

Structural plasticity in root-fungal symbioses: diverse interactions lead to improved plant fitness

Article

Published Version

Creative Commons: Attribution 4.0 (CC-BY)

Open Access

Kariman, K., Barker, S. J. and Tibbett, M. ORCID: https://orcid.org/0000-0003-0143-2190 (2018) Structural plasticity in root-fungal symbioses: diverse interactions lead to improved plant fitness. PeerJ, 6. e6030. ISSN 2167-8359 doi: https://doi.org/10.7717/peerj.6030 Available at https://centaur.reading.ac.uk/81001/

It is advisable to refer to the publisher's version if you intend to cite from the work. See <u>Guidance on citing</u>.

To link to this article DOI: http://dx.doi.org/10.7717/peerj.6030

Publisher: PeerJ

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the <u>End User Agreement</u>.

www.reading.ac.uk/centaur

CentAUR



Central Archive at the University of Reading

Reading's research outputs online

Peer

Structural plasticity in root-fungal symbioses: diverse interactions lead to improved plant fitness

Khalil Kariman¹, Susan Jane Barker¹ and Mark Tibbett²

¹ School of Agriculture and Environment, The University of Western Australia, Crawley, Western Australia, Australia

² Centre for Agri-Environmental Research & Soil Research Centre, School of Agriculture Policy and Development, University of Reading, Berkshire, United Kingdom

ABSTRACT

Root-fungal symbioses such as mycorrhizas and endophytes are key components of terrestrial ecosystems. Diverse in trophy habits (obligate, facultative or hemibiotrophs) and symbiotic relations (from mutualism to parasitism), these associations also show great variability in their root colonization and nutritional strategies. Specialized interface structures such as arbuscules and Hartig nets are formed by certain associations while others are restricted to non-specialized intercellular or intracellular hyphae in roots. In either case, there are documented examples of active nutrient exchange, reinforcing the fact that specialized structures used to define specific mycorrhizal associations are not essential for reciprocal exchange of nutrients and plant growth promotion. In feremycorrhiza (with Austroboletus occidentalis and eucalypts), the fungal partner markedly enhances plant growth and nutrient acquisition without colonizing roots, emphasizing that a conventional focus on structural form of associations may have resulted in important functional components of rhizospheres being overlooked. In support of this viewpoint, mycobiome studies using the stateof-the-art DNA sequencing technologies have unearthed much more complexity in root-fungal relationships than those discovered using the traditional morphologybased approaches. In this review, we explore the existing literature and most recent findings surrounding structure, functioning, and ecology of root-fungal symbiosis, which highlight the fact that plant fitness can be altered by taxonomically/ecologically diverse fungal symbionts regardless of root colonization and interface specialization. Furthermore, transition from saprotrophy to biotrophy seems to be a common event that occurs in diverse fungal lineages (consisting of root endophytes, soil saprotrophs, wood decayers etc.), and which may be accompanied by development of specialized interface structures and/or mycorrhiza-like effects on plant growth and nutrition.

Subjects Agricultural Science, Ecology, Mycology, Plant Science Keywords Mycorrhiza, Endophyte, Symbiosis, Root colonization, Interface structures

INTRODUCTION

Early terrestrial plants moved from aquatic environments to emerged land about 400 million years ago, when the incipient soil was severely deficient in nutrients and organic matter. Early colonizers were bryophytes such as mosses, liverworts and hornworts,

Submitted 19 February 2018 Accepted 30 October 2018 Published 4 December 2018

Corresponding author Khalil Kariman, khalil.kariman@uwa.edu.au

Academic editor Jorge Curiel Yuste

Additional Information and Declarations can be found on page 23

DOI 10.7717/peerj.6030

Copyright 2018 Kariman et al.

Distributed under Creative Commons CC-BY 4.0

OPEN ACCESS

and were composed of a few cells with no true roots, leaves or stems (*Kenrick & Crane*, 1997). Fossil records indicate that lineages of early land plants established symbiosis with arbuscular mycorrhizal (AM) fungi during the Ordovician period (460 mya) (*Redecker, Kodner & Graham, 2000*), suggesting that AM fungi aided early colonization of nutrient/water-deficient land by plants via enhancing their nutrient and water uptake. As the ancient soil had an extremely limited reserve of organic matter, the central function of AM fungi presumably was to forage soil for inorganic nutrients, reflected in the functional capacity of extant AM associations.

Mycorrhizal and other (non-pathogenic) root-inhabiting fungi (such as endophytes) continue to play a vital role in soil nutrient cycling, remineralization of organic matter, shaping plant and microbial communities and ultimately safeguarding the stability and functionality of the entire land ecosystem (*Jumpponen & Trappe, 1998; Van der Heijden, Bardgett & Straalen, 2008; Weiss et al., 2011; Zuccaro, Lahrmann & Langen, 2014*).

Fungal partners can be obligate biotrophs i.e., entirely dependent on living root cells as in AM symbiosis, in which cell architecture and physiology is intensively reorganized to arrange the biotrophic interface (Genre et al., 2005). Some fungal symbionts are facultative biotrophs or partly dependent on their living host such as some ECM fungi or dark septate endophytes (DSE) (Jumpponen & Trappe, 1998; Koide et al., 2008). Sebacinalean endophytes (SE) have both biotrophic and necrotrophic (preceded by pre-programmed death of cortical cells) habits during their interaction with plant roots (*Weiss et al., 2011*; Lahrmann & Zuccaro, 2012). In return for the assorted benefits conferred to the host plant, the root-associated fungi may depend on their host as the carbon (C) source. Simple sugars (hexoses) were presumed to be the sole C type received by fungal partners in mycorrhizal associations (*Smith & Read*, 2008), perhaps due to a primary research focus on carbohydrates as a possible food source rather than other organic molecules such as fatty acids (FAs) that were not technically feasible to detect at the time. However, Keymer et al. (2017) fed plants with $[U^{-13}C6]$ glucose and monitored the ¹³C patterns of fungal FAs in Lotus japonicus wild-types and mutants defective in AM-specific paralogs of lipid biosynthesis genes (KASI and GPAT6), and demonstrated that plants transfer 16:0 FAs to AM fungi. Accordingly, sugars are now known not to be the only C form provided by host plants in mycorrhizal symbiosis.

Fungal trophic habits are associated with presence/absence of genes involved in degradation of plant cell wall components. Phylogenetic analyses have provided evidence for genomic modifications in certain root fungal symbionts in order to switch from saprotrophic/pathogenic lifestyles towards symbiotic lifestyles (*Kohler et al., 2015*; *Hacquard et al., 2016*; *Weiss et al., 2016*). Convergent loss of saprotrophic traits such as genes encoding plant cell wall degrading enzymes has been documented in ECM fungi (*Kohler et al., 2015; Fesel & Zuccaro, 2016*), which is a genomic signature for ECM evolutionary transition via saprotrophy to biotrophy, but not in root endophytes such as *Colletotrichum tofieldiae and Serendipita indica (Lahrmann et al., 2015; Hacquard et al., 2016*).

Interface structures have been considered to be the defining features of root-fungal interactions, however the underlying mechanisms of nutrient exchange vary across different

associations. Interface structures can be specialized (arbuscules, Hartig nets and fungal pegs), non-specialized (hyphae and hyphal coils), or totally absent. In this review, we examine a range of symbiotic relationships between soil-inhabiting fungi and plant roots, focusing primarily on root colonization and interface structures, to address the question of whether the focus on interface structures has limited our understanding of the wider diversity of these symbioses. To date, the types of root-fungal symbioses have been defined by the species involved and the structures developed; namely AM, ECM, ectendomycorrhiza (EEM), arbutoid mycorrhiza (ABM), monotropoid mycorrhiza (MTM), orchid mycorrhiza (OM), ERM (Smith & Read, 2008), sheathed ericoid mycorrhiza (SERM) (Vohnik et al., 2012), SE (Weiss et al., 2011; Zuccaro, Lahrmann & Langen, 2014), DSE (Jumpponen & Trappe, 1998; Koide et al., 2008), fine root endophytes (FRE) (Crush, 1973; Gianinazzi-Pearson et al., 1981; Orchard et al., 2017), fire-associated mutualism (FAM) (Baynes et al., 2011), and a non-colonizing symbiosis (hereafter named "feremycorrhiza", FM) described recently (Kariman et al., 2014a). Figure 1 illustrates the root colonization features in currently described plant-fungal associations, and Tables 1 and 2 summarize their main characteristics and benefits for host plants, respectively.

The location of the plant-fungal interaction on the mutualism–parasitism spectrum ultimately depends on the nutritional balance achieved by the partnership rather than the type of interface structure that is formed (*Smith & Smith*, 1996). Regardless of the symbiosis type and morphological traits, the net outcome of root-fungal interactions for host plants (positive, neutral, or negative responses) is determined by environmental conditions (e.g., nutrient availability in soil), plant/fungus genetics, and temporal relationships during mycorrhizal development (*Johnson, Graham & Smith*, 1997; *Klironomos*, 2003).

Three waves of mycorrhizal evolution have been proposed by Brundrett & Tedersoo (2018) including (i) the origin of AM associations in early terrestrial plants over 450 Mya, (ii) evolution of ECM (except Pinaceae), nonmycorrhizal (NM) roots, ERM, and OM associations along the period of major root diversification in the Late Cretaceous, and iii) development of specialized nutrition strategies and multifunctional (e.g., AM and ECM) roots in a few plant families. The third wave is an ongoing trend that is related to substantial climate change since the Palaeocene. Recent studies have revealed that the actual niches of different root symbionts could extend beyond those our respective domains of research predict (Selosse, Schneider-Maunoury & Martos, 2018). Evolutionary tendency towards shifting ecological niches (evolutionary trajectories) seems to be a common event in fungi that occurs convergently in numerous independent taxa. In fungal root symbionts, the key evolutionary trajectories include (i) additional food source plus protection against soil adversities and (ii) regressive evolution, such as that of enzymes involved in saprotrophic nutrition (Selosse, Schneider-Maunoury & Martos, 2018). Transitions between nutritional strategies in root-fungal relationships, especially gains or losses of ECM and NM strategies, are more common than previously thought (Brundrett & Tedersoo, 2018). In this review, we have briefly mentioned the ecological niches of certain root symbionts, which seem to have been overlooked.

The majority of plants may be simultaneously associated with a multitude of symbiotic fungal clades in their natural ecosystems. Mycobiome studies using the state-of-the-art



Figure 1 Schematic representation of root colonization strategies in plant-fungal symbioses. The diagram illustrates the interface structures, root cell penetration features of hyphae (i.e., intercellular or intracellular), and also indicates to what extent (epidermis, outer cortex or inner cortex) fungal structures develop. In feremycorrhiza, however, root colonization does not occur. Abbreviations for the symbioses (in blue) are as follows: AM, arbuscular mycorrhiza; ABM, arbutoid mycorrhiza; DSE, dark septate endophytes; ECM, ectomycorrhiza; EEM, ectendomycorrhiza; ERM, ericoid mycorrhiza; FRE, fine root endophytes; FM, feremycorrhiza; MTM, monotropoid mycorrhiza; OM, orchid mycorrhiza; SE, sebacinalean endophytes; and SERM, sheathed ericoid mycorrhiza. Abbreviations for fungal structures (in black): A, arbuscules; ERH, extraradical hyphae; FP, fungal peg; HC, hyphal coils; HN, Hartig net; M, mantle; MS, microsclerotia; and V, vesicles.

Full-size DOI: 10.7717/peerj.6030/fig-1

"omics" technologies have unearthed a range of root endophytic and root-colonizing saprotrophic relationships involving diverse fungal lineages in both mycorrhizal and NM plants (*Shakya et al., 2013; Toju et al., 2013; Oliveira et al., 2014; Toju, Sato & Tanabe, 2014; Coleman-Derr et al., 2016; Glynou et al., 2016; Almario et al., 2017*). For example, two independent studies using 454-pyrosequencing have revealed diverse mycorrhizal and endophytic taxa associated with roots of 36 co-occurring plant species in an oak-dominated forest in northern Japan (*Toju, Sato & Tanabe, 2014*), and three endangered orchid species in the Atlantic Forest, in Brazil (*Oliveira et al., 2014*). These studies support the proposition that beneficial root-fungal interactions could extend far beyond the well-established associations mentioned above (Fig. 1). It is increasingly apparent that study of plant performance in the absence of the co-evolved rhizosphere biota will give a limited and

Interface structures in predominantly beneficial root-fungal associations cat- egorized by symbiosis type and part- ner taxa. Symbiosis	Plant Taxa	Fungal Taxa	Interface Structures	Intracellular Hyphae	Fungal Sheath
Arbuscular Mycorrhiza (AM) Bryophytes, Pteridophytes, Angiosperms, Gymnosperms	Mucoromycota: Glom- eromycotina	Arbuscules	+	+	-
Fine Root Endophytes (FRE)	Angiosperms ^b	Mucoromycota: Mucoromy- cotina	Arbuscules	+	_
Ectomycorrhiza (ECM)	Angiosperms, Gymnosperms	Basidiomycota, Ascomycota, Mucoromycota	Hartig net	_	+
Ectendomycorrhiza (EEM)	Angiosperms, Gymnosperms	Basidiomycota, Ascomycota, Mucoromycota	Hartig net & Hyphal coils	+	±
Arbutoid Mycorrhiza (ABM)	Ericales: Ericaceae, Pyro- laceae	Basidiomycota	Hartig net & Hyphal coils	+	±
Monotropoid Mycorrhiza (MTM)	Ericales: Ericaceae	Basidiomycota	Hartig net & Fungal peg	_	+
Orchid mycorrhiza (OM)	Asparagales: Orchidaceae	Basidiomycota Ascomycota	Hyphal coils (Pelotons)	+	_
Ericoid Mycorrhiza (ERM)	Ericales: Ericaceae	Ascomycota Basidiomycota: Sebacinales	Hyphal coils	+	_
Sheathed Ericoid Mycorrhiza (SERM)	Ericales: Ericaceae	Basidiomycota	Hyphal coils	+	+
Sebacinalean Endophytes (SE)	Bryophytes, Pteridophytes, Angiosperms, Gymnosperms	Basidiomycota	Hyphal coils	+	_
Dark Septate Endophytes (DSE)	Angiosperms, Gymnosperms,	Ascomycota	Hyphae & Microsclero- tia	+	_
Fire-Associated Mutualism (FAM) ^a	Angiosperms: ^b Poaceae	Ascomycota	Unknown	Unknown	_
Feremycorrhiza (FM)	Angiosperms: ^b Myrtaceae	Basidiomycota	Absent	No root col- onization	-

Table 1 Interface structures in predominantly beneficial root-fungal associations categorized by symbiosis type and partner taxa.

Notes.

^aRoot colonization features need to be clarified. ^bThe host plant range needs to be investigated.

even skewed understanding of plant functioning in their natural environments (*Smith et al., 2011*) e.g., for applications such as increasing sustainability of food production in low input agroecosystems, and habitat restoration for recovery of endangered species (*Philippot et al., 2013*). Efforts such as those to ameliorate degraded lands may be further hampered by insufficient understanding of the complex variety of plant-fungal interactions that may also need to be restored (*Bever et al., 2010*).

