INTRODUCTION

Plant cell walls form a dynamic extracellular matrix that actively controls growth and development, and are essential for the functionality of plants (Keegstra, 2010). Cell walls provide shape to the many different cell types needed to form tissues and organs, and form the interface between neighboring cells, they control intercellular communication. Therefore, cell walls mediate most plant–microbe interactions. However, cell walls are not exclusive to photosynthetic organisms: fungi also have walls that determine hyphal growth, shape and responses (Durán and Nombela, 2004).

Unlike pathogenic interactions, where the fungal pathogen may be effective even with a limited presence in the plant tissues, in mycorrhizae, i.e., the widespread symbiotic associations established between plant roots and soil fungi, has been investigated extensively. All mycorrhizal interactions achieve full symbiotic functionality through the development of an extensive contact surface between the plant and fungal cells, where signals and nutrients are exchanged. The exchange of molecules between the fungal and the plant cytoplasm takes place both through their plasma membranes and their cell walls; a functional compartment, known as the symbiotic interface, is thus defined. Among all the symbiotic interfaces, the complex intracellular interface of arbuscular mycorrhizal (AM) symbiosis has received a great deal of attention since its first description. Here, in fact, the host plasma membrane invaginates and proliferates around all the developing intracellular fungal structures, and cell wall material is laid down between this membrane and the fungal cell surface. By contrast, in ectomycorrhizae (ECM), where the fungus grows outside and between the root cells, plant and fungal cell walls are always in direct contact and form the interface between the two partners. The organization and composition of cell walls within the interface compartment is a topic that has attracted widespread attention, both in ecto- and endomycorrhizae. The aim of this review is to provide a general overview of the current knowledge on this topic by integrating morphological observations, which have illustrated cell wall features during mycorrhizal interactions, with the current data produced by genomic and transcriptomic approaches.

Keywords: cell wall, mycorrhizal interactions, fungal genomes, interface, gene expression
THE SYMBIOTIC INTERFACE: HOW TO INCREASE THE PARTNERS’ CONTACTS WHILE MAINTAINING BIOTROPHY

Among all the mycorrhizal interfaces, the complex intracellular interface of AM symbiosis has received considerable attention since its first descriptions in the seventies. Following the findings on fungal pathogens (Bracker and Littlefield, 1973; Scannerini and Bonfante, 1976) observed that the AM fungus is always surrounded by a plant-derived membrane, which leads to an interfacial zone consisting of a fungal plasma membrane, a specialized interfacial matrix, and a plant membrane, which was called the periarbuscular membrane (Figure 1). At that time, observations were mostly made on the cortical cells that host branched fungal arbuscules. The presence of this interface compartment is a typical feature of all endomycorrhizae (Scannerini and Bonfante-Fasolo, 1983; Peterson and Massicotte, 2004). In orchid, ericoid and arbutoid interactions, the intracellular fungus resulted to be confined within this compartment, that provides the structural basis of biotrophic interactions, since both partners maintain their individuality and remain alive. In the meantime, it causes a huge increase in the contact surface between the two partners, and the plant membrane increases in length several-fold during arbuscule development (Cox and Sanders, 1974).

The improved knowledge on the AM colonization process has allowed to demonstrate that the symbiotic interface is not limited to the arbusculated stage (Gutjahr and Parniske, 2013). When the AM germ-tube comes into contact with the epidermal cells, forming hyphopodia (Genre and Bonfante, 2007), these cells generate a colonization structure, the prepenetration apparatus (PPA), which is a transient formation that comprises cytoskeletal and endoplasmic reticulum (ER) components (Genre et al., 2005, 2008). Following this event, the hypha enters and crosses the epidermal cell, but prevents direct contact with the host cytoplasm thanks to a newly synthesized membrane of host origin. The biosynthesis of this novel perifungal membrane is the result of a process which involves exocytosis of the Golgi vesicles at

![FIGURE 1](image-url)
the growing tips of the AM fungus. Using different GFP Medicago constructs, Genre et al. (2012) and Ivanov et al. (2012) have demonstrated that two VAMPs (vesicle-associated membrane proteins), belonging to R-SNAREs, are required to assemble the perifungal membrane. Interestingly, these proteins have also been detected at the cell plate of dividing meristematic root cells (Ivanov et al., 2012), thus offering the first molecular demonstration of the similarities between cell division leading to the construction of a new cell wall and development of the symbiotic interface.

