



Review

The role of ectomycorrhizal communities in forest ecosystem processes: New perspectives and emerging concepts

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ABSTRACT

The fungal symbionts forming ectomycorrhizas, as well as their associated bacteria, benefit forest trees in a number of ways although the most important is enhancing soil nutrient mobilization and uptake. This is reciprocated by the allocation of carbohydrates by the tree to the fungus through the root interface, making the relationship a mutualistic association. Many field observations suggest that ectomycorrhizal fungi contribute to a number of key ecosystem functions such as carbon cycling, nutrient mobilization from soil organic matter, nutrient mobilization from soil minerals, and linking trees through common mycorrhizal networks. Until now, it has been very difficult to study trees and their fungal associates in forest ecosystems and most of the work on ECM functioning has been done in laboratory or nursery conditions. In this review with discuss the possibility of working at another scale, in forest settings. Numerous new techniques are emerging that makes possible the *in situ* study of the functional diversity of ectomycorrhizal communities. This approach should help to integrate developing research on the functional ecology of ectomycorrhizas and their associated bacteria with the potential implications of such research for managing the effects of climate change on forests.

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1. Introduction

Land colonisation by plants would probably not have been possible without fungi. When moving from the aquatic to the aerial habitat, phototrophs faced considerable difficulties, among them the limited water supply and the scarcity of soluble minerals, especially P. The photosynthesizing organisms overcame these difficulties by forming mutualistic associations with fungi, called *mycorrhizas*. The two partners display complementary adaptations to live on land: the fungal mycelium is well adapted to the three-dimensional exploration of the substrate and some species have a weathering potential which may allow access to non-soluble mineral elements (Lapeyrie et al., 1991; Hoffland et al., 2004). Phototrophs are well adapted to gas exchange and photon collection, which allows the exploitation of atmospheric resources. Moreover they display conducting structures that link aerial- and soil-based parts.

At the present time, among the various types of mycorrhizal symbioses, the primitive non-septate fungi that form arbuscular mycorrhizas (AMs) are largely dominant and are involved with about 80–90% of the phototrophs (Mosse, 1973; Mosse et al., 1981). The AM symbiosis is so widespread that it has been suggested to be ancestral in Plantae (Pirozinski and Malloch, 1975; Selosse and Le Tacon, 1998; Heckman et al., 2001; Wang and Qiu, 2006).

More recently, in some groups of Gymnosperms and Angiosperms, a different symbiosis arose: the association with septate ectomycorrhizal fungi (ECM fungi). In such associations, the fungus forms a sheath around the root and penetrates into the cortex but remains intercellular, forming the Hartig net. Basidiomyceta and Ascomycota have partly replaced the primitive arbuscular mycorrhizal associations (AMs) in numerous trees and some shrub species. The rise of ECM fungi is not easy to date (Alexander, 2006), but it may be speculated that it originated between 220 and 150 Myr (Selosse and Le Tacon, 1998; Bruns and Shefferson, 2004; Alexander, 2006). This replacement of AMs by ECMs favoured the colonisation of lands areas where organic matter accumulates (such as in temperate and boreal zones). Indeed, the saprotrophic

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abilities of the septate fungi give access to organic N as well as P, which are then transferred to the host.

At present, the ECM symbiosis forms a significant component of forest ecosystems in the boreal, temperate and Mediterranean climate zones. In these regions, ECM fungi are found associated with trees belonging to the families Pinaceae, Abietaceae, Fagaceae, Tiliaceae, Betulaceae and Myrtaceae. The Salicaceae and some of the Rosaceae form both ECMs and AMs as does the genus *Alnus* (Betulaceae). However, ECM fungi could also be regionally present in the tropics, where some tree families such as the Dipterocarpaceae are exclusively associated with ECM fungi.

The main groups of fungi that form ECMs in temperate regions have been listed by Trappe (1977). Each ECM tree species may form symbiotic associations with several hundreds of fungal species. While some ECM fungi are associated with all the hosts able to form ECM associations, others are restricted to a single tree genus or even species. Consequently, a mixed forest stand is richer in species of ECM fungi than a pure stand (Le Tacon et al., 1984; Bruns, 1995; Massicotte et al., 1999; Dahlberg, 2001; Richard et al., 2005).