Overemphasizing the visibility of symbioses (i.e., root colonization and interface specialization) could have hindered our understanding of the actual functional contribution of root-associated fungi towards health and performance of terrestrial ecosystems. This review examines the morphological (interfacial matrix) and functional (primary focus on plant fitness) aspects of diverse symbioses with the aim of engendering discussion about a broader view of plant-fungal root symbioses that emphasizes both form and function. Furthermore, our modest knowledge of fungal taxonomy and ecology also contributes

Symbiosis	Benefits for host	Reference
ABM: Arbutoid Mycorrhiza	^a Presumably, similar benefits as the ECM symbiosis	Münzenberger, Kottke & Oberwinkler (1992)
AM: Arbuscular Mycorrhiza	Improved mineral nutrition (P and Zn, in particular); tolerance against biotic (pathogens) and abiotic stresses such as drought, salinity, and heavy metals; improved soil health and structure	Smith & Read (2008), Sikes (2010), Hilde- brandt, Regvar & Bothe (2007)
DSE: Dark Septate Endophytes	Breaking down various organic substances and releasing nutrients; protection against plant pathogens, herbivores, and abiotic stresses such as heat, presumably due to the fungal capability of synthesizing antibacterial and antifungal compounds, toxic secondary metabolites, or high melanin contents of hyphae	Jumpponen & Trappe (1998), Newsham (1999), Newsham (2011)
ECM: Ectomycorrhiza	Improved plant vigour and access to nutrients that are tightly fixed in complex organic matter or soil particles (N and P in particular); alleviating stresses caused by soil-borne pathogens and abiotic stresses such as drought and salinity; ameliorating the CO_2 fertilization effect; accelerating weathering of rocks and releasing essential nutrients; decomposition of soil organic matter, tolerance to P toxicity	Landeweert et al. (2001), Smith & Read (2008), Terrer et al. (2016), Kariman et al. (2014b)
EEM: Ectendomycorrhiza	Hydrolyzing complex polysaccharides and supplying C to young host seedlings prior to the beginning of their autotrophism; possibly involved in revegetation of disturbed sites and establishment of conifer seedlings post-fire	Trevor et al. (2001); Navarro-Ródenas et al. (2012)
ERM: Ericoid Mycorrhiza	Assisting plants to survive in nutrient impoverished habitats through mineralization and acquisition of nutrients from soil organic sources	Read, Leake & Perez-Moreno (2004)
FAM: Fire-Associated Mutualism	Thermotolerance and fire adaptation by enhancing both probability of fire (via increased plant biomass) and plant survival (larger underground seed bank)	Baynes et al. (2011)
FM: Feremycorrhiza	Improved plant growth and nutrition mainly via increasing nutrient solubilization and mobilization; tolerance to P toxicity	Kariman et al. (2014a), Kariman et al. (2014b)
FRE: Fine Root Endophytes	Possibly involved in tolerance against extreme environmental conditions such as high altitude, soil acidity, cold temperatures, and waterlogging. Functional traits are not well known	Postma, Olsson & Falkengren-Grerup (2007), Orchard et al. (2016)
MTM: Monotropoid Mycorrhiza	Supplying C (sourced from neighbouring trees) to mycoheterotrophic host plants	Tedersoo et al. (2007), Hynson et al. (2013)
OM: Orchid mycorrhiza	Feeding host plants during their mycoheterotrophic phase, mainly through breaking down simple/complex organic matter	Cameron, Leake & Read (2006)
SE: Sebacinalean Endophytes	Improved growth and resistance against biotic and abiotic stresses such as salinity	Varma et al. (2001), Weiss et al. (2011), Weiss et al. (2016)
SERM: Sheathed Ericoid Mycorrhiza	^a Presumably, similar benefits as the ERM symbiosis	Vohnik et al. (2012)

Table 2 Key benefits of different root-fungal symbioses for host plants.

Notes.

^aThere is limited experimental evidence about the potential benefits for host plants.

to our limited understanding of the functioning of root fungal symbionts, hence we will explore the taxonomically/ecologically diverse interactions observed recently by aid of high-throughput "omics" technologies.

Current definition of symbiosis

It is necessary to mention the current definition of symbiosis, which is arguably the most controversial term in the history of biological terminology (Martin & Schwab, 2013). The term "symbiotismus" was coined by Albert Bernhard Frank in 1877 to describe the mutualistic relationship in lichens, whereas the word "symbiosis" is credited to Anton de Bary who, one year later, defined symbiosis as "the living together of unlike named organisms" (Sapp, 1994; Sapp, Carrapico & Zolotonodov, 2002). While some scientists persisted in the opinion that "symbiosis" should only be used for mutualistic relationships, others extended the definition to encompass commensalistic and parasitic interactions (Douglas, 2010). The 130-year-old debate is over now and the current general biology and ecology textbooks use the broader definition of symbiosis that includes all possible interaction types, and the restrictive definition (equalizing symbiosis with mutualism) has essentially disappeared (Martin & Schwab, 2013). Symbiosis (which literally means "living together", derived from the Greek word "sym": together, and "biosis": living) is currently defined as any type of close and long-term ecological relationship between two living organisms of different species. Here, we explore the root-fungal symbioses that are predominantly beneficial to host plants i.e., mutualistic and commensalistic symbioses, where the fungal partner may or may not benefit from the association, respectively.

Interfacial and functional properties of root-fungal symbioses Arbuscular mycorrhiza (AM)

Approximately 80% of all vascular plant species establish AM symbiosis (72% are AM consistently, while 7% form inconsistent NM-AM associations) including bryophytes, pteridophytes, gymnosperms and angiosperms (Brundrett & Tedersoo, 2018) with the fungi that were, until very recently, classified within the phylum Glomeromycota (Smith & Read, 2008; Schussler & Walker, 2010). Spatafora et al. (2016) conducted extensive phylogenetic analyses of a broad range of fungal taxa and consequently split zygomycetes into two phyla Mucoromycota (mainly mycorrhizas, root endophytes and saprotrophs) and Zoopagomycota (mainly pathogens of small animals and fungi), and placed AM fungi (AMF) within Mucoromycota as a subphylum i.e., Glomeromycotina. Although AMF are considered to be nonspecific or have very low species-level specificity (Smith & Read, 2008), the extent of colonization and AMF composition may vary for different plant-fungus combinations. AMF communities can be influenced by plant identity, ecological groups (e.g., habitat generalist plants vs habitat specialist plants) or the ecosystem type (Gollotte, Van Tuinen & Atkinson, 2004; Öpik et al., 2009; Veresoglou & Rillig, 2014). For example, Vandenkoornhuyse et al. (2003) demonstrated that even coexisting grass species can have significantly different AMF communities. With respect to ecological preferences, specialist AMF taxa were shown to have a tendency towards habitat specialist plants, while generalist AMF prefer habitat generalist plants in both forest and grassland ecosystems (*Öpik et al.*, 2009; Vályi, Rillig & Hempel, 2015).

The main benefits plants receive from AM symbiosis include access to the soil nutrients that are otherwise unavailable and resistance against pathogens and environmental stresses such as drought, salinity and heavy metal toxicity (*Smith & Read, 2008*). AM fungi are not able to complete their lifecycle in the absence of a host and this effect has not been able to be overcome by tissue culture techniques. The close evolutionary relationship extending over the entire period of plant evolution on land, and the remarkable intracellular development of these fungi that involves very close interaction between the plant and fungal nuclei suggests this symbiosis has evolved towards the same host nucleus dependence that have eukaryote cell organelle symbioses (*Barker, Tagu & Delp, 1998*), and other specialized microbial symbioses such as legume-rhizobium associations (*Coba de la Peña et al., 2017*).

Although AM fungi generally colonize roots, colonization of root hairs has also been documented (Guinel & Hirsch, 2000). Hyphae grow inter- and intracellularly through living epidermal and cortical cells, in which they produce specialized shrub-shaped structures called arbuscules. Prior to hyphal penetration, host epidermal cells located immediately below the fungal appressorium undergo intensive re-programming, such as remodeling of actin filaments and microtubules, and form a pre-penetration apparatus (PPA, Genre et al., 2005). Therefore, PPA formation is an appropriate cellular marker indicating which epidermal cells are about to be colonized. The PPA development includes differential expression of genes involved in cell wall modification such as expansin-like gene and cellulose synthase (Siciliano et al., 2007). Following penetration into the root cortex via extracellular or intracellular hyphal growth, and depending on the plant-fungus combination, AM associations may produce arbuscules (Arum-type), thick hyphal coils (Paris-type), or intermediate structures (such as arbusculate coils) that cannot be easily defined (Smith & Smith, 1997; Dickson, 2004; Karandashov et al., 2004). Arbuscules are separated from the cytoplasm by a pre-arbuscular membrane, originated by invagination of plant plasma membrane, and are specialized interface structures where the fungal partner trades nutrients such as P, taken up from soil using its extensive extraradical hyphae, for simple carbohydrates from the host plant (Harrison, 2012). Arbuscules are preferentially formed inside inner cortical cells. Similar to arbuscules, hyphal coils are surrounded by plant plasma membranes. The morphological variability of AM structures may be influenced by plant cultivars, fungal isolates and soil conditions (Dickson, 2004). Arum-type associations may be superior in supplying nutrients to their host due to growing intercellularly in a longitudinal pattern (a feature missing in the Paris-type), leading to higher colonized root length. The Paris-type structures, however, live longer than arbuscules. Although the total percentage of root colonization (counting all intraradical structures) is generally considered to be an indicator of the AM presence and functionality, the extent of colonization does not necessarily reflect the physiological responses of the plant host (Jakobsen, 1995; Smith, Smith & Jakobsen, 2004; Kariman et al., 2014b). This could be related to relative abundance and activity of arbuscules as well as the extent of development of extraradical hyphae and their effectiveness in nutrient uptake.

Recent work highlights the fungal influence on nutrient transporters in roots, which differs for different species interactions (*Smith, Smith & Jakobsen, 2004; Smith et al., 2011; Kariman et al., 2014a*). Nutrient-related signals seem to control the development

of AM symbiosis. Two conserved cis-elements (MYCS and P1BS) in the promoter regions of AM-inducible phosphate transporter genes are required simultaneously for symbiotic gene expression and root colonization (*Karandashov et al., 2004; Chen et al., 2011*). Coordination of inorganic P (Pi) starvation and AM signalling pathways appears to be the prerequisite for establishment of the symbiosis, but the precise regulatory mechanisms underlying this phenomenon are not known. Although generally considered a beneficial association for host plants, the net effects of AM associations on the host plant can be positive, neutral, or even negative depending on the plant-fungus combination and genetics, origin of the fungal isolates, and environmental context (*Klironomos, 2003; Smith, Grace & Smith, 2009*).

Fine Root endophytes (FRE)

Fine endophytes are root endophytic fungi associated with angiosperms that have been traditionally classified as AM fungi (Glomus tenue) (Crush, 1973; Gianinazzi-Pearson et al., 1981), but their taxonomic position has been quite ambiguous (Schussler & Walker, 2010) until recently. Orchard et al. (2017) clarified the phylogenetic position of FRE and demonstrated that these fungi belong to Mucoromycotina, not Glomeromycotina. Typical features of FRE include fine hyphae of less than 1.5 μ m in diameter, intracellular colonization of epidermal and cortical cells in a fan-like branching pattern, and production of arbuscule- and vesicle-like structures (Gianinazzi-Pearson et al., 1981; Abbott, 1982; Orchard et al., 2017). Capability of Mucoromycotina to establish symbiosis with early terrestrial plants has raised the hypothesis that Mucoromycotina may be predecessors of Glomeromycotina (Bidartondo et al., 2011; Hoysted et al., 2018). The hypothesis is further supported by the close phylogenetic relationship between Mucoromycotina and AM fungi (Lin et al., 2014; Spatafora et al., 2016), recent demonstration of a mutually beneficial symbiosis between Mucoromycotina and Haplomitriopsida liverworts (Field et al., 2015), and their arbuscule-forming feature (Orchard et al., 2017). Improved growth of ryegrass (Lolium perenne), cocksfoot (Dactylis glomerata), and sweet vernal (Anthoxanthum odoratum) associated with FRE has been observed under P-deficient conditions (Crush, 1973). FRE may have important ecological functions in plants exposed to abiotic stresses due to their ubiquitous presence under extreme environmental conditions such as high altitude, soil acidity, cold temperatures, and water-logging (Crush, 1973; Postma, Olsson & Falkengren-Grerup, 2007; Newsham, Upson & Read, 2009; Orchard et al., 2016). The available evidence suggests that the role of FRE fungi in supporting healthy plant communities should be further examined (Orchard et al., 2016).

Ectomycorrhiza (ECM)

Around 2% of all vascular plant species (~8,500 species) form ECM symbiosis (*Brundrett* & *Tedersoo*, 2018). ECM hosts are mostly woody species belonging to *Betulaceae*, *Fagaceae*, *Dipterocarpaceae*, *Myrtaceae*, *Pinaceae*, *Salicaceae*, *Cupressaceae*, *Rosaceae*, *Fabaceae*, *Aceraceae*, *Euphorbiaceae*, and *Ulmaceae*, whilst there are up to 20,000 basidiomycetous, ascomycetous and Mucoromycotina fungi involved in this symbiosis (*Rinaldi, Comandini* & *Kuyper, 2008; Tedersoo, May & Smith, 2010*). Climatic factors have been suggested as the

main drivers of ECM diversity and distribution globally, and the species richness of ECM fungi peak at mid-latitudes, especially in temperate forests and Mediterranean biomes of the Northern Hemisphere i.e., where pine forests are the dominant vegetation (*Tedersoo et al., 2014; Mello & Balestrini, 2018*). Environmental and host factors have been shown to drive ECM diversity across the European forests (*Van der Linde et al., 2018*).

A sheath of organized hyphae called a mantle is formed around fine lateral roots. The colonized lateral roots have restricted apical growth (referred to as "short roots"), are thicker than non-colonized roots and have no root hairs. Some short roots have bifurcating branching patterns, which is an ontogenetic plant trait (*Smith & Read*, 2008). Mantle functions as a transitory storage compartment for metabolites received from the host and also the nutrients absorbed from soil by extraradical hyphae (Smith & Read, 2008; Nehls & Bodendiek, 2012). Mantle might be less developed (sparse and loose) in some ECM associations (*Walker*, 1985). The presence of fifteen genes encoding putative hexose transporters and the absence of genes involved in sucrose hydrolysis (invertases) in the genome of the model ECM fungus Laccaria bicolor suggest that this fungus receives its C source as simple six-C sugars such as glucose and fructose (Martin et al., 2008). However, this does not seem to be a general trend. An invertase gene is present in the genome of the ascomycetous ECM fungus Tuber melanosporum, making it capable of hydrolyzing sucrose and potentially less dependent on the host plant (Martin et al., 2010). Furthermore, carbohydrates might not be the sole C form provided by host plants, considering the evidence of FAs transfer from host plants to AM fungi (Keymer et al., 2017). From the mantle, extraradical hyphae extend outward into soil, and also intraradical hyphae grow between the root epidermal and cortical cells. The biotrophic interface is called a Hartig net. It is composed of highly branched labyrinthine hyphae that grow between epidermal cells (angiosperms) or penetrate in the epidermis and surround several layers of cortical cells (gymnosperms). The Hartig net is well-known as the active site for nutrient exchange between the two symbiotic partners (Smith & Read, 2008). However, there are reports of unusual ECM associations lacking a Hartig net, where positive growth and nutritional responses have been observed (Brundrett, 2009). ECM symbiosis is crucial for the succession of land ecosystems as it improves plant vigor and access to nutrients that are tightly fixed in complex organic matter or soil particles (N and P in particular), alleviates stresses caused by soil-borne pathogens and abiotic stresses such as drought and salinity, ameliorate the CO₂ fertilization effect, and can have a role in weathering of rocks and decomposition of organic matter in soil (Landeweert et al., 2001; Tibbett & Sanders, 2002; Smith & Read, 2008; Terrer et al., 2016). Saprotrophy to biotrophy transition seems to be a central trend in evolution of ECM fungi. Multigene phylogenetic analyses have suggested that ECM fungi have evolved independently from their saprotrophic and wood decaying ancestors (James et al., 2006), at least 80 times (Tedersoo & Smith, 2013). Recently, some wood-decaying fungi were shown to colonize the roots of coniferous seedlings in a mycorrhizal manner, some of which formed typical ECM structures (Smith et al., 2017). ECM-forming Tuber species have also been observed to colonize the roots of herbaceous plants in an endophytic manner (Gryndler et al., 2014; Schneider-Maunoury et al., 2018). An endophytic interaction has been documented between the ECM fungus Tricholoma

matsutake and the AM tree *Cedrela odorata* (*Murata et al., 2013*). These examples support proposals that (i) there is a wider ecological niche for ECM fungi i.e., some also act as a saprotroph/endophyte probably depending on fungal requirement for C and/or (ii) some ECM fungi are at different transitory stages within the saprotrophy-biotrophy continuum.

