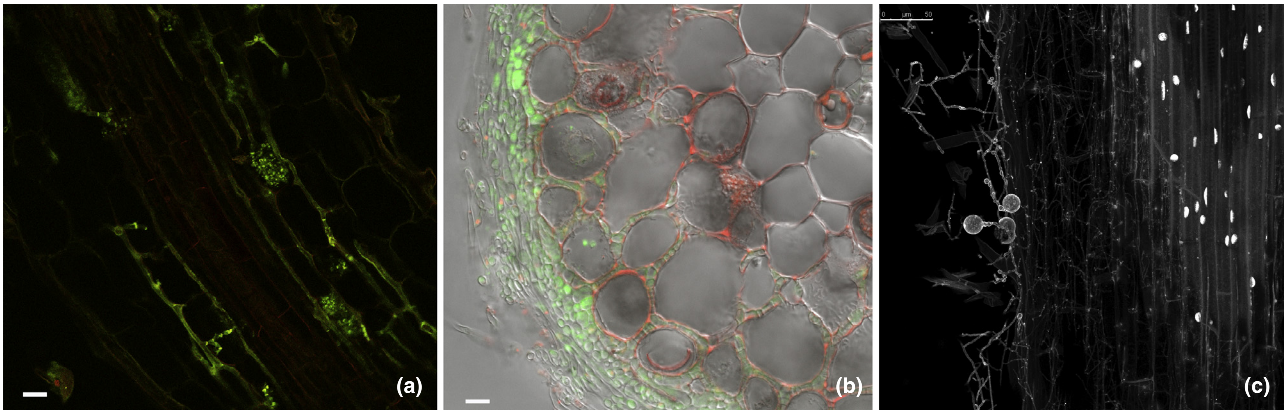
Beneficial root-associated fungi perform vital functions in host mineral nutrient uptake, carbon (C) cycling, plant growth promotion and/or increased resistance against plant pathogens that are fundamental to sustainable plant productivity. This is achieved by the establishment of an intimate interaction between the host cells and the fungal hyphae that can be more or less extensive and limited to the epidermis or include the cortex layers. These multifaceted fungal symbioses comprise a full spectrum of variation forming a continuum of interactions with highly distinct anatomical features and separate evolutionary histories [1–4]. The obligate biotrophic arbuscular mycorrhizal (AM) fungi belong to the Glomeromycota phylum, one of the oldest fungal lineages, and form the most widespread and common root–fungus associations. AM fungi have evolved an efficient means of acquiring inorganic nutrients from soil to supply plants, but cannot grow apart from their hosts [3,5,6]. Therefore, they are thought to have none or very little saprotrophic capability [7••,8••]. Ectomycorrhizal (ECM) fungi have arisen independently several times from saprotrophic ancestors and can be found in the phyla Ascomycota and Basidiomycota [9,10]. These fungi are important in forest ecosystems and, although they are capable to colonize the surface of non-host roots without penetrating them, intercellular growth is restricted to specific plant families, mostly trees [6]. These dual soil–plant inhabitants are efficient at deriving nutrients saprotrophically from soil organic matter, where they live transitorily, and biotrophically from plants, during mutualistic interactions. Thus, they display a strong adaptation to life within hosts but have maintained saprotrophic characters [11••,12••]. Depending on environmental conditions and host partners, ECM fungi can additionally be involved in parasitism where fungal infections may lead to the production of severe necrosis in the root cortices [13–16], indicating potential for mutualism and pathogenicity in this group of fungi. A different class of root associations is represented by the non-mycorrhizal endophytes. This group of fungi can be of beneficial nature and while the underpinning mechanisms are largely unknown, plant benefits range from growth promotion to increased resistance to biotic and abiotic stresses [17]. By definition root endophytes do not form an interface of specialized hyphae and are thought to colonize the host without efficient means for nutrient transfer towards the host [18]. Yet recent evidence shows that these fungi can form extensive biotrophic interfaces with plant cells, during which fungal hyphae are encased by the host plasma membrane [19,20•]. Indeed in several endophytic interactions nutrient transfer between the two partners was reported, but the means of transfer at the biotrophic interface is still unclear [21–23]. These fungi are widespread root inhabitants closely related to, but not restricted to ECM, orchid mycorrhiza (OM) and ericoid fungi, and also insect-parasitic fungi can act as beneficial plant endophytes delivering the roots with insect-derived nitrogen (N) [21,24]. Some mycoparasitic fungi feeding on other fungi can also be classified as beneficial root endophytes. These fungi are widely used in agriculture as biocontrol agents and whereas the mycoparasitism represents the ancestral life style they have acquired the ability to grow between cortical cells of their plant hosts [25•,26]. Like the AM fungi, root endophytes have a wide host range and can be found associated with the so-called non-mycorrhizal (NM) plants where they are able to establish biotrophy [19,20•,27]. Endophytic colonization of NM plants by AM fungi has also been reported, but it is considered to be functionally less significant as no arbuscules are formed in these hosts and hyphae typically occur in moribund cells with no plant growth promotion [18,28].