Detailed electron microscope observations had already shown that the interfacial compartment contains cell-wall like material (Scannnerini and Bonfante-Fasolo, 1983; Balestrini and Bonfante, 2005), and this has led to the question about whether the perifungal membrane maintains the capacity to synthesize and deliver cell wall-related molecules, like the peripheral membrane, (i.e., the plasma membrane of the host cell), but directed towards the interface space. The development of many in situ techniques (enzymes, lectins, and antibodies) has made it possible to validate this hypothesis: β-1,4-glucans, nonesterified homogalacturonan, xyloglucans, proteins rich in hydroxyproline (HRGPs), and arabinogalactan proteins (AGPs) have been located at the interface in many different plant/AM fungus combinations, as on peripheral cell wall, i.e., the cell wall of host cells containing the fungal structures (Bonfante et al., 1990a; Bonfante-Fasolo et al., 1991; Balestrini et al., 1994, 1996b; Gollotte et al., 1995; Balestrini and Bonfante, 2005). Expansins, which are extracellular proteins involved in cell wall-loosening and in the growth of plant cells (Cosgrove et al., 2002), have also been located in AM roots: they are present both in the cell walls of the host cells and in the interface, suggesting that this class of proteins, involved in cell wall loosening, may be crucial in the accommodation process of the fungus inside the cortical cells (Balestrini et al., 2005).

Although the molecular content of the interface reflects the composition of the host cell wall, the morphology of the interface material indicates that its components are assembled differently, and this leads to a more amorphous structure (Figures 2 and 3). In addition, this cell wall-like material changes in morphology during the arbuscule’s life cycle: it is very thick and compact around the arbuscule trunk, it becomes very thin around the fungal branches, and it again becomes thicker when the arbuscule collapses. Such dynamics probably mirror the uneven distribution of plant membrane proteins along the perifungal membrane (see Gutjahr and Parniske, 2013 for a review). Expansins and/or secreted proteins of fungal origin (see below) could also play a role in keeping the interfacial material loose.

In liverworts, the disappearance of cell wall autofluorescence, which is a normal feature of non-colonized parenchyma cells, has been observed in the fungus-colonized areas, suggesting changes in cell wall composition upon fungal colonization, and a localized decrease in cell wall-bound phenolic compounds (Ligrone et al., 2007).

Compared to AM symbiosis, the symbiotic interface in ECM appears much simpler, at least on a morphological level: the plant and fungal cell walls are always in direct contact, since the ECM fungus remains apoplastic (Balestrini et al., 1996a; Peterson et al., 2004; Figures 2 and 3). When the hyphae penetrate between the root cells, only subtle alterations can be observed in the PCW, although a localized loosening has been reported in several ECMs (Balestrini et al., 1996a). Ultra-structural observations of ECMs formed by Hieiella cylindrosorum IAA-overproducing mutants suggest that fungal IAA may play a role in Hartig net development by affecting PCW loosening (Gea et al., 1994). Components specific to both plant (e.g., cellulose and pectins) and fungal (e.g., SRAPs and hydrophobins) cell walls have been identified in the cell walls at the symbiotic interface (Balestrini et al., 1996a; Laurent et al., 1999; Tagu et al., 2001; Figure 3).

In conclusion, functioning mycorrhizal symbiosis requires both partners to be alive in order to exchange nutrients in a balanced way (Kiers et al., 2011). From a structural point of view, this requires the partners to maintain their individuality: this is guaranteed by a simple wall-to-wall contact during intercellular interactions and by a more sophisticated interface when the fungus becomes intracellular. Interestingly, the development of such a complex interface is also characteristic of biotrophic pathogenic interactions (Yi and Valent, 2013), suggesting that some plant responses reflect ancient mechanisms which are independent of the outcome of the interaction. Quoting Yi and Valent (2013) “…the interface is the site of active secretion by both players. This cross-talk at the interface determines the winner in adversarial relationships and establishes the partnership in mutualistic relationships.”