Ectendomycorrhiza (EEM)

The EEM association is formed between gymnosperms/angiosperms, including plant species belonging to *Pinus* (pine), *Picea* (spruce) and *Larix* (larch), and certain members of the fungal taxa Ascomycota, Basidiomycota and Mucoromycota (previously within Zygomycota), including species of Wilcoxina, Sphaerosporella, Phialophora and Chloridium (Egger & Fortin, 1988; Trevor et al., 2001; Navarro-Ródenas et al., 2012). Hartig net and mantle develop in EEM associations similar to the ECM, and hyphae also penetrate epidermal and cortical cells as observed in AM symbiosis. The mantle is quite thin and sometimes absent. The Hartig net grows distal to the root apical meristem between the epidermal and outer cortical cells and may progress deeper between inner cortical cells resulting in short roots as seen in ECM associations. Intracellular hyphae are highly branched, and usually develop in the vicinity of the cells surrounded by the Hartig net. Dense bodies of polysaccharides (probably glycogen) were detected in the mantle and Hartig net in the Pinus banksiana-Wilcoxina association (Scales & Peterson, 1991). However, there is no direct evidence for nutrient exchange at the symbiotic interface and like the majority of features of less common symbioses, this potential process needs to be further investigated. EEM fungi can hydrolyze complex polysaccharides, so they have been proposed to be the suppliers of C to young seedlings prior to the beginning of their autotrophism (Egger, 1986). Presence of EEM symbiosis in seedlings regenerating from burned coniferous/deciduous forests suggests that EEM fungi may play a role in revegetation of disturbed sites and establishment of conifer seedlings post-fire (Mikola, 1965; Lobuglio & Wilcox, 1988; Trevor et al., 2001).

Arbutoid mycorrhiza (ABM)

Plants from *Ericaceae* and *Pyrolaceae*, mostly species of *Comarostaphylis*, *Arctostaphylos* and *Arbutus*, establish ABM associations with diverse basidiomycetous fungi (*Münzenberger*, *Kottke & Oberwinkler*, 1992). ECM-forming fungi may mediate the interactions between ABM and ECM plants as they establish ECM symbiosis with trees, and can also form ABM associations with ericaceous plants from the Arbutoidea suborder (*Richard et al.*, 2005). The mycorrhizal structures are very similar to those of ECM and the fungal species involved are also capable of forming ECM associations, so the plant species often determines the type of the association present in a given area of forest. In these associations, a hyphal mantle covers the root surface but might be missing, and a Hartig net is usually restricted to epidermal and outer cortical cells due to the presence of suberin deposits and Casparian strips in the outer cortex of host roots (*Münzenberger*, 1991). Furthermore, hyphae also penetrate the outer cortical cells and fill them with coils, which is the distinguishing feature of ABM as compared to ECM symbiosis (*Münzenberger*, *Kottke & Oberwinkler*, 1992) and is reminiscent of the Arum-Paris division of AM symbioses that is also host-driven (*Smith*

& *Smith*, 1997). Although the ABM symbiosis is presumed to be functionally similar to ECM, there is very limited knowledge about the exchange of nutrients and possible benefits for each partner.

Monotropoid mycorrhiza (MTM)

Achlorophyllous plants from Ericaceae, such as Monotropa, Pterospora and Sarcodes establish MTM symbiosis with several basidiomycetous fungi (that also form ECM symbioses with neighboring photosynthetic plants) including species of Boletus, Lactarius, Rhizopogon, Russula, and Tricholoma (Cullings & Bruns, 1996; Bidartondo & Bruns, 2002; Bidartondo, 2005; Yang & Pfister, 2006). A dense fungal sheath is formed around roots that may or may not enclose the root apex, depending on the plant species involved. A Hartig net develops but is confined to the outer epidermal cells and does not extend deeper into cortex presumably due to presence of cell wall modifications such as Casparian strips (Bonfante & Perotto, 1995). Individual hyphae from the Hartig net or inner mantle grow into epidermal cells but do not penetrate cell walls i.e., cell walls bend to accommodate the penetrated hyphae, a structure designated as a "fungal peg". This results in increased surface area of the cell, which can potentially facilitate nutrient transfer at the interfacial matrix although there is no direct contact with the plant cytoplasm. Fungal pegs are presumed to be the active site for nutrient exchange. There is no direct evidence in this regard but the development of additional structures supports this proposal. A membranous sac is extended from the fungal peg into the host cytoplasm and, small wall ingrowths (protuberances) grow from the invaginated cell walls into epidermal cells (Hynson et al., 2013). Presence of a fungal peg and lack of intracellular hyphal structures are the main features distinguishing MTM from ABM and as the same fungi can produce both types of association (below), this is another example where symbiotic structures are directed by the host.

In MTM associations, the host plants contain no chlorophyll and are mycoheterotrophic i.e., they rely on their fungal partners for the C to be sourced through neighboring autotrophic plants such as *Pinus*, *Picea*, *Fagus*, *Quercus*, *Cedrus*, and *Salix* (*Leake*, *1994*; *Tedersoo et al.*, 2007; *Hynson et al.*, 2013). Mycoheterotrophic plants are considered as the only unambiguous examples for the potentially wide-spread phenomenon of plant-to-plant C transfer via hyphal networks of mycorrhizal fungi (*Bidartondo*, 2005). Glucose molecules labeled with ¹⁴C radioisotope were injected into the phloem of pine and spruce trees, and were subsequently detected in the mycoheterotrophic *Monotropa* plants within five days (*Bjorkman*, 1960), demonstrating that the MTM host receives its C from the neighboring plants through the common fungal hyphae. The saprotrophic capacity of the fungal symbiont, therefore, seems very unlikely and it is not also clear whether the plant partner supplies any types of C to the fungus or it comes entirely from the neighboring trees. The relationship between the host plant and the neighboring trees could be of a reciprocal nature as ³²P injected into flowering stems of the MTM host *Monotropa uniflora* was detected in the neighboring *Quercus* trees (*Furman*, 1966).

Orchid mycorrhiza (OM)

Orchids from the plant family Orchidaceae, that encompasses 10% of vascular plant species, establish OM symbiosis (*Brundrett & Tedersoo*, 2018), with a variety of basidiomycete

(including *Ceratobasidium, Russula, Sebacina* and *Tulasnella*), and ascomycete (including *Tuber, Peziza* and *Tricharina* species) fungi (*Selosse et al., 2004; Smith & Read, 2008; Waterman et al., 2011*). Fungal hyphae colonize newly formed root hairs soon after seed germination. Hyphae penetrate cells and become surrounded by the invaginated plasma membrane. Coarse hyphal coils (pelotons) are formed within cells and dramatically increase the interfacial surface between the two partners (*Rasmussen, 2002; Smith & Read, 2008*). Similar to arbuscules, pelotons have short life-spans of a few days, then are degenerated and digested by the host cells, which remain functional and can be recolonized by other hyphae (*Rasmussen, 2002*).

Unlike most plants, all orchids have a mycoheterotrophic stage at some point during their life cycle. Orchid seeds have a very limited reserve of nutrients, so all orchids are completely reliant on their mycorrhizal partners during their early growth stage, which is called a protocorm (Smith & Read, 2008; McCormick et al., 2012). Similar to what we may expect in other plant-fungal interactions, three possible outcomes from the initial contact between the fungus and imbibed seeds are: formation of functional mycorrhiza; seed parasitism; rejection of fungal colonization. Only seeds involved in functional mycorrhizal interactions successfully germinate and grow. After the protocorm stage, the majority of the adult orchids become autotrophic and putatively independent of C supply from the fungal partners, however, some orchids (mycoheterotrophic species) remain totally dependent on the mycorrhizal fungus to gain C and nutrients such as phosphate and N (Alexander, Alexander & Hadley, 1984; Cameron, Leake & Read, 2006; Rasmussen & *Rasmussen*, 2009). As in most mycorrhizal associations, the plant and fungal supply of organic and mineral nutrients can originate from the fungal capability to utilize simple and complex carbohydrates such as glucose, mannose, cellobiose, cellulose, CMC, xylan, pectin and starch, and also inorganic/organic sources of N (ammonium, amino acids and proteins) and P (orthophosphate, DNA and phytic acid) (*Nurfadilah et al.*, 2013). Studies by Cameron, Leake & Read (2006) showed that considerable quantities of fixed C in green forest orchid (Goodyera repens) were allocated to the extraradical mycelium of the OM fungi involved, demonstrating mutualism in OM symbiosis. Taken together, OM fungi can acquire their C source through either their heterotrophic activities or the autotrophic partner, and the extent of contribution of each route could be context-dependent.

Some mycoheterotrophic orchids are not fungal-specific, and can be associated with diverse saprophytic fungi. For instance, an OM association between the Asiatic *Epipogium roseum* and the saprotrophic *Psathyrellaceae* was successfully established and developed (*Yamato et al., 2005; Yagame et al., 2007*). Furthermore, diverse saprotrophic lineages have been identified in orchids including *Psathyrellaceae* (*Ogura-Tsujita & Yukawa, 2008*), *Mycenaceae* (*Ogura-Tsujita et al., 2009; Selosse et al., 2010*), *Marasmiaceae* (*Dearnaley & Bougoure, 2010*), *Resinicium* spp (*Martos et al., 2009*), and *Gymnopus*-related fungi (*Dearnaley, 2006*). These studies indicate less specificity in OM associations, and further highlight the fact that mycorrhizal fungi can be quite versatile in terms of their nutritional lifestyles, and may behave as saprotrophs or biotrophs.

Ericoid mycorrhiza (ERM)

Plants from *Ericaceae* (1.5% of vascular plant species) such as *Calluna* (heather), *Vaccinium* (bilberry) and *Erica* (heath) form ERM symbiosis with various ascomycetous fungi including *Rhizoscyphus ericae*, *Meliniomyces variabilis*, and *Oidiodendron maius* (*Rice* & *Currah*, 2006; *Brundrett & Tedersoo*, 2018). Although many sebacinalean taxa have also been detected in ERM roots in DNA-based molecular studies (*Bruzone*, *Fontenla & Vohník*, 2015), it is still unclear whether they form true ERM associations or they are common mycobionts or endophytes associated with roots. ERM fungi may form a loose hyphal network around the fine hair root surfaces. They penetrate the epidermal/cortical cells (without penetrating plasma membrane) and fill them with dense hyphal coils. ERM colonization is restricted to expanded (mature) cells, so the root apical region remains uncolonized. Recently, a new symbiosis with distinct morphological characteristics was discovered between *Vaccinium* spp. and an undescribed non-sebacinalean basidiomycete, termed "sheathed ericoid mycorrhiza" (SERM) (*Vohnik et al.*, 2012). In this symbiosis, fungal hyphae produce 1- to 3-layer sheaths around the terminal parts of hair roots and fill rhizodermal cells with hyphal coils.

Reciprocal exchange of C and P has been demonstrated in an ERM association between *R. ericae* and *Calluna vulgaris* (*Pearson & Read, 1973*). Similarly, a reciprocal exchange of C and P has been observed between the ERM fungus *Pezoloma ericae* and the leafy liverwort *Cephalozia bicuspidata* (*Kowal et al., 2018*). ERM fungi enhance fitness and nutrient acquisition of *Ericaceae* plants in their natural habitats through decomposition of complex organic compounds by secreting a broad range of enzymes including cellulases, proteases, polyphenol oxidases and phosphatases (*Read, Leake & Perez-Moreno, 2004; Martino et al., 2018*). They also protect host plants against heavy metal toxicity (*Perotto, Girlanda & Martino, 2002*) and may have a role in the restoration of ericaceous heaths (*Diaz et al., 2006; Diaz, Green & Tibbett, 2008*).

ERM fungi play a vital role in survival of ERM plants growing in nutrient impoverished habitats (typically having low soil pH and slow turnover of organic matter), through mineralization of soil organic matter. *Martino et al. (2018)* compared the genomes of four ERM fungi (*Meliniomyces bicolor, Meliniomyces variabilis, Oidiodendron maius* and *Rhizoscyphus ericae*) with those of fungi with different lifestyles (mycorrhizas, endophytes, saprotrophs, and pathogens). The ERM fungal genes related to saprotrophy (such as those encoding polysaccharide-degrading enzymes, lipases, and proteases) and secondary metabolism were shown to be closer to those of saprotrophs and pathogens than those found in the ECM fungi. The most highly upregulated genes in the ERM symbiosis (biotrophic interaction) were those encoding fungal and plant cell wall-degrading enzymes (CWDEs), lipases, proteases, nutrient transporters and mycorrhiza-induced small secreted proteins (MiSSPs). Accordingly, as reflected in the ERM fungal gene repertoire, conservation of a dual lifestyle capacity (saprotrophic and biotrophic) in ERM fungi seems to be a necessity for mutual plant-fungus fitness.

Sebacinalean endophytes (SE)

SE fungi, such as *Serendipita indica*, belong to Sebacinales (Hymenomycetes, Basidiomycota). These fungi colonize a broad range of bryophytes, pteridophytes, angiosperms (monocots and dicots) and gymnosperms, including the non-mycorrhizal plant *Arabidopsis thaliana*, without causing disease symptoms (*Varma et al., 2001*; *Weiss et al., 2011*; *Lahrmann et al., 2013*). A loose hyphal network is formed around the roots and hyphae grow inter- and intracellularly in the epidermis and also the outer layer of cortex in some plant species, but do not colonize the root tips and meristematic zones (*Deshmukh et al., 2006*; *Zuccaro et al., 2011*). Morphologically-distinct interface structures have not been detected at the symbiotic interface.