Commonalities and differences in AM, ECM and endophytic fungi, while sometimes difficult to grasp, are important to understand the impact of individual symbiotic interactions in the ecosystem and might be reflected in their genomic and transcriptomic traits. The recent release of the genomes of the AM fungus *Rhizophagus irregularis* (formerly known as *Glomus intraradices*) [7••,8••], the ECM fungi, *Laccaria bicolor* [11••] and *Tuber melanosporum* [12••], and the root endophyte *Piriformospora indica* [29••] provides unprecedented insights into how these beneficial root symbionts penetrate and establish within their hosts and to which extent their lifestyles are encoded in their genomes. This review describes current advances in understanding the components of root endophytic lifestyles from biological and comparative genomic analyses.

Biology of the symbiotic interface

The obligate biotrophic AM fungus *R. irregularis* (Glomeromycota, Glomerales) forms highly branched, tree-shaped structures, the arbuscules, inside living cortical cells, preferentially in the inner layers (Figures 1a, 2a). This extensive interface was shown to be the site of symbiotic nutrient transfer where phosphate and N are actively transferred to the plant in exchange for simple carbohydrates [3,5,30,31]. These fascinating fungal structures are associated with dramatic reprogramming of the host cell to accommodate intracellular hyphae which start even before actual penetration, resulting in the so-called pre-penetration apparatus [32]. Host cell rearrangement includes remodeling of actin filaments and microtubules, movement of the host nucleus to the center of the cell and site of fungal penetration, and deformation of the vacuole with proliferation of plastids and mitochondria. Intense re-organization of host cell architecture and physiology seems to be characteristic of obligate biotrophy and can be paralleled in mutualists and pathogens (e.g. powdery mildew fungi) [33], reflecting a continued coevolution with the hosts that led to the development of fungal and plant tools efficiently tailored to each other. Successful colonization and beneficial outcome by AM fungi is indeed dependent on the presence of a common symbiosis signaling pathway (SYM pathway) in the hosts [34,35]. This pathway is functionally conserved in several plant families and has homologs in bryophytes and green algae of the order Charales, suggesting the remote possibility of symbiotic associations in green algae [36].

Figure 1



Current Opinion in Plant Biology

(a) Section of paraffin-embedded root of *M. truncatula* inoculated with *R. irregularis* after staining with fluorescein isothiocyanate conjugate-wheat germ agglutinin, WGA-FITC. Scale bar, 10 μm. Photo kindly provided by Raffaella Balestrini and Paola Bonfante. **(b)** Laser-scanning confocal microscopy image of a transverse section of 12-week-old *L. bicolor*–*Populus trichocarpa* ectomycorrhiza root tip. Green signal corresponds to indirect immunolocalization of *L. bicolor* MiSSP8 protein (unpublished data) and plant root cells are counterstained with propidium iodide in red. Scale bar, 10 μm. Photo kindly provided by Claire Veneault-Fourrey. **(c)** Maximum projection of a barley root colonized by *P. indica* at 30 days post inoculation. Broad extraradical hyphae are visible at the boundary of the epidermis, whereas thin secondary hyphae are filling the cortical cells. Host nuclei are absent in the cortex cells, while the cylinder is undamaged and preserves intact nuclei. Scale bar, 50 μm.