FROM STRUCTURE TO BIOSYNTHESIS: PLANT CELL WALL RELATED GENES RESPOND TO SYMBIOSIS

Starting from in situ localization data, attention has been focused on the genesis of the interfacial material, and in particular on the plant genes involved in the cell wall metabolism. Using targeted approaches, it was found that genes encoding a putative AGP and an HRGP were induced in mycorrhizal roots of Medicago truncatula and maize, respectively, and the transcripts were specifically localized in arbusculated cells (Balestrini et al., 1997; van Buuren et al., 1999). An endotransglucosylase/hydrolase gene, Mt-XHT1, induced in M. truncatula roots during AM symbiosis, was identified (Maldonado-Mendoza et al., 2005). The analysis of transgenic roots expressing an Mt-XHT1 fusion promoter has shown that expression is enhanced not only in the root regions colonized by the fungus, but also at distal sites. On the basis of this expression pattern, it was suggested that Mt-XHT might be involved in the systemic modification of a cell wall structure in order to enable fungal penetration.

Coming to the availability of sequenced genomes for several plants that are AM hosts, and the possibility of obtaining global transcriptional profiling of mycorrhizal roots, the regulation of cell-wall related genes has been studied at a larger scale. On the basis of localization data, an expansin gene has been found among the most up-regulated genes in M. truncatula mycorrhizal roots (Liu et al., 2003). Similarly, expansin/expansin-like genes were up-regulated during the early symbiotic stages in both M. truncatula (Weidmann et al., 2004; Siciliano et al., 2007) and tomato roots (EXL1; Dermatsev et al., 2009), suggesting that an increase in PCW plasticity is a prerequisite to the accommodation of the
fungus in the plant. *In situ* hybridization experiments on *Medicago* roots have in fact revealed that an expansin-like protein was preferentially expressed in epidermal cells in contact with the hyphopodium (Siciliano et al., 2007). A cellulose synthase-like gene was also shown to be up-regulated at the same stage (Siciliano et al., 2007). In agreement with the proposed role played by the PPA, the up-regulation of genes involved in cell wall synthesis/remodeling, during hyphopodium development, suggests that the building of the interface starts prior to fungal colonization. The symbiosis-dependent expression of an early nodulation gene (*ENOD11*), induced during the early stages of root nodulation and coding for a putative proline-rich protein (PRP), has also been detected in epidermal and cortical cells during root colonization by AM fungi (Journet et al., 2001; Chabaud et al., 2002). However, the role of these PRP proteins remains purely hypothetical. Thanks to a cDNA microarray experiment on *Lotus japonicus*, Guether et al. (2009) have demonstrated that a large number of genes related to membrane dynamics and cell wall metabolism are induced in mycorrhizal roots. These data support the hypothesis of plant cells having an active role in fungus accommodation *via* membrane proliferation and cell wall construction. Among the up-regulated genes related to cell wall metabolism, transcripts encoding for an endo-β-1,4-beta-glucanase (*LjCel1*) and a putative cellulose synthase (*LjCesA*) were detected exclusively in arbusculated cells, using a microdissection approach. These data are in agreement with those previously observed for *M. truncatula*, where the homologous gene *MtCell1* was found to be specifically expressed during symbiosis and, more specifically, within arbusculated cells (Liu et al., 2003). Considering the membrane domain, it was suggested that MtCell1 was located in the periarbuscular membrane and that it was directly involved in the assembly of the cellulose/hemicellulose matrix detected at the interface through *in situ* methods. Similarly, transcripts of a putative cellulose synthase, *LjCesA*, were also found to accumulate in arbusculated cells. CesA proteins are part of the cellulose synthase complex in higher plants (Taylor, 2008), which is a membrane-located enzymatic system that is responsible for cellulose synthesis.

Morphometric analyses have suggested an increase in the size of cells containing arbuscules (Balestrini et al., 2005). The authors hypothesized that *LjCesA* plays a role in cell expansion during arbuscule development, in conjunction with other proteins involved in cell wall remodeling (Balestrini and Bonfante, 2005). The role of two apoplastic plant proteases of the subtilase family (*LjSbtM1* and *LjSbtM3*) during AM fungal colonization was also reported (Takeda et al., 2009). The members inside this protease family, as extracellular enzymes, are expressed during organ development and may be involved in the modification of cell wall structure, thus contributing to cell wall dynamics (Schaller et al., 2012). It has been proposed that these two *Lotus* genes, which are specifically expressed during the symbiosis, could play a role in cell wall modifications: they could facilitate fungal growth, or communication between the symbiotic partners, e.g., through the generation of peptides with a signaling role. Localization data have also shown that LjSbtM1, which is targeted for secretion, is localized in the apoplastic compartments, including the PCWs of the colonized cells, the intercellular spaces and the periarbuscular space.