Host plants gain various benefits from the SE partners including improved growth and resistance against various biotic and abiotic stresses such as salinity (Waller et al., 2005; Deshmukh et al., 2006; Weiss et al., 2011). Bi-directional exchange of nutrients/C has been observed between SE fungi and their hosts (Yadav et al., 2010; Zuccaro et al., 2011; Zuccaro, Lahrmann & Langen, 2014), however a specialized means of nutrient transfer has not been reported. Within cells, hyphae are enveloped by host plasma membrane and establish a biotrophic interaction. They also cause pre-programmed cell death of cortical cells, in which they subsequently degrade organic compounds in a saprotrophic manner via secretion of extracellular enzymes such as proteases and metalloproteases (Zuccaro et al., 2011; Lahrmann & Zuccaro, 2012; Zuccaro, Lahrmann & Langen, 2014). Accordingly, the fungal symbiont is known to possess a dual lifestyle involving biotrophic and hemibiotrophic (necrotrophic) phases. Sebacinales is an important fungal order for evolutionary studies of root symbionts, consisting of lineages that have highly diverse interactions with plants including saprotrophism, endophytism, and mycorrhizal associations (Weiss et al., 2016). In contrast to facultative and obligate biotrophic symbionts, genes associated with saprotrophy and necrotrophy habits are well represented in the genome of the hemibiotrophic endophyte S. indica including members of the glycoside hydrolase families, metallo-endopeptidase families, and caspase family (Kohler et al., 2015; Lahrmann et al., 2015; Van der Heijden et al., 2015). However, genes that are strictly involved in lignin degradation such as those encoding class II peroxidases (PODs) are absent from the genome of S. indica, similar to most ECM fungi (Kohler et al., 2015). This might underly loss of the wood-decaying capacity of these fungi during evolution towards the biotrophy/hemibiotrophy traits.

Dark septate endophytes (DSE)

DSE are polyphyletic aggregates of fungi belonging to Ascomycota, conidial or sterile, and share melanized and septate hyphae as their common morphological traits (*Rodriguez & White, 2009*). Acephala applanata, A. macrosclerotiorum, Phialocephala fortinii, P. glacialis Vibrissea truncorum, and Meliniomyces variabilis are among the ascomycetous fungi forming DSE associations (*Grunig, Queloz & Sieber, 2011*). They colonize roots from a variety (nearly 600 species) of angiosperms and gymnosperms without causing any apparent disease symptoms (*Jumpponen & Trappe, 1998*). Hyphae grow in roots inter- and intracellularly and like SE do not form specialized interface structures for nutrient exchange.

There are four distinct fungal structures formed by DSE (*Jumpponen & Trappe, 1998*). Runner hyphae are individual hyphal strands linked to depressions between epidermal cells. Appressoria are swollen structures from which thin penetration tubes grow into plant cell walls. Intracellular hyphae produce clusters of rounded thick-walled cells within cortical cells, called microsclerotia, which may serve a storage function.

DSE fungi can break down various organic substances including cellulose, starch, xylan, and gelatine by secreting enzymes such as laccases, lipases, amylases and polyphenol oxidases (*Jumpponen & Trappe, 1998*). The interaction between DSE fungi and their host occurs along the mutualism-parasitism continuum. As with AM, positive, neutral and negative effects on plant biomass have been documented, which may depend on the plant-fungus combinations and environmental conditions (*Newsham, 1999; Newsham, 2011; Jumpponen, 2001; Tellenbach, Grünig & Sieber, 2011*). DSE also protect their hosts against plant pathogens, herbivores, and abiotic stresses such as heat that could be linked to their capability of synthesizing antibacterial and antifungal compounds, toxic secondary metabolites, or high melanin contents of their hyphae (*Mandyam & Jumpponen, 2005*).

DSE may also form hyaline (non-melanized) structures along with their typical dark septate structures, sometimes referred to as hyaline endophytes (HE) (*Haselwandter & Read, 1982; Newsham, 1999; Yu, Nassuth & Peterson, 2001; Lukesova et al., 2015*). While axenic cultures of the DSE fungus *Phialocephala fortinii* are generally darkly pigmented, some hyaline thin-walled hyphae were noticed to become thick-walled and melanized on PDA cultures (*Currah & Tsuneda, 1993*). However, it has also been proposed that HE may be formed by fungal taxa different from the DSE (*Vare, Vestberg & Eurola, 1992*).

Whether these hyaline septate hyphae are a phase of DSE or an independent entity (HE), they have been underestimated or ignored because their hyaline structures are not usually visible under the ordinary light microscopy and also due to the limitation of staining techniques such as use of Trypan blue. The lipid specific stain Sudan IV and differential interface contrast are required for detection and quantification of HE within roots (*Barrow & Aaltonen, 2001; Barrow, 2003*).

Fire-associated mutualism (FAM)

FAM is a recently discovered symbiosis that occurs between cheatgrass (*Bromus tectorum*) and certain isolates of the ascomycetous fungus *Morchella* (*Baynes et al., 2011*). Fungal hyphae extensively colonize roots in a manner not seen in other mycorrhiza and can further extend towards stem tissues. *Morchella* species may form a weak and probably facultative boitrophic association with plant roots. An EEM-like association (patchy mantle, poorly developed Hartig net, and intracellular colonization) has been observed in pure culture synthesis trials between *Morchella* spp. and *Pinaceae* (*Dahlstrom, Smith & Weber, 2000*). ECM structures were not detected in synthesis experiments involving other *Morchella* species (*Godbout & Fortin, 1985; Warcup, 1990; Yamada & Katsuya, 1995*).

As mycorrhizal structures are largely missing in the FAM association, details of root colonization features need to be further investigated. The *Morchella* isolates were shown to significantly increase the biomass of cheatgrass, fecundity of its local population, and also enhance survival rate of seeds exposed to heat. FAM is an evolutionarily novel interaction

associated with fire adaptation in which both probability of fire (via increased plant biomass) and plant survival (larger under-ground seed bank) are enhanced, simultaneously (*Baynes et al., 2011*). Thermotolerance in plants can be possibly linked to production of secondary metabolites (such as monocillin I) by their symbiotic fungal partners (*McLellan et al., 2007*).

Feremycorrhiza (FM)

Feremycorrhiza is a plant-fungus symbiosis discovered recently, between jarrah (Eucalyptus marginata) and the basidiomycetous fungus Austroboletus occidentalis (Kariman et al., 2014a). The term "Feremycorrhiza" originates from "fere" (meaning nearly in Latin and companion in Middle English) and "mycorrhiza", and refers to basic commonalities shared with mycorrhizal associations in terms of plant growth and nutritional benefits. The potential range of host plants and fungal partners capable of forming FM symbiosis needs to be investigated. A Scleroderma species was observed to establish FM or ECM symbiosis with jarrah, depending on the experimental conditions (*Kariman et al., 2012*; Kariman et al., 2014a; Kariman et al., 2016). This is an example where the symbiosis type (here, presence or absence of fungal interface structures) differs according to environment rather than host. Likewise, Navarro-Ródenas et al. (2012) demonstrated that the type of mycorrhizal association (ECM or EEM) between Helianthemum almeriense and Terfezia *claveryi* is determined by the P source where the organic P form can lead to intracellular (EEM) colonization. In FM symbiosis, fungal hyphae live in the rhizosphere soil and vicinity but do not penetrate plant roots. Lack of root colonization was observed microscopically and further confirmed biochemically. Mannitol, a sugar alcohol found in hyphae of A. occidentalis and many ECM fungi, was not detected in FM roots whereas it was abundant in ECM roots (colonized by Scleroderma sp.), supporting the lack of direct association (Kariman et al., 2014a).

The FM symbiosis can dramatically enhance plant biomass and uptake of nutrients such as N, P, K, S, Mg, Fe, and Zn (Kariman et al., 2012; Kariman et al., 2014a). A study using ³³P-labelled phosphate revealed that fungal hyphae do not extend far beyond the rhizosphere and do transfer nutrients to the host. The transcript abundances of two plant phosphate transporter (PHT1) genes (EmPHT1 and EmPHT2) were not affected in FM roots but were significantly reduced in ECM roots. Enhanced concentration of carboxylates (citrate, in particular) in the rhizosphere of FM plants was correlated with positive nutritional responses. The lack of detectable PHT1 gene response in FM roots coupled with enhanced carboxylate concentrations in the rhizosphere soil suggests that plant roots function as the active pathway of nutrient uptake in FM symbiosis, i.e., enhanced nutrient solubilization and mobilization seem to be the main functional mechanisms. In ECM symbiosis, however, the reduced concentration of carboxylates in the rhizosphere soil compared to NM (control) plants and down-regulation of two PHT1 genes in ECM roots (Kariman et al., 2014a) indicates a hyphal pathway as the main route of nutrient acquisition. Improved host performance was observed for FM plants under P-deficiency (Kariman et al., 2012; Kariman et al., 2014a) and phosphate/phosphite toxicity conditions (Kariman et al., 2014b; Kariman et al., 2016). Ability of Scleroderma sp. to form FM or

ECM associations in the same host (jarrah) depending on the experimental conditions (*Kariman et al., 2012; Kariman et al., 2014a; Kariman et al., 2016*) suggests a complexity to the detail of the potential fungal-host interactions that deserves further investigation.

In our previous studies, A. occidentalis was found to have similar (Kariman et al., 2014a) or superior (Kariman et al., 2012) positive effects on growth of jarrah seedlings compared with the ECM fungus Scleroderma sp. Furthermore, both FM and ECM symbioses significantly improved shoot content of P, K, Mg, S, Fe, Zn, and Cu compared to NM jarrah plants (Kariman et al., 2012; Kariman et al., 2014a), whereas improved N nutrition was only observed in the FM symbiosis (Kariman et al., 2014a). Except for N, all these plant nutrients are ultimately derived from weathering of primary minerals in soil. Ectomycorrhizal fungi, mostly basidiomycetes, can mobilize nutrients from insoluble mineral sources (such as apatite, biotite and muscovite) via excretion of carboxylates (low molecular weight organic acid anions) and protons, which results in acidolysis of soil minerals by dismantling their crystalline structure and subsequent release of immobile essential nutrients for plant uptake (Landeweert et al., 2001; Van Scholl, Smits & Hoffland, 2006; Courty et al., 2010). The FM fungus seems to have a remarkable capacity for biological weathering of soil minerals and nutrient mobilization, which was reflected in the significant growth and nutritional benefits for host plants (Kariman et al., 2012; Kariman et al., 2014a; Kariman et al., 2016). Improved P nutrition of jarrah plants associated with the FM fungus could be due to the fungal role in dissolution of phosphate-bearing minerals such as apatite (Newman, 1995; Landeweert et al., 2001; Courty et al., 2010). Feremycorrhiza is an interesting example indicating how an invisible plant-fungus association (no root colonization) can significantly enhance plant fitness, i.e., an important ecological phenomenon that has been missed by traditional structure-focused approaches.

Recent observations on root endophytes and root-colonizing saprotrophic fungi

Mycobiome studies using the state-of-the-art "omics" technologies (e.g., metagenomics and transcriptomics) have unearthed much more complexity in root and rhizosphereassociated mycobiome than previously presumed. Other than the well-studied root endophytic associations described here (SE and DSE), a multitude of root endophytic and root-colonizing saprotrophic relationships involving diverse fungal lineages have been revealed in root endosphere and rhizosphere of mycorrhizal and NM plants in both natural and farming ecosystems. Similar to SE and DSE, these endophytic associations do not form specialized interface structures in roots (with a few exceptions, see below), but they might possess plant growth-promoting capabilities. However, we should bear in mind that "omics" studies usually do not discriminate between fungal mycelia (active stage) and spores (dormant stage). Accordingly, the "root-colonizing saprotrophs" might be just a biased conclusion of a casual encounter between fungi and plant roots, unless specific microscopic localization probes are employed. In vitro and "omics" studies can reveal the fungal genetic potential for a specific trait, and subsequent research under natural conditions can determine if the identified traits are functional in nature or not, and if so, how these potentials can be exploited to improve or sustain farming/natural systems.

Here, we briefly explore several examples of root endophytic/rhizospheric associations discovered recently.

Almario et al. (2017) studied the root-associated mycobiome of the NM plant Arabis alpina (Brassicaceae) using the amplicon sequencing of the fungal ITS2 region. Fifteen fungal taxa were consistently recovered from roots of Arabis alpina plants growing in P-impoverished soils, including a highly abundant Helotiales taxon. The mycobiome associated with roots and rhizosphere of A. alpina was dominated by ascomycetes, which is similar to those of the mycorrhizal plants poplar, agave, and plants from an oak-dominated temperate forest (Shakya et al., 2013; Toju, Sato & Tanabe, 2014; Coleman-Derr et al., 2016). The fungal isolate F229 (belonging to Helotiales) showed a mycorrhiza-like activity that included colonization of the root endosphere (inter- and intracellularly) and P transfer to roots. This association improved P uptake and growth of A. alpina plants grown in native low-P soil i.e., commensalism. However, potential benefits to the fungal partner have not been investigated. Likewise, the root endophyte Collectotrichum tofieldiae transfers P to the NM plant A. thaliana and improves its growth only under P-limiting conditions, where the plant growth promotion property of the fungus requires both host plant's phosphate starvation and innate immune responses (*Hiruma et al.*, 2016). Thus, establishment of this C. tofieldiae-A. thaliana association seems to somehow depend on P starvation signalling pathway as also observed in AM symbiosis (Karandashov et al., 2004; Chen et al., 2011). Net negative effects of certain root endophytes on growth of A. thaliana, Microthlaspi erraticum, and Hordeum vulgare have also been documented, which were attributed to incompatibility between symbionts (Kia et al., 2016).

Toju et al. (2013) studied the root mycobiome of 12 plant species from an oakdominated temperate forest and observed diverse ECM taxa including clades of *Russula*, *Lactarius, Cortinarius, Tomentella, Amanita, Boletus*, and *Cenococcum*. Interestingly, the root mycobiome was dominated by endophytic ascomycetes belonging to Helotiales, Chaetothyriales, and Rhytismatales. Similarly, sequencing of the ITS and/or D1-D2 regions of the LSU rDNA using a 454 sequencing platform revealed that endophytic ascomycetes were dominant in root endosphere and rhizosphere mycobiome of *Populus deltoides*, *P. trichocarpa, Quercus alba*, and *Pinus taeda (Bonito et al., 2016)*. *Glynou et al. (2016)* recovered 296 operational taxonomic units (OTUs) of root endophytes from roots of the NM plant *Microthlaspi*, which were dominated by six widespread OTUs belonging to the orders Pleosporales, Hypocreales and Helotiales. Here, the local environment was found to be the main factor determining root-endophytic diversity.

Grelet et al. (2017) investigated the associations of *Mycena* species with *Ericaceae* plants, and suggested that *Mycena* species operate along the saprotrophic-symbiotic continuum. A *M. galopus* isolate promoted the growth of *Vaccinium corymbosum* seedlings. The fungus colonizes plant roots and forms distinctive peg-like structures. The positive growth response in plants inoculated with *M. galopus* was similar to that of the plants inoculated with the ERM fungus *Rhizoscyphus ericae*. A shift from saprotrophy towards biotrophy has also been suggested for wood-decaying basidiomycetes. *Smith et al. (2017)* investigated this phenomenon by using 201 wood-decaying basidiomycetes and monitored their root colonization capacity in two conifers (*Picea abies* and *Pinus sylvestris*). Interestingly,

thirty-four fungal species colonized the roots of at least one tree species. Two species formed a mantle around roots and one species (*Phellinus igniarius*) formed Hartig net-like structures. These typical endophytic associations between wood-decaying fungi and roots of ECM hosts have been proposed to be an intermediary step between saprotrophic and biotrophic (mycorrhizal) strategies (*Selosse, Dubious & Alvarez, 2009; Baldrian & Kohout, 2017*). Here, the emerged endophytic behavior of these fungi could be driven by easily available C source from roots, which is rendered inaccessible to competing saprotrophs by active plant defense pathways (*Baldrian & Kohout, 2017*). *Hacquard et al. (2016*) compared the transcriptomes of the beneficial root endophyte C olletotrichum tofieldiae and its pathogenic relative Colletotrichum incanum, and found genomic signatures dealing with transition from pathogenic to beneficial lifestyles including a narrowed repertoire of secreted effector proteins, and expanded families of genes related to chitin binding and secondary metabolism.

