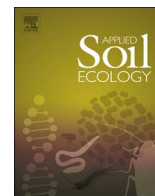




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Review

Focus on mycorrhizal symbioses

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ABSTRACT

A large proportion of the genetic diversity on Earth is represented by fungi. The true magnitude of fungal diversity has only recently been appreciated thanks to next-generation sequencing (NGS) and the development of large-scale DNA sequence datasets. In the last years, a great deal of effort has been dedicated to characterizing the fungal communities in soil. Fungal activity influences the structure of plant communities and provides various ecosystem processes. Mycorrhizal fungi are specialized root symbionts that interact with a great diversity of plants, forming the “mycorrhizae”. The development of several genome/transcriptome projects on soil fungi with different lifestyles is allowing to identify new functions and to verify how different mycorrhizal fungi interact and communicate with their host plants. In this brief note, attention will focus on some old and new aspects related to these widespread symbioses, highlighting some of their potentialities in agro-forest environments.

1. Introduction

The associations between soil mycorrhizal fungi and roots, referred to as mycorrhizae, are an essential feature of the biology of most terrestrial plants (Smith and Read, 2008; Bucher et al., 2014; van der Heijden et al., 2015). The classification of mycorrhizal types mostly depends on the structures formed inside or outside the plant roots and on the taxonomic position of the partners (Smith and Read, 2008; van der Heijden et al., 2015). Traditionally, the variety of mycorrhizal associations is divided into two main types, according to their ability to colonize the root cells: ecto- and endomycorrhizae, which form two different types of plant-fungus interface (Smith and Read, 2008; Balestrini and Bonfante, 2014). More specifically, four major mycorrhizal types have been described on the basis of their symbiotic structure and function: arbuscular mycorrhiza (AM), ectomycorrhiza (EM), orchid mycorrhiza and ericoid mycorrhiza (Table 1; BOX 1). A detailed description of the main structural features that characterize mycorrhizal morphologies can be found in Peterson et al. (2004). The symbiotic nature of the interaction between plant roots and mycorrhizal fungi is based on nutritional exchanges. The extraradical mycorrhizal mycelium, which grows out from the roots in soil, has access to mineral nutrients that are delivered to the host plants in exchange for carbon compounds (Smith and Read, 2008; Balestrini et al., 2013; van der Heijden et al., 2015). Nutrients are exchanged across the symbiotic interface between the plant and the fungus inside the roots (Smith and Read, 2008; Bonfante and Genre, 2010; Balestrini and Bonfante, 2014;

Rich et al., 2017). In addition to sugars, lipids have been recently demonstrated to be an additional source of organic carbon delivered to the fungus in AM symbiosis (Luginbuehl et al., 2017), and they are thought to be exported out of the root cell across the periarbuscular membrane for the use by the fungus (Bravo et al., 2017). Jiang et al. (2017) have reported that fatty acids produced by the host plants can be transferred to the AM fungus *Rhizophagus irregularis*, which lacks of the type I fatty acid synthase (FAS-I) complex, to sustain colonization. However, plant fatty acids can also be transferred to the pathogenic fungus *Golovinomyces cichoracerum* and are required for invasion by the pathogen, suggesting that both mycorrhizal and pathogenic fungi recruit the plant fatty acid biosynthesis program to facilitate colonization in a similar fashion (Jiang et al., 2017).

Mycorrhizal fungi play an important role in terrestrial ecosystems as they regulate nutrient and carbon cycles, and influence various ecosystem processes (van der Heijden et al., 2015), e.g. soil aggregation (Rillig and Mummey, 2006), litter decomposition (Lindahl et al., 2007) and seedling survival (van der Heijden et al., 2015 and references therein). Mycorrhizal symbioses influence plant growth and performance (including plant productivity), and increase the tolerance to biotic (Poza et al., 2009) and abiotic stresses, e.g. water deficit (Porcel et al., 2006; Kivlin et al., 2013; Rapparini and Peñuelas, 2014). However, effects are often variable between studies and are related to the context (e.g. plant and fungal species, environmental conditions, resources availability) (van der Heijden et al., 2015; Walder and van der Heijden, 2015; Berruti et al., 2016). In addition to improve plant

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Table 1
Biodiversity of mycorrhizal symbioses.

Mycorrhizal Type	Plants	Fungi	Fungal colonization
Arbuscular mycorrhiza (AM)	Most herbs, grasses and several trees, hornworts and liverworts	Glomeromycota	Endo-
Ectomycorrhiza	Pinaceae and Angiosperms (mostly shrubs and trees, mostly temperate), some liverworts	Basidiomycota and Ascomycota	Ecto-
Orchid mycorrhiza	Orchids	Basidiomycota ^a	Endo-
Ericoid mycorrhiza	Members of the Ericaceae, some liverworts	Mainly Ascomycota, some Basidiomycota	Endo-
Nonmycorrhizal plant species	Brassicaceae, Crassulaceae, Orobanchaceae, Proteaceae etc.		

Modified by van der Heijden et al. (2015).

^a Individual of ascomycetes genus *Tuber* has been also found in association with forest orchids (Selosse et al., 2004).

BOX 1

Definitions for mycorrhizal symbioses.