Considering these data, it is tempting to suggest that the AM fungus not only leads to the construction of the interface compartment, but may also have the peripheral cell wall as an additional target. This has also been suggested for an ascorbate oxidase gene (*LjAO1*), which is up-regulated during AM symbiosis, where it shows a double location: in the apoplast and in the interface. This suggests that AO is possibly involved in the accommodation...
of fungal structures, with the role of maintaining the structure of the interface compartment, as well as in cell wall loosening and extension, as observed in arbusculated cells (Balestrini et al., 2012a).

The activation of a β-xylosidase α-L-arabinosidase (which can contribute to the turnover of cell wall xylose and arabinose) has also been shown to be induced in tomato mycorrhizal roots (Fiorilli et al., 2009); the corresponding transcripts were localized exclusively in the arbuscule-containing cells, suggesting its involvement during the formation of the periarbuscular matrix, although involvement in the remodeling of the peripheral wall cannot be excluded. A monosaccharide transporter, MST2, which has been identified in an AM fungus (Helber et al., 2011), has been shown to transport not only glucose, but also cell wall monosaccharides, i.e., xylose. This result is in agreement with the fact that the plant-fungal interface in AM symbiosis contains primary PCW components (Balestrini and Bonfante, 2005). The authors have suggested that a versatile sugar transporter – capable of transporting monosaccharides from the apoplast – might be an optimal adaptation to the biotrophic life style of AMF (Helber et al., 2011).

Changes in the plant transcriptomic profiles of ECM roots have been well documented (Voiblet et al., 2001; Johansson et al., 2004; Duplessis et al., 2005; Le Quéré et al., 2005; Tuskan et al., 2006;
investigated. Although the mechanisms at the base of this response still have to be studied, the expression of cell wall-related genes in AM roots (Willmann et al., 2013), maize demonstrated that a loss in function mutation in a mycorrhiza-specific cell wall relaxation. Interestingly, it has recently been demonstrated that symbiotic interactions are not limited to the sym-biotic interface, since a still not fully acknowledged aspect is the cell wall metabolism does not seem to be limited to the sym-biotic interface in ECMs, where no conspicuous morphological modifications have been described. Finally, the impact of mycorrhizal fungi on the cell wall metabolism does not seem to be limited to the sym-biotic interfaces, since a still not fully acknowledged aspect is the increase in size of the colonized cells, which likely results from cell wall relaxation. Interestingly, it has recently been demonstrated that a loss in function mutation in a mycorrhiza-specific maize Pt transporter gene (Pt1;6) leads to a down-regulation of cell wall-related genes in AM roots (Willmann et al., 2013), although the mechanisms at the base of this response still have to be investigated.

**DECRYPTION OF GENOMES OF MYCORRHIZAL FUNGI SHEDS LIGHT ON CELL WALL DYNAMICS**

The sequenced genomes of mycorrhizal fungi are crucial tools to obtain a deeper understanding of the molecular mechanisms that underlie the symbiotic lifestyle. Focusing on cell wall genes, the so far sequenced fungi have allowed new information to be obtained on the fungal cell wall machinery, including genes that potentially code for fungal cell wall proteins involved in the interaction with plants, and those that may code for enzymes which act on PCW. This is a great step forward, since unlike for pathogenic fungi, a biochem-i-cal characterization of the main cell wall components, (i.e., polysaccharides and proteins) is not yet available for mycorrhizal fungi.

The involvement of fungal cell wall proteins, mainly small secreted proteins, (e.g., SRAPs and hydrophobins), has been well studied during the development of the symbiotic interface in ECM associations (Martin et al., 1999; Laurent et al., 1999; Tagu et al., 2001). Hydrophobins are morphogenetic small-secreted and moder-ately hydrophobic proteins that are typically present in fungi and which are involved in several aspects of fungal biology (Wösten, 2001). They are also thought to play important roles during ECM establishment (Tagu et al., 2001; Voiblet et al., 2001; Plett et al., 2012). They have been localized on the fungal cell wall in the sym-biotic structures formed by *Pisolithus tinctorius* and *Eucalyptus globulus* (Tagu et al., 2001), and several hydrophobins are currently considered to belong to apoplastic MiSSPs (Mycorrhizal-induced Small Secreted Proteins; Plett et al., 2012). A genome-wide inven-tory of hydrophobin genes from two different genomes of the ECM fungus *L. bicolor* (Martin et al., 2008) has recently been obtained. This inventory shows a complex diversity and a range of expression profiles inside this multi-gene family (Plett et al., 2012).