Mycobiome studies have unearthed another class of fungal lineages i.e., Archaeorhizomycetes that occurs ubiquitously in different terrestrial ecosystems. These fungi have saprotrophic potential, occupy roots and rhizosphere soil, but do not form recognizable mycorrhizal structures (*Schadt et al., 2003*; *Rosling et al., 2011*). Due to their dominance in summer and absence during other times of the year, Archaeorhizomycetes have been suggested to be dependent on root-derived C compounds as the main C source (*Schadt et al., 2003*). Several members of Archaeorhizomycetes have been cultured *in vitro* (*Rosling et al., 2011*), which can facilitate studying their functioning, that is rather vague currently.

All these examples indicate that root-associated fungi and free-living saprotrophic fungi may have evolved the capacity to form facultative biotrophic or mycorrhiza-like associations, which could enhance plant phenotype as reported for *Mycena galopus* (*Grelet et al., 2017*). Development of peg-like structures in *Mycena* species (*Grelet et al., 2017*), Hartig net-like structures in *Phellinus igniarius* (*Smith et al., 2017*), and formation of arbuscule-like structures in FRE belonging to Mucoromycotina (*Orchard et al., 2017*) suggest that mycorrhiza and mycorrhiza-like associations might have evolved in numerous fungal lineages independently.

Root-fungal symbioses and ecosystem functioning

Mycorrhizas and other fungal root symbionts are involved in key ecosystem processes including mineralization of organic matter, biological weathering of soil minerals, solubilization of mineral nutrients, soil acidification, C cycling, interactions with mycoheterotrophic plants, mediation of plant responses to biotic and abiotic stresses, tolerance to heavy metals, shaping plant and microbial communities, and enhancing biodiversity (*Landeweert et al., 2001; Finlay, 2008; Van der Heijden, Bardgett & Straalen, 2008*). Most studies dealing with root-fungal interactions have focused on plant performance at the individual level, and the ecosystem-scale effects warrant further and more in-depth investigations. AM and ECM associations seem to be key players in this regard, while certain less-explored associations (e.g., complex endophytic mycobiomes, FE, and DSE) could also play a major role in ecosystem functioning due to their ubiquitous presence across various ecosystems.

Different associations may function differently in ecosystem processes. A typical example for differential impact of root-fungal symbioses on a key ecosystem process has been presented by *Phillips, Midgley & Brozstek (2013)*, who classified the temperate forests based on their mycorrhizal associations of the dominant trees and their contrasting effects on the nutrient economy. Their framework suggested that forests dominated by AM trees have an inorganic nutrient economy, in which plant-derived C is rapidly decomposed by saprotrophs followed by rapid cycling of the inorganic nutrients. However, forests dominated by ECM trees have an organic nutrient economy, due to slow turnover of plant-derived C and enhanced root/rhizosphere couplings, leading to higher availability of organic nutrients.

Soil microbes (including fungal root symbionts) and N availability are among the main factors controlling decomposition of organic matter in soil (*Allison et al., 2010*; *Lindahl, De Boer & Finlay, 2010*). ECM and ERM fungi have greater access to organic N sources than AM fungi, due to possession of N-degrading enzymes and proteases (*Read & Perez-Moreno, 2003*), suggesting that soil C storage is greater in ecosystems dominated by EEM fungi compared with those dominated by AM fungi (*Averill, Turner & Finzi, 2014*).

Soil microorganisms, mycorrhizas in particular, are the key factors determining P cycling in forest soil ecosystems, rather than the annual uptake of trees. *Rosling et al.* (2016) uncovered significant differences in P cycling and mycorrhizal functioning in plots dominated by AM and ECM-associated trees in hardwood forests. Their results showed higher phosphatase activities and a larger organic P pool in ECM plots than in AM plots, while inorganic P decreased and organic P increased over the growing season in both ECM and AM plots. Interestingly, a similar microbial biomass (including symbiotic and saprotrophic microbiota) was observed for both AM and ECM plots and the microbial P pool was almost three times larger than the annual P uptake by the existing vegetation. Although this large microbial biomass can potentially exacerbate P-limitation for plant growth, these forests are still productive based on the annual litter fall datasets (*Rosling et al., 2016*). This is possibly because the soil available P pool is being continuously topped up mainly through mobilization of phosphate-bearing minerals, rather than mineralization of organic P compounds in soil that may not meet both microbial and plant P demands.

These examples suggest that functional traits, trophic habits and enzymatic properties of different mycorrhizal types determine their role and significance in key ecosystem processes such as N, P, and C cycling. These studies provide useful models for measuring the impact of other less-studied root-fungal symbioses at an ecosystem scale. The studies mentioned above have primarily focused on nutrient cycling, while these frameworks/models can be potentially employed to determine fungal effects on plant communities subjected to environmental constraints within diverse ecosystems. For instance, FRE are ubiquitous in harsh environments (*Crush, 1973; Postma, Olsson & Falkengren-Grerup, 2007; Newsham, Upson & Read, 2009; Orchard et al., 2016*), and it would be interesting to explore their role in functionality of stressful ecosystems such as those with high altitude, soil acidity or cold temperatures.

CONCLUSIONS

Our review of the current literature suggests that the potential exchange of nutrients/metabolites and beneficial interactions in plant-fungal relationships can occur via specialized interface structures or simple non-specialized hyphae inside or outside roots. This fundamental fact has been either missed or neglected (due to invisibility of certain symbioses or sole focus on specialized structures), but it is essential for a proper understanding of the actual contribution of fungal root symbionts to nutrient cycling and plant fitness in terrestrial ecosystems. Nevertheless, we do emphasize that while interface morphological characteristics are not a direct indicator or prerequisite for enhancing plant phenotype, certain highly efficient structures (such as those in AM and ECM associations) are key elements for mycorrhizal functionality at both plant and ecosystem levels. Overall, interface structures can be morphologically diverse, specialized (arbuscules, Hartig nets and fungal pegs: AM, ECM, EEM, ABM, MTM and FRE), non-specialized (hyphae and hyphal coils: ERM, SERM, OM, DSE and SE), or totally absent (FM) in root-fungal relationships, suggesting plasticity in interface structures as well as functional traits of root-associated fungi i.e., employing different strategies such as direct nutrient transfer and/or rhizosphere modification to benefit their host plants. To shed more light on the nature of a given root-fungal relationship including some currently known associations, it is crucial to explore mutualism (i.e., a reciprocal exchange of nutrients/metabolites) as the definitive feature in mycorrhizal symbiosis.

Specialized structures such as arbuscules could be a more efficient means of nutrient transfer due to their specific features such as increased intimate surface area at the symbiotic interface. To date, most studies have focused on AM, ECM, OM and SE, and further research is required to unearth the cellular mechanisms behind exchange of nutrients in the other root-fungal interactions. Sequencing the genome of representative fungi will identify the potential trophic habits of the fungal partner, and, in a given association, the symbiotic characteristics can be explored via transcriptomic analyses whilst proteomic studies focusing on nutrient/hexose transporters at the interfacial matrix will explore further the symbiotic benefits. Comparative genomics of the fungal symbionts and their hosts would provide key insights into their life-style and evolution.

State-of-the-art molecular approaches have unearthed much more complexity and diversity in root-fungal relationships than previously thought, and suggest that mycorrhizal capacity (or saprotrophy to biotrophy transition) has possibly evolved in highly diverse fungal lineages across the kingdom Mycota. This includes the recent discoveries of diverse root endophytes and root-colonizing saprotrophic fungi, some with peg-like (*Mycena galopus*), Hartig net-like (*Phellinus igniarius*), or arbuscule-like (FRE belonging to Mucoromycotina) structures, which could possibly be of a mutualistic nature. Moreover, dual niches for mycorrhizal and root endophytic fungi seems to be a common strategy, and could be a key capacity, aiding them to cope with environmental constraints and ecological restrictions.

ACKNOWLEDGEMENTS

The authors are thankful to Atefeh Fazelnia and Behzad Zohouri for their assistance in preparation of the schematic picture.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

The authors received no funding for this work.

Competing Interests

Mark Tibbett is an Academic Editor for PeerJ.

Author Contributions

- Khalil Kariman conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Susan Jane Barker and Mark Tibbett conceived and designed the experiments, analyzed the data, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

Data Availability

The following information was supplied regarding data availability:

This is a review paper and the research in this article did not generate any data or code.

REFERENCES

- Abbott L. 1982. Comparative anatomy of vesicular-arbuscular mycorrhizas formed on subterranean clover. *Australian Journal of Botany* **30**:485–499 DOI 10.1071/BT9820485.
- Alexander C, Alexander IJ, Hadley G. 1984. Phosphate uptake by *Goodyera* repens in relation to mycorrhizal infection. *New Phytologist* **97**:391–400 DOI 10.1111/j.1469-8137.1984.tb03605.x.
- Allison SD, Gartner TB, Mack MC, McGuire K, Treseder K. 2010. Nitrogen alters dynamics during early succession in boreal forest. *Soil Biology and Biochemistry* 42:1157–1164 DOI 10.1016/j.soilbio.2010.03.026.
- Almario J, Jeena G, Wunder J, Langen G, Zuccaro A, Coupland G, Bucher M. 2017. Root-associated fungal microbiota of nonmycorrhizal Arabis alpina and its contribution to plant phosphorus nutrition. *Proceedings of the National Academy of Sciences of the United States of America* **114(44)**:E9403–E9412 DOI 10.1073/pnas.1710455114.
- Averill C, Turner BL, Finzi AC. 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* **505**:543–545 DOI 10.1038/nature12901.

- Baldrian P, Kohout P. 2017. Interactions of saprotrophic fungi with tree roots: can we observe the emergence of novel ectomycorrhizal fungi? *New Phytologist* 215:511–513 DOI 10.1111/nph.14665.
- Barker SJ, Tagu D, Delp G. 1998. Regulation of root and fungal morphogenesis in mycorrhizal symbioses. *Plant Physiology* 116:1201–1207 DOI 10.1104/pp.116.4.1201.
- Barrow JR. 2003. Atypical morphology of dark septate fungal root endophytes of Bouteloua in arid southwestern U.S.A. rangelands. *Mycorrhiza* 13:239–247 DOI 10.1007/s00572-003-0222-0.
- **Barrow JR, Aaltonen RE. 2001.** Evaluation of the internal colonization of Atriplex canescens (Pursh) Nutt. roots by dark septate fungi and the influence of host physiological activity. *Mycorrhiza* **11**:199–205 DOI 10.1007/s005720100111.
- Baynes M, Newcombe G, Dixon L, Castlebury L, O Donnell K. 2011. A novel plantfungal mutualism associated with fire. *Fungal Biology* 116:133–144.
- Bever JD, Dickie IA, Facelli E, Facelli JM, Klironomos J, Moora M, Rillig MC, Stock WD, Tibbett M, Zobel M. 2010. Rooting theories of plant community ecology in microbial interactions. *Trends in Ecology and Evolution* 25:468–478.
- Bidartondo MI. 2005. The evolutionary ecology of myco-heterotrophy. *New Phytologist* 167:335–352 DOI 10.1111/j.1469-8137.2005.01429.x.
- Bidartondo M, Bruns T. 2002. Fine-level mycorrhizal specificity in the Monotropoideae (Ericaceae): specificity for fungal species groups. *Molecular Ecology* 11:557–569 DOI 10.1046/j.0962-1083.2001.01443.x.
- Bidartondo MI, Read DJ, Trappe JM, Merckx V, Ligrone R, Duckett JG. 2011. The dawn of symbiosis between plants and fungi. *Biology Letters* **7**:574–577 DOI 10.1098/rsbl.2010.1203.
- **Bjorkman E. 1960.** Monotropa hypopitys L., an epiparasite on tree roots. *Physiologia Plantarum* **13**:308–327 DOI 10.1111/j.1399-3054.1960.tb08034.x.
- **Bonfante P, Perotto S. 1995.** Strategies of arbuscular mycorrhizal fungi when infecting host plants. *New Phytologist* **130**:3–21 DOI 10.1111/j.1469-8137.1995.tb01810.x.
- Bonito G, Hameed K, Ventura R, Krishnan J, Schadt C, Vilgalys R. 2016. Isolating a functionally relevant guild of fungi from the root microbiome of Populus. *Fungal Ecology* 22:35–42 DOI 10.1016/j.funeco.2016.04.007.
- **Brundrett MC. 2009.** Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant and Soil* **320**:37–77 DOI 10.1007/s11104-008-9877-9.
- Brundrett M, Tedersoo L. 2018. Evolutionnary history of mycorrhizal symbiosis and global host plant diversity. *New Phytologist* 220(4):1108–1115 DOI 10.1111/nph.14976.
- **Bruzone MC, Fontenla SB, Vohník M. 2015.** Is the prominent ericoid mycorrhizal fungus Rhizoscyphus ericae absent in the Southern Hemisphere's Ericaceae? A case study on the diversity of root mycobionts in Gaultheria spp. from northwest Patagonia, Argentina. *Mycorrhiza* **25**:25–40 DOI 10.1007/s00572-014-0586-3.