Arbuscular mycorrhiza (AM): The most widespread mycorrhizal interaction formed by fungi of the phylum Glomeromycota (arbuscular mycorrhizal fungi), which are obligate symbiotic fungi. Most of the mycorrhizal plants form endosymbiosis with AM fungi, including many important crop plants (e.g., maize, wheat, soybean, rice, tomato, etc.). The AM fungi colonize the roots developing inter- and intracellular hyphae, arbuscules and, in some species, vesicles.

Arbuscule. Highly branched structure produced by AM fungi inside the host plant root cells (mainly in the inner cortical layers) that represents functional symbiotic structure. Arbuscules are considered to be the main site where plant and fungus exchanges occur.

Spores. Subcellular thick-walled multi-nucleate resting structures (<http://invam.wvu.edu/>; <http://schuessler.userweb.mwn.de/amphylo/>).

Ectendomycorrhiza: A mycorrhizal type where „the sheath may be reduced or absent, the Hartig net is usually well developed, but the hyphae penetrate into the cells of the plants” (Smith and Read, 2008).

Ectomycorrhiza (ECM): ECM fungi dominate in forests, representing one of the main functional group in northern forest, and form symbiotic interactions mostly with woody plants. Although ECMs are made up of a relatively small number of plants these symbiotic interactions have an extensive occupancy of biomes (Martin et al., 2007). The ECM tree species, thanks to the mutualistic symbioses with ECM fungi, have been able to acquire metabolic capabilities that, in turn, have allowed otherwise unavailable ecological niches to be utilized (Smith and Read, 2008). ECM fungi are mainly known for their fruiting structures, e.g. truffles, bolets, chantarellas, amanitas. During the development of the ECMs, fungal hyphae surround the root tips, forming the mantle, and some hyphae penetrate between epidermal and outer cortical cells to form the Hartig net, which is considered the site for nutrient exchanges. <https://unite.ut.ee/>

Endomycorrhiza: Mycorrhizal symbiotic interaction that involve fungal penetration inside living root epidermal and cortical cells.

Ericoid mycorrhiza: Mycorrhizal fungi form endomycorrhizae with plants of the genus Ericales and play an important ecological role (i.e., as efficient SOM degraders), but are mainly restricted to heathlands (Read and Perez-Moreno, 2003).

Extraradical mycelium: Network of hyphae that develops in the soil, where the fungus absorbs nutrients that are transferred to the host plant through intraradical hyphae.

Orchid mycorrhiza: In nature orchids (i.e. members of the Orchidaceae plant family) establish a typical type of symbiotic interaction with specific soil fungi that allow seeds germination and development of adult plants. Orchids seeds, called “dust seeds”, contain little stored food reserves because lack the endosperm, and colonisation by a compatible fungus is essential for the provision of major nutrients such as carbon (C) and nitrogen (N), and, as a consequence, for their germination.

Pelotons. Fungal coils formed inside the orchid cells in germinating seeds, protocorms, and roots. The pelotons are thought to be the site of nutrient transfer between the symbionts that is essential for the perpetuation of orchids in their natural habitats (Dearnaley, 2007; Dearnaley et al., 2017).

mineral nutrition, AM fungi can alleviate heavy metal toxicity to the host plants and can tolerate high metal concentrations in the soil (references in Tamayo et al., 2014; Cicatelli et al., 2014; Meier et al., 2015; Ferrol et al., 2016). The availability of the genome sequence for the AM fungus *Rhizophagus irregularis* (Tisserant et al., 2013) has recently allowed researchers to identify several putative fungal genes coding for Cu, Fe, and Zn transporters (Tamayo et al., 2014). Although metal-tolerant plant species and ecotypes are known in the Ericaceae, metal tolerance in these plants has been mainly attributed to their association with ericoid mycorrhizal fungi (Daghino et al., 2016). The mechanisms underlying plant protection by the fungal symbiont are still poorly understood, while some insights have been obtained on the molecular mechanisms involved in heavy metal tolerance in the fungal symbiont, mainly thanks to “omics” approaches and the heterologous expression in model organisms (Daghino et al., 2016 and references therein). Metal tolerance and adaptation has also been studied in ECM species (i.e., *Suillus* species) that colonize the host plants in harsh environments

(Colpaert et al., 2004, 2011) and *Suillus luteus* was recently found to be a dominant member of the fungal communities from young pine plantation in soil polluted with zinc and cadmium (Op De Beeck et al., 2015). Additionally, some symbiotic fungi produce fruiting bodies with a high economical value, such as truffles and bolets (Mello et al., 2015).

2. Current research highlights

The development of DNA and RNA sequencing tools, such as the new sequencing techniques (next-generation sequencing, NGS), which produce short-read sequences in large quantity, as well as the advances in bioinformatics, have allowed to improve knowledge on the biology, ecology and biodiversity of mycorrhizal associations (Balestrini et al., 2013; van der Heijden et al., 2015). Great efforts have been dedicated to the characterization of soil fungal communities, including mycorrhizal fungi (Balestrini et al., 2015; Peay et al., 2016 and references therein). Soil fungi can in fact influence different ecosystem functions,

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