The authors suggest that, during evolution, some hydrophobin proteins might have acquired new roles that are specific of the mutualistic lifestyle. Hydrophobin genes have been identified in the *Tuber melanosporum* genome (Martin et al., 2010; Balestrini et al., 2012b), and, among these genes, *TmlHYD3* seems to be slightly up-regulated in ECMs vs the free-living mycelium. However, these proteins seem to be absent in *Rhizophagus irregularis*, as in mildew where hydrophobins are lacking (Spanu et al., 2010).

The main carbohydrate components of fungal cell walls are chitin and glucans, and these have been localized in the cell walls of different mycorrhizal fungi (Bonfante et al., 1990b; Balestrini et al., 1994, 1996a, 2012b; Lemoine et al., 1995; Figures 1 and 2).

Taking advantage of the genome sequence, a genome-wide inventory of the proteins involved in cell wall synthesis and remodel-eling has been obtained for the *T. melanosporum* black truffle, while expression results have revealed that cell wall-related genes can be involved in the morphogenetic transition from mycelium growth to the ectomycorrhizal branched hyphae (Balestrini et al., 2012b).

In addition to their structural role, chitin-derived molecules are widespread microbial signals that trigger various defense responses in plant cells (Shimizu et al., 2010; Hayafune et al., 2014). In *Rhizobium*-legume symbiosis, the nitrogen-fixing bacte-ria produce lipochitooligosaccharides (LCOs), which are termed Nod factors (Dénarié and Cullimore, 1993). It has long been proposed that AM fungi also release signal molecules (Myc factors), which are essential for the recognition of the fungal partner (Catoira et al., 2000b; Parniske, 2008). These molecular signals have recently been characterized as a mixture of sul-fated and non-sulfated LCOs (Maillet et al., 2011). Myc-LCOs, which are present at very low concentrations in the exudates of mycorrhizal carrot roots and *R. irregularis* germinated spores, stimulate AM symbiosis formation, and increase root branch-ing in *M. truncatula* (Maillet et al., 2011). Fungal orthologs of bacterial genes coding for enzymes involved in symbiotic LCO factors synthesis have not been identified so far in the genome of *R. irregularis*, the first AM fungus to be sequenced (Tisserant et al., 2013). Additionally, it has recently been observed...
that short-chain chitin oligomers (COs) of AM fungus origin activate a response (Ca$^{2+}$ spiking) in root epidermal cells, with the maximum activity being observed for CO4 and CO5 (Genre et al., 2013). Short-chain COs are therefore part of the molecular dialog with the host plant, that leads to the activation of the common symbiosis signaling pathway: these data reveal that AM fungi may produce different chitin-based signals (Genre et al., 2013). The R. irregularis genome (Tisserant et al., 2013; Lin et al., 2014) has revealed many genes involved in the chitin metabolism. In addition, transcriptomic data have shown that several of these genes, including, e.g., chitin synthases and putative chitin deacylases, are expressed during the different stages of the fungal life cycle, including the pre-symbiotic stage (Tisserant et al., 2012). Further investigation on the regulation of specific members inside these gene families, will provide new information on the relationships between the generation of chitin-derived signals by AM fungi and their life cycle. It is interesting to note that, until now, the production of chitin-related molecules with a signaling meaning has not been described in ECM fungi.

Fungal cell wall-related signals therefore seem to play an important role in pre-symbiotic communication between the AM symbiosis partners. This also seems to be true for the plant side: cutin monomers, which are hydrophobic components of the cell walls that are mostly present in epidermal cells, have been identified as signal molecules that induce hyphopodium differentiation (Wang et al., 2012; Murray et al., 2013).