- **Cameron DD, Leake JR, Read DJ. 2006.** Mutualistic mycorrhizal in orchids: evidence from plant–fungus carbon and nitrogen transfers in the greenleaved terrestrial orchid *Goodyera* repens. *New Phytologist* **171**:405–416 DOI 10.1111/j.1469-8137.2006.01767.x.
- **Chen A, Gu M, Sun S, Zhu L, Hong S, Xu G. 2011.** Identification of two conserved cis-acting elements, MYCS and P1BS, involved in the regulation of mycorrhiza-activated phosphate transporters in eudicot species. *New Phytologist* **189**:1157–1169 DOI 10.1111/j.1469-8137.2010.03556.x.
- **Coba de la Peña T, Fedorova E, Pueyo JJ, Lucas MM. 2017.** The Symbiosome: Legume and Rhizobia Co-evolution toward a Nitrogen-Fixing Organelle? *Frontiers in Plant Science* **8**:2229.
- Coleman-Derr D, Desgarennes D, Fonseca-Garcia C, Gross S, Clingenpeel S, Woyke T, North G, Visel A, Partida-Martinez LP, Tringe SG. 2016. Plant compartment and biogeography affect microbiome composition in cultivated and native Agave species. *New Phytologist* 209:798–811 DOI 10.1111/nph.13697.
- Courty PE, Buée M, Diedhiou A, Frey-Klett P, Le Tacon F, Rineau F, Turpault MP, Uroz S, Garbaye J. 2010. The rôle of ectomycorrhizal communities in forest ecosystems: new perspectives and emerging concepts. *Soil Biology and Biochemistry* 42:679–698 DOI 10.1016/j.soilbio.2009.12.006.
- Crush JR. 1973. The effect of Rhizophagus tenuis mycorrhizas on ryegrass, cocksfoot and sweet vernal. *New Phytologist* 72:965–973 DOI 10.1111/j.1469-8137.1973.tb02073.x.
- **Cullings K, Bruns T. 1996.** Evolution of extreme specialization within a lineage of ectomycorrhizal epiparasites. *Nature* **379**:63–67 DOI 10.1038/379063a0.
- **Currah RS, Tsuneda A. 1993.** Vegetative and reproductive morphology of Phialocephala fortinii (Hyphomycetes, Mycelium radicis atrovirens) in culture. *Transactions of the Mycological Society of Japan* **34**:345–356.
- **Dahlstrom JL, Smith JE, Weber NS. 2000.** Mycorrhiza-like interaction by Morchella with species of the Pinaceae in pure culture synthesis. *Mycorrhiza* **9**:279–285 DOI 10.1007/PL00009992.
- **Dearnaley JDW. 2006.** The fungal endophytes of Erythrorchis *cassythoides*-is this orchid saprophytic or parasitic? *Australasian Mycologist* **25**:51–57.
- Dearnaley JDW, Bougoure JJ. 2010. Isotopic and molecular evidence for saprotrophic Marasmiaceae mycobionts in rhizomes of Gastrodia sesamoides. *Fungal Ecology* 3:288–294 DOI 10.1016/j.funeco.2009.11.003.
- Deshmukh S, Huckelhoven R, Schafer P, Imani J, Sharma M, Weiss M, Waller F, Kogel K. 2006. The root endophytic fungus *Serendipita indica* requires host cell death for proliferation during mutualistic symbiosis with barley. *Proceedings of the National Academy of Sciences of the United States of America* 103:18450–18457 DOI 10.1073/pnas.0605697103.
- Diaz A, Green ID, Benvenuto M, Tibbett M. 2006. Are ericoid mycorrhizas a factor in the success of *Calluna vulgaris* heathland restoration? *Restoration Ecology* 14:187–195 DOI 10.1111/j.1526-100X.2006.00120.x.

- Diaz A, Green ID, Tibbett M. 2008. Re-creation of heathland on improved pasture using topsoil removal and sulphur amendments: Edaphic drivers and impacts on ericoid mycorrhizas. *Biological Conservation* 141:1628–1635 DOI 10.1016/j.biocon.2008.04.006.
- Dickson S. 2004. The Arum-Paris continuum of mycorrhizal symbioses. *New Phytologist* 163:187–200 DOI 10.1111/j.1469-8137.2004.01095.x.

Douglas A. 2010. The symbiotic habit. New Jersey: Princeton University Press.

- Egger KN. 1986. Substrate hydrolysis patterns of post-fire ascomycetes (Pezizales). *Mycologia* 78:771–780 DOI 10.1080/00275514.1986.12025321.
- **Egger KN, Fortin JA. 1988.** Ectendomycorrhizae: diversity and classification. In: Lalonde M, Piché Y, eds. *Canadian workshop on Mycorrhizae in forestry*. Ste-Foy: C.R.B.F Université Laval, 113–114.
- **Fesel PH, Zuccaro A. 2016.** Dissecting endophytic lifestyle along the parasitism/mutualism continuum in Arabidopsis. *Current Opinions in Microbiology* **32**:103–112 DOI 10.1016/j.mib.2016.05.008.
- Field KJ, Rimington WR, Bidartondo MI, Allinson KE, Beerling DJ, Cameron DD, Duckett JG, Leake JR, Presse S. 2015. First evidence of mutualism between ancient plant lineages (Haplomitriopsida liverworts) and Mucoromycotina fungi and its response to simulated Palaeozoic changes in atmospheric CO2. *New Phytologist* 205:743–756 DOI 10.1111/nph.13024.
- **Finlay RD. 2008.** Ecological aspects of mycorrhizal symbiosis with special emphasis on the functional diversity of interactions involving the extraradical mycelium. *Journal of Experimental Botany* **59**:1115–1126 DOI 10.1093/jxb/ern059.
- Furman TE. 1966. Symbiotic relationships of Monotropa. American Journal of Botany 53:627.
- Genre A, Chabaud M, Timmers T, Bonfante P, Barker DG. 2005. Arbuscular mycorrhizal fungi elicit a novel intracellular apparatus in *Medicago truncatula* root epidermal cells before infection. *The Plant Cell* 17:3489–3499 DOI 10.1105/tpc.105.035410.
- Gianinazzi-Pearson V, Morandi D, Dexheimer J, Gianinazzi S. 1981. Ultrastructural and ultracytochemical features of a Glomus tenuis mycorrhiza. *New Phytologist* 88:633–639 DOI 10.1111/j.1469-8137.1981.tb01739.x.
- Glynou K, Ali T, Buch AK, Haghi Kia S, Ploch S, Xia X, Çelik A, Thines M, Maciá-Vicente JG. 2016. The local environment determines the assembly of root endophytic fungi at a continental scale. *Environmental Microbiology* 18:2418–2434 DOI 10.1111/1462-2920.13112.
- **Godbout C, Fortin JA. 1985.** Synthesized ectomycorrhizae of aspen: fungal genus level of structural characterization. *Canadian Journal of Botany* **63**:252–262 DOI 10.1139/b85-029.
- **Gollotte A, Van Tuinen D, Atkinson D. 2004.** Diversity of arbuscular mycorrhizal fungi colonising roots of the grass species Agrostis capillaris and Lolium perenne in a field experiment. *Mycorrhiza* **14**:111–117 DOI 10.1007/s00572-003-0244-7.

- Grelet GA, Ba R, Goeke DF, Houliston GJ, Taylor AFS, Durall DM. 2017. A plant growth- promoting symbiosis between Mycena galopus and Vaccinium corymbosum seedlings. *Mycorrhiza* 27:831–839 DOI 10.1007/s00572-017-0797-5.
- **Grunig CR, Queloz V, Sieber TN. 2011.** Structure of diversity in dark septate endophytes: from species to genes. *Forestry Sciences* **80**:3–30 DOI 10.1007/978-94-007-1599-8 1.
- Gryndler M, Černá L, Bukovská P, Hršelová H, Jansa J. 2014. *Tuber aestivum* association with non-host roots. *Mycorrhiza* 24:603–610 DOI 10.1007/s00572-014-0580-9.
- **Guinel FC, Hirsch AM. 2000.** The involvement of root hairs in mycorrhizal associations. *Cellular and Molecular Biology* **17**:285–310.
- Hacquard S, Kracher B, Hiruma K, Münch PC, Garrido-Oter R, Thon MR, Weimann A, Damm U, Dallery JF, Hainaut M, Henrissat B, Lespinet O, Sacristán S, Ver Loren van Themaat E, Kemen E, McHardy AC, Schulze-Lefert P, O'Connell RJ. 2016. Survival trade-offs in plant roots during colonization by closely related beneficial and pathogenic fungi. *Nature Communications* 7:11362 DOI 10.1038/ncomms11362.
- Harrison MJ. 2012. Cellular programs for arbuscular mycorrhizal symbiosis. *Current Opinion in Plant Biology* 15:691–698 DOI 10.1016/j.pbi.2012.08.010.
- Haselwandter K, Read DJ. 1982. The significance of a root-fungus association in two Carex species of high-alpine plant communities. *Oecologia* 53:352–354 DOI 10.1007/BF00389012.
- Hildebrandt U, Regvar M, Bothe H. 2007. Arbuscular mycorrhiza and heavy metal tolerance. *Phytochemistry* **68**:139–146 DOI 10.1016/j.phytochem.2006.09.023.
- Hiruma N, Gerlach S, Sacristan RT, Nakano S, Hacquard B, Kracher U, Neumann U, Ramírez D, Bucher M, O'Connell RJ, Schulze-Lefert P. 2016. Root endophyte colletotrichum tofieldiae confers plant fitness benefits that are phosphate status dependent. *Cell* 165:464–474 DOI 10.1016/j.cell.2016.02.028.
- Hoysted GA, Kowal J, Jacob A, Rimington WR, Duckett JG, Pressel S, Orchard S, Ryan MH, Field KJ, Bidartondo MI. 2018. A mycorrhizal revolution. *Current Opinion in Plant Biology* 44:1–6.
- Hynson N, Madsen TP, Selosse MA, Adam IKU, Ogura-Tsujita Y, Roy M, Gebauer
 G. 2013. The physiological ecology of mycoheterotrophy. In: Merckx V, ed.
 Mycoheterotrophy—the biology of plants living on fungi. New York: Springer, 297–342.
- **Jakobsen I. 1995.** Transport of phosphorus and carbon in VA mycorrhizas. In: Varma A, Hock B, eds. *Mycorrhiza, structure, function, molecular biology and biotechnology*. Berlin: Springer, 297–324.
- James TY, Kauff F, Schoch CL, Matheny PB, Hofstetter V, Cox CJ, Celio G, Gueidan C, Fraker E, Miadlikowska J, Lumbsch HT, Rauhut A, Reeb V, Arnold AE, Amtoft A, Stajich JE, Hosaka K, Sung GH, Johnson D, O'Rourke B, Crockett M, Binder M, Curtis JM, Slot JC, Wang Z, Wilson AW, Schüssler A, Longcore JE, O'Donnell K, Mozley-Standridge S, Porter D, Letcher PM, Powell MJ, Taylor JW, White

MM, Griffith GW, Davies DR, Humber RA, Morton JB, Sugiyama J, Rossman AY, Rogers JD, Pfister DH, Hewitt D, Hansen K, Hambleton S, Shoemaker RA, Kohlmeyer J, Volkmann-Kohlmeyer B, Spotts RA, Serdani M, Crous PW, Hughes KW, Matsuura K, Langer E, Langer G, Untereiner WA, Lücking R, Büdel B, Geiser DM, Aptroot A, Diederich P, Schmitt I, Schultz M, Yahr R, Hibbett DS, Lutzoni F, McLaughlin DJ, Spatafora JW, Vilgalys R. 2006. Reconstructing the early evolution of Fungi using a six-gene phylogeny. *Nature* 443:818–822 DOI 10.1038/nature05110.

- Johnson NC, Graham JH, Smith FA. 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist* 135:575–585 DOI 10.1046/j.1469-8137.1997.00729.x.
- Jumpponen A. 2001. Dark-Septate Endophytes—are they mycorrhizal? *Mycorrhiza* 11:207–211 DOI 10.1007/s005720100112.
- Jumpponen A, Trappe JM. 1998. Dark septate endophytes: a review of facultative biotrophic root-colonizing fungi. *New Phytologist* 140:295–310 DOI 10.1046/j.1469-8137.1998.00265.x.
- Karandashov V, Nagy R, Wegmüller S, Amrhein N, Bucher M. 2004. Evolutionary conservation of a phosphate transporter in the arbuscular mycorrhizal symbiosis. *Proceedings of the National Academy of Sciences of the United States of America* 101:6285–6290 DOI 10.1073/pnas.0306074101.
- Kariman K, Barker SJ, Finnegan PM, Tibbett M. 2012. Dual mycorrhizal associations of jarrah (*Eucalyptus marginata*) in a nurse-pot system. *Australian Journal of Botany* 60:661–668 DOI 10.1071/BT12152.
- Kariman K, Barker SJ, Finnegan PM, Tibbett M. 2014b. Ecto- and arbuscular mycorrhizal symbiosis can induce tolerance to toxic pulses of P in jarrah (*Eucalyptus marginata*) seedlings. *Mycorrhiza* 24:501–509 DOI 10.1007/s00572-014-0567-6.
- Kariman K, Barker SJ, Jost R, Finnegan PM, Tibbett M. 2014a. A novel plant-fungus symbiosis benefits the host without forming mycorrhizal structures. *New Phytologist* 201:1413–1422 DOI 10.1111/nph.12600.
- Kariman K, Barker SJ, Jost R, Finnegan PM, Tibbett M. 2016. Sensitivity of jarrah (Eucalyptus marginata) to phosphate, phosphite, and arsenate pulses as influenced by fungal symbiotic associations. *Mycorrhiza* 26:401–415 DOI 10.1007/s00572-015-0674-z.
- Kenrick P, Crane PR. 1997. The origin and early evolution of plants on land. *Nature* 389:33–39 DOI 10.1038/37918.
- Keymer A, Pimprikar P, Wewer V, Huber C, Brands M, Bucerius SL, Delaux PM,
 Klingl V, Röpenack-Lahaye EV, Wang TL, Eisenreich W, Dörmann P, Parniske
 M, Gutjahr C. 2017. Lipid transfer from plants to arbuscular mycorrhiza fungi. *eLife* 6:e29107 DOI 10.7554/eLife.29107.
- **Kia SH, Glynou K, Nau T, Thines M, Piepenbring M, Maciá-Vicente JG. 2016.** Influence of phylogenetic conservatism and trait convergence on the interactions between fungal root endophytes and plants. *ISME* **11**:777–790.

Klironomos JN. 2003. Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology* 84:2292–2301 DOI 10.1890/02-0413.

Kohler A, Kuo A, Nagy LG, Morin E, Barry KW, Buscot F, Canbäck B, Choi C, Cichocki N, Clum A, Colpaert J, Copeland A, Costa MD, Doré J, Floudas D, Gay G, Girlanda M, Henrissat B, Herrmann S, Hess J, Högberg N, Johansson T, Khouja HR, LaButti K, Lahrmann U, Levasseur A, Lindquist EA, Lipzen A, Marmeisse R, Martino E, Murat C, Ngan CY, Nehls U, Plett JM, Pringle A, Ohm RA, Perotto S, Peter M, Riley R, Rineau F, Ruytinx J, Salamov A, Shah F, Sun H, Tarkka M, Tritt A, Veneault-Fourrey C, Zuccaro A, Tunlid A, Grigoriev IV, Hibbett DS, Martin F. 2015. Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. *Nature Genetics* 47:410–415 DOI 10.1038/ng.3223.

- Koide RT, Sharda JN, Herr JR, Malcolm GM. 2008. Ectomycorrhizal fungi and the biotrophy-saprotrophy continuum. *New Phytologist* 178:230–233 DOI 10.1111/j.1469-8137.2008.02401.x.
- Kowal J, Pressel S, Duckett JG, Bidartondo MI, Field KJ. 2018. From rhizoids to roots? Experimental evidence of mutualism between liverworts and ascomycete fungi. *Annals of Botany* 121(2):221–227 DOI 10.1093/aob/mcx126.
- Lahrmann U, Ding Y, Banhara A, Rath M, Hajirezaei MR, Dohlemann S, Von Wirén N, Parniske M, Zuccaroa A. 2013. Host-related metabolic cues affect colonization strategies of a root endophyte. *Proceedings of the National Academy of Sciences of the United States of America* 110:13965–13970 DOI 10.1073/pnas.1301653110.
- Lahrmann U, Strehmel N, Langen G, Frerigmann H, Leson L, Ding Y, Scheel D, Herklotz S, Hilbert M, Zuccaro A. 2015. Mutualistic root endophytism is not associated with the reduction of saprotrophic traits and requires a noncompromised plant innate immunity. *New Phytologist* 207:841–857 DOI 10.1111/nph.13411.
- Lahrmann U, Zuccaro A. 2012. Opprimo ergo sum-evasion and suppression in the root endophytic fungus *Serendipita indica*. *Molecular Plant Microbe Interactions* 25:727–737 DOI 10.1094/MPMI-11-11-0291.
- Landeweert R, Hofflund E, Finlay RD, Van Breemen N. 2001. Linking plants to rocks: ectomycorrhizal fungi mobilize nutrients from minerals. *Trends in Ecology and Evolution* 16:248–254 DOI 10.1016/S0169-5347(01)02122-X.
- Leake JR. 1994. The biology of myco-heterotrophic ('saprophytic') plants. *New Phytologist* 127:171–216 DOI 10.1111/j.1469-8137.1994.tb04272.x.
- Lin K, Limpens E, Zhang ZH, Ivanov S, Saunders DGO, Mu D, Pang L, Cao H, Cha H, Lin T, Zhou Q, Shang Y, Li Y, Sharma T, Van Velzen R, De Ruijter N, Aanen DK, Win J, Kamoun S, Bisseling T, Geurts R, Huang S. 2014. Single nucleus genome sequencing reveals high similarity among nuclei of an endomycorrhizal fungus. *PLOS Genetics* 10:e1004078 DOI 10.1371/journal.pgen.1004078.
- Lindahl BD, De Boer W, Finlay RD. 2010. Disruption of root C transport into forest humus stimulates fungal opportunists at the expense of mycorrhizal fungi. *ISME Journal* 4:872–881 DOI 10.1038/ismej.2010.19.

- Lobuglio KF, Wilcox HE. 1988. Growth and survival of ectomycorrhizal and ectendomycorrhizal seedlings of Pinus resinosa on iron tailings. *Canadian Journal of Botany* 66:55–60 DOI 10.1139/b88-007.
- Lukesova T, Kohout P, Větrovský T, Vohník M. 2015. The potential of Dark Septate Endophytes to form root symbioses with ectomycorrhizal and ericoid mycorrhizal middle European forest plants. *PLOS ONE* 10:e0124752 DOI 10.1371/journal.pone.0124752.
- Mandyam K, Jumpponen A. 2005. Seeking the elusive function of the root-colonising dark septate endophytic fungi. *Studies in Mycology* 53:173–189 DOI 10.3114/sim.53.1.173.
- Martin F, Aerts A, Ahren D, Brun A, Danchin EGJ, Duchaussoy F. Gibon J, Kohler A, Lindquist E, Pereda V, Salamov A, Shapiro HJ, Wuyts J, Blaudez D, Buée M, Brokstein P, Canbäck B, Cohen D, Courty PE, Coutinho PM, Delaruelle C, Detter JC, Deveau A, DiFazio S, Duplessis S, Fraissinet-Tachet L, Lucic E, Frey-Klett P, Fourrey C, Feussner I, Gay G, Grimwood J, Hoegger PJ, Jain P, Kilaru S, Labbé J, Lin YC, Legué V, Le Tacon F, Marmeisse R, Melayah D, Montanini B, Muratet M, Nehls U, Niculita-Hirzel H, Oudot-Le Secq MP, Peter M, Quesneville H, Rajashekar B, Reich M, Rouhier N, Schmutz J, Yin T, Chalot M, Henrissat B, Kües U, Lucas S, Van de Peer Y, Podila GK, Polle A, Pukkila PJ, Richardson PM, Rouzé P, Sanders IR, Stajich JE, Tunlid A, Tuskan G, Grigoriev IV. 2008. The genome of *Laccaria bicolor* provides insights into mycorrhizal symbiosis. *Nature* 452:88–92 DOI 10.1038/nature06556.
- Martin F, Kohler A, Murat C, Balestrini R, Coutinho PM, Jaillon O, Montanini B, Morin E, Noel B, Percudani R, Porcel B, Rubini A, Amicucci A, Amselem J, Anthouard V, Arcioni S, Artiguenave F, Aury JM, Ballario P, Bolchi A, Brenna A, Brun A, Buée M, Cantarel B, Chevalier G, Couloux A, Da Silva C, Denoeud F, Duplessis S, Ghignone S, Hilselberger B, Iotti M, Marçais B, Mello A, Miranda M, Pacioni G, Quesneville H, Riccioni C, Ruotolo R, Splivallo R, Stocchi V, Tisserant E, Viscomi AR, Zambonelli A, Zampieri E, Henrissat B, Lebrun MH, Paolocci F, Bonfante P, Ottonello S, Wincker P. 2010. Perigord black truffle genome uncovers evolutionary origins and mechanisms of symbiosis. *Nature* 464:1033–1038 DOI 10.1038/nature08867.
- Martin BD, Schwab E. 2013. Current usage of symbiosis and associated terminology. *International Journal of Biology* 5:32–45.
- Martino E, Morin E, Grelet GA, Kuo A, Kohler A, Daghino S, Barry KW, Cichocki N, Clum A, Dockter RB, Hainaut M, Kuo RC, LaButti K, Lindahl BD, Lindquist EA, Lipzen A, Khouja HR, Magnuson J, Murat C, Ohm RA, Singer SW, Spatafora JW, Wang M, Veneault-Fourrey C, Henrissat B, Grigoriev IV, Martin FM, Perotto S. 2018. Comparative genomics and transcriptomics depict ericoid mycorrhizal fungi as versatile saprotrophs and plant mutualists. *New Phytologist* 217:1213–1229 DOI 10.1111/nph.14974.
- Martos F, Dulormne M, Pailler T, Bonfante P, Faccio A, Fournel J, Dubois MP, Selosse MA. 2009. Independent recruitment of saprotrophic fungi as mycorrhizal

partners by tropical achlorophyllous orchids. *New Phytologist* **184**:668–681 DOI 10.1111/j.1469-8137.2009.02987.x.

- McCormick MK, Taylor DL, Juhaszova K, Burnett RK, Whigham DF, O'Neill JP. 2012. Limitations on orchid recruitment: not a simple picture. *Molecular Ecology* 21:1511–1523 DOI 10.1111/j.1365-294X.2012.05468.x.
- McLellan CA, Turbyville TJ, Wijeratne EMK, Kerschen A, Vierling E, Queitsch C, Whitesell L, Gunatilaka AAL. 2007. A rhizosphere fungus enhances Arabidopsis thermotolerance through production of an HSP90 inhibitor. *Plant Physiology* 145:174–182 DOI 10.1104/pp.107.101808.
- Mello A, Balestrini R. 2018. Recent insights on biological and ecological aspects of ectomycorrhizal fungi and their interactions. *Frontiers in Microbiology* 9:216 DOI 10.3389/fmicb.2018.00216.
- Mikola P. 1965. Studies on the ectendotrophic mycorrhiza of pine. *Acta Forestalia Fennica* 79:1–56.
- Münzenberger B. 1991. Losliche und zellwandgebundene Phenole in Mykorrhizen und nicht mykorrhizierten Wurzeln der Fichte (Picea abies [L.] Karst.) und des Erdbeerbaumes (Arbutus unedo L.) und ihre Bedeutung in der Pilz-Wurzel-Interaktion. PhD thesis, University of Tübingen, Tübingen, Germany.
- Münzenberger B, Kottke I, Oberwinkler F. 1992. Ultrastructural investigations of Arbutus unedo-Laccaria amethystea mycorrhiza synthezised *in vitro*. *Trees* 7:40–47.
- Murata H, Yamada A, Maruyama T, Endo N, Yamamoto K, Ohira T, Shimokawa T. 2013. Root endophyte interaction between ectomycorrhizal basidiomycete *Tricholoma matsutake* and arbuscular mycorrhizal tree *Cedrela odorata*, allowing *in vitro* synthesis of rhizospheric shiro. *Mycorrhiza* 23:235–242 DOI 10.1007/s00572-012-0466-7.
- Navarro-Ródenas A, Pérez-Gilabert M, Torrente P, Morte A. 2012. The role of phosphorus in the ectendomycorrhiza continuum of desert truffle mycorrhizal plants. *Mycorrhiza* 22:565–575 DOI 10.1007/978-3-642-30826-0.7.
- Nehls U, Bodendiek I. 2012. Carbohydrates exchange between symbionts in ectomycorrhizas. In: Hock B, ed. *Fungal associations*. 9. Berlin: Springer, 119–136.
- Newman EI. 1995. Phosphorus inputs to terrestrial ecosystems. *Journal of Ecology* 83:713–726 DOI 10.2307/2261638.
- Newsham KK. 1999. *Phialophora graminicola*, a dark septate fungus, is a beneficial associate of the grass *Vulpia ciliata* ssp. *ambigua*. *New Phytologist* 144:517–524 DOI 10.1046/j.1469-8137.1999.00537.x.
- Newsham KK. 2011. A meta-analysis of plant responses to dark septate root endophytes. *New Phytologist* **190**:783–793 DOI 10.1111/j.1469-8137.2010.03611.x.
- Newsham KK, Upson R, Read DJ. 2009. Mycorrhizas and dark septate root endophytes in polar regions. *Fungal Ecology* 2:10–20 DOI 10.1016/j.funeco.2008.10.005.
- Nurfadilah S, Swarts N, Dixon KW, Lambers H, Merritt D. 2013. Variation in nutrientacquisition patterns by mycorrhizal fungi of rare and common orchids explains diversification in a global biodiversity hotspot. *Annals of Botany* 111:1233–1241 DOI 10.1093/aob/mct064.

- Ogura-Tsujita Y, Gebauer G, Hashimoto T, Umata H, Yukawa T. 2009. Evidence for novel and specialized mycorrhizal parasitism: the orchid Gastrodia confusa gains carbon from saprotrophic Mycena. *Proceedings of the Royal Society of London B* 276:761–767 DOI 10.1098/rspb.2008.1225.
- Ogura-Tsujita Y, Yukawa T. 2008. High mycorrhizal specificity in a widespread mycoheterotrophic plant, Eulophia zollingeri (Orchidaceae). *American Journal of Botany* 95:93–97 DOI 10.3732/ajb.95.1.93.
- Oliveira SF, Bocayuva MF, Veloso TGR, Bazzolli DMS, Da Silva CC, Pereira OL, Kasuya MC. 2014. Endophytic and mycorrhizal fungi associated with roots of endangered native orchids from the Atlantic Forest, Brazil. *Mycorrhiza* 24:55–64.
- Öpik M, Metsis M, Daniell TJ, Zobel M, Moora M. 2009. Large-scale parallel 454 sequencing reveals host ecological group specificity of arbuscular mycorrhizal fungi in a boreonemoral forest. *New Phytologist* 184:424–437 DOI 10.1111/j.1469-8137.2009.02920.x.
- Orchard S, Hilton S, Bending GD, Dickie IA, Standish RJ, Gleeson DB, Jeffery RP, Powell JR, Walker C, Bass D, Monk J, Simonin A, Ryan MH. 2017. Fine endophytes (Glomus tenue) are related to Mucoromycotina, not Glomeromycota. *New Phytologist* 213:481–486 DOI 10.1111/nph.14268.
- Orchard S, Standish RJ, Nicol D, Gupta VVSR, Ryan MH. 2016. The response of fine root endophyte (Glomus tenue) to waterlogging is dependent on host plant species and soil type. *Plant and Soil* 403:305–315 DOI 10.1007/s11104-016-2804-6.
- **Pearson V, Read D. 1973.** Biology of mycorrhiza in the Ericaceae. II. Transport of C and phosphorus by endophyte and mycorrhiza. *New Phytologist* **72**:1325–1331 DOI 10.1111/j.1469-8137.1973.tb02110.x.
- Perotto S, Girlanda M, Martino E. 2002. Ericoid mycorrhizal fungi: some new perspectives on old acquaintances. *Plant and Soil* 244:41–53 DOI 10.1023/A:1020289401610.
- Philippot L, Raaijmakers JM, Lemanceau P, Van der Putten WH. 2013. Going back to the roots: the microbial ecology of the rhizosphere. *Nature Reviews Microbiology* 11:789–799 DOI 10.1038/nrmicro3109.
- Phillips RP, Midgley MG, Brozstek E. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in forests. *New Phytologist* 199:41–51 DOI 10.1111/nph.12221.
- **Postma JWM, Olsson PA, Falkengren-Grerup U. 2007.** Root colonisation by arbuscular mycorrhizal, fine endophytic and dark septate fungi across a pH gradient in acid beech forests. *Soil Biology and Biochemistry* **39**:400–408 DOI 10.1016/j.soilbio.2006.08.007.
- Rasmussen HN. 2002. Recent developments in the study of or-chid mycorrhiza. *Plant and Soil* 244:149–163 DOI 10.1023/A:1020246715436.
- Rasmussen HN, Rasmussen FN. 2009. Orchid mycorrhiza: implications of a mycophagous life style. *Oikos* 118:334–345 DOI 10.1111/j.1600-0706.2008.17116.x.

- Read DJ, Leake JR, Perez-Moreno J. 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany* 82:1243–1263 DOI 10.1139/b04-123.
- Read DJ, Perez-Moreno J. 2003. Mycorrhizas and nutrient cycling in ecosystems—a journey towards relevance? *New Phytologist* 157:475–492 DOI 10.1046/j.1469-8137.2003.00704.x.
- Redecker D, Kodner R, Graham LE. 2000. Glomalean fungi from the Ordovician. *Science* 289:1920–1921 DOI 10.1126/science.289.5486.1920.
- **Rice AV, Currah RS. 2006.** In: Schulz BJE, Boyle CJC, Sieber TN, eds. *Oidiodendron maius: saprobe in Sphagnum peat, mutualist in ericaceous roots?* Heidelberg: Springer, 227–246.
- Richard F, Millot S, Gardes M, Selosse MA. 2005. Diversity and specificity of ectomycorrhizal fungi retrieved from an old-growth Mediterranean forest dominated by Quercus ilex. *New Phytologist* 166:1011–1023 DOI 10.1111/j.1469-8137.2005.01382.x.
- **Rinaldi AC, Comandini O, Kuyper TW. 2008.** Ectomycorrhizal fungal diversity: separating the wheat from the chaff. *Fungal Diversity* **33**:1–45.
- Rodriguez R, White J. 2009. Fungal endophytes: diversity and functional roles. *New Phytologist* 182:314–330 DOI 10.1111/j.1469-8137.2009.02773.x.
- Rosling A, Cox F, Cruz-Martinez K, Ihrmark K, Grelet GA, Lindahl BD, Menkis A, James TY. 2011. Archaeorhizomycetes: unearthing an ancient class of ubiquitous soil fungi. *Science* 333:876–879 DOI 10.1126/science.1206958.
- Rosling A, Midgley MG, Cheeke T, Urbina H, Fransson P, Phillips RP. 2016. Phosphorus cycling in deciduous forest soil differs between stands dominated by ecto- and arbuscular mycorrhizal trees. *New Phytologist* 209:1184–1195 DOI 10.1111/nph.13720.
- **Sapp J. 1994.** *Evolution by association: a history of symbiosis.* New York: Oxford University Press.
- Sapp J, Carrapiço F, Zolotonodov M. 2002. Symbiogenesis: the hidden face of Constantin Merezhkowsky. *History and Philosophy of the Life Sciences* 24:421–449.
- Scales PF, Peterson RL. 1991. Structure and development of Pinus banksiana– Wilcoxina ectendomycorrhizae. *Canadian Journal of Botany* 69:2135–2148 DOI 10.1139/b91-268.
- Schadt CW, Martin AP, Lipson DA, Schmidt SK. 2003. Seasonal dynamics of previously unknown fungal lineages in tundra soils. *Science* 301:1359–1361 DOI 10.1126/science.1086940.
- Schneider-Maunoury L, Leclercq S, Clément C, Covès H, Lambourdière J, Sauve M, Richard F, Selosse M, Taschen E. 2018. Is *Tuber melanosporum* colonizing the roots of herbaceous, non-ectomycorrhizal plants? *Fungal Ecology* 31:59–68 DOI 10.1016/j.funeco.2017.10.004.
- Schussler A, Walker C. 2010. *The Glomeromycota: a species list with new families and new genera*. Edinburgh & Kew: The Royal Botanic Garden Munich, Germany: Botanische Staatssammlung Munich; Oregon: Oregon State University.