Several fungal genes encoding enzymes involved in cell wall metabolism are expressed during AM fungal colonization, suggesting a role in the remodeling of the fungal cell wall during intracellular colonization (Lanfranco et al., 1999; Tisserant et al., 2012, 2013). AM fungal cell walls undergo a conspicuous change in their organization during their life cycle: the spore wall is thick and layered with a highly fibrillar chitin, while the hyphal wall becomes progressively thinner during the intracellular phase, reaching a thin amorphous structure in the thinner arbuscular branches (Bonfante et al., 1990b). This would seem to suggest that fungal growth inside the root cells requires a strict regulation of the genes related to both cell wall synthesis and degradation. Additionally, the expression of plant chitinase genes has been reported in arbuscule-containing cells, suggesting a putative role in fungal cell wall modification, during the development of the arbuscule branches, as well as in reducing the amount of chitin-derived elicitors, during the intracellular colonization and the development of the symbiotic interface (Bonanomi et al., 2001; Hogekamp et al., 2011).

As far as the R. irregularis genome is concerned, a surprising observation is the loss of glycosyl hydrolase (GH) genes and – among them – genes known to be involved in degrading PCW polysaccharides (Tisserant et al., 2013). PCW degradation requires the production of different enzymes that are regulated by the type and complexity of the plant material, and fungi can produce these enzymes (Tian et al., 2009). A decreased repertoire of PCW degrading enzymes, compared to saprotrophic and pathogenic fungi, has also been reported for the ECM fungi L. bicolor and T. melanosporum (Martin et al., 2008, 2010). Although both genomes have shown a reduced set of enzymes that target PCW components, subtle differences have been observed in the enzyme repertoire between the two fungi and in their expression (Martin et al., 2010; Plett and Martin, 2011). Despite the similarity of the symbiotic structures that they form, the expression results suggest differences in the mode of interaction with the respective host plants. For example, a limited number of PCW degrading enzymes are expressed in truffle symbiotic tissues, while L. bicolor expresses very few PCW degrading enzymes, and mainly secretes expansin-like proteins that may play a role in cell wall remodeling during hyphal penetration (Plett and Martin, 2011). Similarly, the ECM fungus Amanita bisporigina (Nagendran et al., 2009) lacks genes that code for extracellular enzymes which are active on cell wall linkages. A reduced set of PCW-degrading enzymes has also been found in some obligate biotrophic pathogens, i.e., B. graminis (Spanu et al., 2010). Unlike the enzymatic arsenal observed in other pathogenic fungi, the great reduction in PCW-degrading enzymes in fungi that are phylogenetically and functionally diverse suggests that this feature is related to their biotrophic life style. This could be one of the strategies that biotrophic fungi adopt to lower the defense reactions of their hosts.

In conclusion, genome sequence projects have, for the first time, allowed hypotheses to be formulated on the meaning of biotrophy in mycorrhizal fungi. They may use chitin-related molecules to dialog with their plant partners, but in spite of their deep intra-root habit, they do not possess PCW-degrading enzymes that can act on the PCW. It can be hypothesized that the signal molecules released by mycorrhizal fungi are perceived by the plant cells, which – in turn – elicit the activation of their own PCW-degrading enzymes. This indirect mechanism should prevent the activation of strong defense reactions.

**CONCLUSION**

Genome/transcriptome approaches applied to mycorrhizal fungi, and not only to the green partners, have had a profound effect on our knowledge of the biology of mycorrhizal symbiosis. As expected, the formation of the complex intracellular interface present in AMs is accompanied by a profound modulation of the PCW related genes (as well as the membrane-related ones). Surprisingly, important transcriptional changes have been detected in ECMs, where cell wall remodeling does not lead to evident morphological changes. The production of signaling molecules (Maillet et al., 2011; Genre et al., 2013), whose composition is related to the fungal cell wall, is probably a key element in the understanding of biotrophism. The mechanisms thanks to which the plant releases PCW enzymes, which allow fungal colonization, merit further detailed investigation. New genome data sets from several mycorrhizal fungi (ECM and AM), which are currently being sequenced (see http://genome.jgi.doe.gov/, http://mycor.nancy.inra.fr/genomeResources.html web sites), and from other non-AM endomycorrhizal fungi, e.g., Oidiodendron maius (ericoid symbiont) and Tulasnellla calospora (orchid symbiont), will increase the knowledge on how different mycorrhizal fungi have an impact on PCW remodeling, and, consequently, on how the different mycorrhizal strategies have developed during the evolution.
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