- Selosse MA, Dubious MP, Alvarez N. 2009. Do Sebacinales commonly associate with plant roots as endophytes? *Mycological Research* 113:1062–1069 DOI 10.1016/j.mycres.2009.07.004.
- Selosse MA, Faccio A, Scappaticci G, Bonfante P. 2004. Chlorophyllous and achlorophyllous specimens of Epipactis microphylla (Neottieae, Orchidaceae) are associated with ectomycorrhizal septomycetes, including truffles. *Microbial Ecology* **47**:416–426.
- Selosse MA, Martos F, Perry B, Maj P, Roy M, Pailler T. 2010. Saprotrophic fungal symbionts in tropical achlorophyllous orchids. *Plant Signaling & Behavior* 5:349–353 DOI 10.4161/psb.5.4.10791.
- Selosse MA, Schneider-Maunoury L, Martos F. 2018. Time to re-think fungal ecology? Fungal ecological niches are often prejudged. *New Phytologist* 217:968–972 DOI 10.1111/nph.14983.
- Shakya M, Gottel N, Castro H, Yang ZK, Gunter L, Labbé J, Muchero W, Bonito G, Vilgalys R, Tuskan G, Podar M, Schadt CW. 2013. A multifactor analysis of fungal and bacterial community structure in the root microbiome of mature Populus deltoides trees. *PLOS ONE* 8:e76382 DOI 10.1371/journal.pone.0076382.
- Siciliano V, Genre A, Balestrini R, Cappellazzo G, DeWitt P, Bonfante P. 2007. Transcriptome analysis of arbuscular mycorrhizal roots during development of the prepenetration apparatus. *Plant Physiology* 144:1455–1466 DOI 10.1104/pp.107.097980.
- **Sikes BA. 2010.** When do arbuscular mycorrhizal fungi protect plant roots from pathogens? *Plant Signaling and Behavior* **5**:763–765 DOI 10.4161/psb.5.6.11776.
- Smith GR, Finlay RD, Stenlid J, Vasaitis R, Menkis A. 2017. Growing evidence for facultative biotrophy in saprotrophic fungi: data from microcosm tests with 201 species of wood-decay basidiomycetes. *New Phytologist* 215:747–755 DOI 10.1111/nph.14551.
- Smith FA, Grace EJ, Smith SE. 2009. More than a carbon economy: nutrient trade and ecological sustainability in facultative arbuscular mycorrhizal symbioses. *New Phytologist* 182:347–358 DOI 10.1111/j.1469-8137.2008.02753.x.
- Smith SE, Jakobsen I, Grønlund M, Smith FA. 2011. Roles of arbuscular mycorrhizas in plant phosphorus nutrition: Interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulation plant phosphorus acquisition. *Plant Physiology* **156**:1050–1057 DOI 10.1104/pp.111.174581.
- Smith SE, Read DJ. 2008. Mycorrhizal symbiosis. London: Academic Press.
- Smith FA, Smith SE. 1996. Mutualism and parasitism: diversity in function and structure in the "arbuscular" (VA) mycorrhizal symbiosis. *Advances in Botanical Research* 22:1–43 DOI 10.1016/S0065-2296(08)60055-5.
- Smith FA, Smith SE. 1997. Structural diversity in (vesicular)-arbuscular mycorrhizal symbioses. New Phytologist 137:373–388 DOI 10.1046/j.1469-8137.1997.00848.x.
- **Smith SE, Smith FA, Jakobsen I. 2004.** Functional diversity in arbuscular mycorrhizal (AM) symbioses: the contribution of the mycorrhizal P uptake pathway is not

correlated with mycorrhizal responses in growth or total P uptake. *New Phytologist* **162**:511–524 DOI 10.1111/j.1469-8137.2004.01039.x.

- Spatafora JW, Chang Y, Benny GL, Lazarus K, Smith ME, Berbee ML, Bonito G, Corradi N, Grigoriev I, Gryganskyi A, James TY, O'Donnell K, Roberson RW, Taylor TN, Uehling J, Vilgalys R, White MM, Stajich JE. 2016. A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. *Mycologia* 108:1028–1046 DOI 10.3852/16-042.
- Tedersoo L, Bahram M, Põlme S, Kõljalg U, Yorou NS, Wijesundera R, Ruiz RV, Vasco-Palacios AM, Thu PQ, Suija A, Smith ME, Sharp C, Saluveer E, Saitta A, Rosas M, Riit T, Ratkowsky D, Pritsch K, Põldmaa K, Piepenbring M, Phosri C, Peterson M, Parts K, Pärtel K, Otsing E, Nouhra E, Njouonkou AL, Nilsson RH, Morgado LN, Mayor J, May TW, Majuakim L, Lodge DJ, Lee SS, Larsson KH, Kohout P, Hosaka K, Hiiesalu I, Henkel TW, Harend H, Guo L, Greslebin A, Grelet G, Geml J, Gates G, Dunstan W, Dunk C, Drenkhan R, Dearnaley J, De Kesel A, Dang T, Chen X, Buegger F, Brearley FQ, Bonito G, Anslan S, Abell S, Abarenkov K. 2014. Global diversity and geography of soil fungi. *Science* 346:6213.
- Tedersoo L, May TW, Smith ME. 2010. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. *Mycorrhiza* 20:217–263 DOI 10.1007/s00572-009-0274-x.
- Tedersoo L, Pellet P, Koljalg U, Selosse M. 2007. A Parallel evolutionary paths to mycoheterotrophy in understorey Ericaceae and Orchidaceae: ecological evidence for mixotrophy in Pyroleae. *Oecologia* 151:206–217 DOI 10.1007/s00442-006-0581-2.
- **Tedersoo L, Smith ME. 2013.** Lineages of ectomycorrhizal fungi revisited: foraging strategies and novel lineages revealed by sequences from belowground. *Fungal Biology Reviews* **27**:83–99 DOI 10.1016/j.fbr.2013.09.001.
- Tellenbach C, Grünig CR, Sieber TN. 2011. Negative effects on survival and performance of Norway spruce seedlings colonized by dark septate root endophytes are primarily isolate dependent. *Environmental Microbiology* 13:2508–2517 DOI 10.1111/j.1462-2920.2011.02523.x.
- **Terrer C, Vicca S, Hungate BA, Phillips RP, Prentice IC. 2016.** Mycorrhizal association as a primary control of the CO2 fertilization effect. *Science* **353**:72–74 DOI 10.1126/science.aaf4610.
- **Tibbett M, Sanders FE. 2002.** Ectomycorrhizal symbiosis can enhance plant nutrition through improved access to discrete organic nutrient patches of high resource quality. *Annals of Botany* **89**:783–789.
- **Toju H, Sato H, Tanabe AS. 2014.** Diversity and spatial structure of belowground plant– fungal symbiosis in a mixed subtropical forest of ectomycorrhizal and arbuscular mycorrhizal plants. *PLOS ONE* **9**:e86566 DOI 10.1371/journal.pone.0086566.
- Toju H, Sato H, Yamamoto S, Kadowaki K, Tanabe AS, Yazawa S, Nishimura O, Agata K. 2013. How are plant and fungal communities linked to each other in belowground ecosystems? A massively parallel pyrosequencing analysis of the

association specificity of root-associated fungi and their host plants. *Ecology and Evolution* **3**:3112–3124 DOI 10.1002/ece3.706.

- Trevor E, Yu JC, Egger KN, Peterson LR. 2001. Ectendomycorrhizal associations characteristics and functions. *Mycorrhiza* 11:167–177 DOI 10.1007/s005720100110.
- Vályi K, Rillig MC, Hempel S. 2015. Land-use intensity and host plant identity interactively shape communities of arbuscular mycorrhizal fungi in roots of grassland plants. *New Phytologist* 205:1577–1586 DOI 10.1111/nph.13236.
- **Van der Heijden MGA, Bardgett RD, Straalen NM. 2008.** The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters* **11**:296–310 DOI 10.1111/j.1461-0248.2007.01139.x.
- Van der Heijden MGA, Martin F, Selosse MA, Sanders I. 2015. Mycorrhizal ecology and evolution: the past, the present and the future. *New Phytologist* 205:1406–1423 DOI 10.1111/nph.13288.
- Van der Linde S, Laura MS, Orme CDL, Cox F, Andreae H, Asi E, Atkinson B, Benham S, Carroll C, Cools N, De Vos B, Dietrich HP, Eichhorn J, Gehrmann J, Grebenc T, Gweon HS, Hansen K, Jacob F, Kristöfel F, Lech P, Manninger M, Martin J, Meesenburg H, Merilä P, Nicolas M, Pavlenda P, Rautio P, Schaub M, Schröck HW, Seidling W, Šrámek V, Thimonier A, Thomsen IM, Titeux H, Vanguelova E, Verstraeten A, Vesterdal L, Waldner P, Wijk S, Zhang Y, Žlindra D, Bidartondo MI. 2018. Environment and host as large-scale controls of ectomycorrhizal fungi. Nature 558:243–248 DOI 10.1038/s41586-018-0189-9.
- Van Scholl L, Smits MM, Hoffland E. 2006. Ectomycorrhizal weathering of the soil minerals muscovite and hornblende. *New Phytologist* 171:805–814 DOI 10.1111/j.1469-8137.2006.01790.x.
- Vandenkoornhuyse P, Ridgway KP, Watson IJ, Fitter AH, Young JPW. 2003. Coexisting grass species have distinctive arbuscular mycorrhizal communities. *Molecular Ecology* 12:3085–3095 DOI 10.1046/j.1365-294X.2003.01967.x.
- Vare H, Vestberg M, Eurola S. 1992. Mycorrhiza and root associated fungi in Spitsbergen. *Mycorrhiza* 1:93–104 DOI 10.1007/BF00203256.
- Varma A, Singh A, Sudha M, Sahay NS, Sharma J, Roy A, Kumari M, Rana D, Thakran S, Deka D, Bharati K, Franken P, Hurek T, Blechert O, Rexer KH, Kost G, Hahn A, Maier W, Walter M, Strack D, Kranner I. 2001. Serendipita indica: a cultivable mycorrhiza-like endosymbiotic fungus. In: Hock B, ed. *The Mycota IX*. Berlin: Springer-Verlag, 125–150.
- Veresoglou SD, Rillig MC. 2014. Do closely related plants host similar arbuscular mycorrhizal fungal communities? A meta-analysis. *Plant and Soil* 377:395–406 DOI 10.1007/s11104-013-2008-2.
- Vohnik M, Sadowsky JJ, Kohout P, Lhotakova Z, Nestby R, Kolarik M. 2012. Novel root-fungus symbiosis in Ericaceae: sheathed ericoid mycorrhiza formed by a hitherto undescribed Basidiomycete with affinities to Trechisporales. *PLOS ONE* 7:e39524 DOI 10.1371/journal.pone.0039524.

- Walker C. 1985. Endogone lactiflua forming ectomycorrhizas with Pinus contorta. *Transactions of the British Mycological Society* 84:353–355 DOI 10.1016/S0007-1536(85)80091-7.
- Waller F, Achatz B, Baltruschat H, Fodor J, Becker K, Fischer M, Heier T, Hückelhoven R, Neumann C, Von Wettstein D, Franken P, Kogel K. 2005. The endophytic fungus Piriformospora indica reprograms barley to salt-stress tolerance, disease resistance, and higher yield. *Proceedings of the National Academy of Sciences of the United States of America* 102:13386–13391 DOI 10.1073/pnas.0504423102.
- Warcup JH. 1990. Occurrence of ectomycorrhizal and saprophytic discomycetes after a wild fire in an eucalypt forest. *Mycological Research* 94:1065–1069 DOI 10.1016/S0953-7562(09)81334-8.
- Waterman RJ, Bidartondo MI, Stofberg J, Combs JK, Gebauer G, Savolainen V,
 Barraclough TG, Pauw A. 2011. The effects of above- and belowground mutualisms on orchid speciation and coexistence. *American Naturalist* 177:E54–E68.
- Weiss M, Sýkorová Z, Garnica S, Riess K, Martos F, Krause C, Oberwinkler F, Bauer R, Redecker D. 2011. Sebacinales everywhere: previously overlooked ubiquitous fungal endophytes. *PLOS ONE* 6:e16793 DOI 10.1371/journal.pone.0016793.
- Weiss M, Waller F, Zuccaro A, Selosse MA. 2016. Sebacinales-one thousand and one interactions with land plants. *New Phytologist* 211:20–40 DOI 10.1111/nph.13977.
- Yadav V, Kumar M, Deep DK, Kumar H, Sharma R, Tripathi T, Tuteja N, Saxena AK, Johri AK. 2010. A phosphate transporter from the root endophytic fungus Serendipita indica plays a role in phosphate transport to the host plant. *The Journal of Biological Chemistry* 285:26532–26544 DOI 10.1074/jbc.M110.111021.
- Yagame T, Yamato M, Mii M, Suzuki A, Iwase K. 2007. Developmental processes of achlorophyllous orchid, Epipogium roseum: from seed germination to flowering under symbiotic cultivation with mycorrhizal fungus. *Journal of Plant Research* 120:229–236 DOI 10.1007/s10265-006-0044-1.
- Yamada A, Katsuya K. 1995. Mycorrhizal association of isolates from sporocarps and ectomycorrhizas with Pinus densifolia seedlings. *Mycoscience* **36**:315–323 DOI 10.1007/BF02268607.
- Yamato M, Yagame T, Suzuki A, Iwase K. 2005. Isolation and identification of mycorrhizal fungi associating with an achlorophyllous plant, Epipogium roseum (Orchidaceae). *Mycoscience* **46**:73–77 DOI 10.1007/S10267-004-0218-4.
- Yang S, Pfister D. 2006. Monotropa uniflora plants of eastern Massachusetts form mycorrhizae with a diversity of russulacean fungi. *Mycologia* 98:535–540 DOI 10.1080/15572536.2006.11832656.
- Yu T, Nassuth A, Peterson RL. 2001. Characterization of the interaction between the dark septate fungus Phialocephala fortinii and Asparagus officinalis roots. *Canadian Journal of Microbiology* 47:741–753 DOI 10.1139/w01-065.
- Zuccaro A, Lahrmann U, Guldener U, Langen G, Pfiffi S, Biedenkopf D, Wong P, Samans B, Grimm C, Basiewicz M, Murat C, Martin F, Kogel KH. 2011. Endophytic

life strategies decoded by genome and transcriptome analyses of the mutualistic root symbiont Serendipita indica. *PLOS Pathogens* **7**:e1002290.

Zuccaro A, Lahrmann U, Langen G. 2014. Broad compatibility in fungal root symbioses. *Current Opinion in Plant Biology* 20:135–145 DOI 10.1016/j.pbi.2014.05.013.