In nature, ECM fungi are essential to the health and growth of forest trees. They can benefit forest trees in a number of ways although the most important is enhancing soil nutrient uptake, particularly for elements with a low mobility in the soil such as P and micronutrients (Smith and Read, 2008) and also for N (Martin, 1985; Chalot and Bran, 1998). This is reciprocated by the allocation of carbohydrates by the tree to the fungus through the root interface, making the relationship a mutualistic association. The ectomycorrhizosphere, which forms a very specific interface between the soil and the trees, hosts a large and diverse community of micro-organisms (fungi and bacteria) that can inhibit or stimulate each other. Some of the ectomycorrhizosphere bacteria consistently promote mycorrhizal development, leading to the concept of 'mycorrhization' helper bacteria (MHBs) (Garbaye, 1994; Frey-Klett and Garbaye, 2005). ECM fungi and bacteria also jointly contribute to weathering and solubilization processes (Calvaruso et al., 2006; Uroz et al., 2009).

The high species richness of ECM communities, the high functional diversity of ECM fungi, and the lack of appropriate investigation methods, have so far limited studies of their functional structure and their precise role in ecosystem processes and biogeochemical cycling. However, new techniques have recently been developed and allow to explore *in situ* the functional diversity of ECM communities. This functional diversity is the key to understanding their contribution to ecological processes of interest for sustainable forest management, soil and landscape conservation. The possible role of associated bacteria in ECM functions has also recently been studied and revealed some interesting interactions.

Here, we aim to review the most recent findings in this field, such as strategies to study ECM communities *in situ* and their roles in (1) C cycling, (2) nutrient mobilization from soil organic matter, (3) nutrient mobilization from soil minerals, (4) common mycorrhizal networks and their role in the functioning of forest plant communities, and (5) the functions of ECM communities following climate change. This new knowledge will be put in perspective within the concepts of functional ecology as well as their implications in sustainable forest management.

Our focus on ecosystem processes in terms of tree nutrition and nutrient cycling does not extend to include the non-nutritional functions of ECMs, such as exploitation of soil water and solutes, water use by trees (Brownlee et al., 1983; Waringer et al., 1994; Unestam and Sun, 1995; Smith and Read, 2008), the production of fungal auxins and their effects on tree development (Slankin, 1973; Gay et al., 1994; Karabaghli-Degron et al., 1998; Barker and Tagu, 2000) or the protection of roots against soil-borne pathogens (Marx, 1969; Sen, 2001).

2. Strategies for *in situ* studies of ectomycorrhizal communities and their functions

Since the early 1990s, studies of ECMs have entered a new period with the use of increasingly powerful molecular tools and other techniques. The most exciting development is the possibility of using genomic tools in forests. Until now, it has been very difficult to study trees and their fungal associates in forest ecosystems and most of the work on ECM functioning has been done in laboratory or nursery conditions. Currently, the possibility exists to work at another scale, in forest settings. Methods for studying mycorrhizas have been extensively published (Varma and Hock, 1999). The main objective of this section is to provide insights on the possibility of using emerging methods to investigate ECM communities. The challenge is to provide the data required for modelling the structure–function relationships within ECM communities and the role of these communities in the functioning of forest ecosystems, according to the across-scale approach proposed by Johnson et al. (2006).

2.1. Describing the biodiversity of ECM fungi in forest ecosystems

Describing the biodiversity of ECM fungi in forest ecosystems is a prerequisite to analysing their functional structure. This can first be assessed by counting fungal fruiting bodies of known ECM fungal species (Straatsma et al., 2001; Smith et al., 2002). Traditional mycological identification methods can be used for taxonomic identification. But a large proportion of fungi forming ECMs do not fructify and many form un conspicuous fruitbodies. The ECM root tips can be morphologically described and classified into morphotypes or anatomotypes (Agerer, 2001). However, most of the time, ECM root tips cannot be identified at the fungal species level solely by morphological or anatomical descriptions. PCR-based techniques have been extensively used for almost 20 years (Gardes et al., 1991; Gardes and Bruns, 1993). The most common approach for the species level is the amplification of the internal transcribed spacer (ITS) region of the ribosomal genes. Identifying ECM fungi following extraction of DNA from a single mycorrhizal tip, PCR-amplifying, sequencing and comparing it with the sequences of databases (NCBI: <http://www.ncbi.nlm.nih.gov/>; UNITE: <http://unite.zbi.ee/>; Kõljalg et al., 2005) allowed the discovery of numerous abundant ECM fungi such as *Tomentella* sp. (Tedersoo et al., 2003, 2006; Courty et al., 2008a) or *Clavulina* sp. (Buée et al., 2005). The recent advances in sequencing technologies, the increase of sequence data and the progress in database searches allow assessing ECM diversity in many forest ecosystems. Similarly, 16S rDNA gene analyses extensively contribute to the understanding of the bacterial diversity in the ectomycorrhizosphere (Uroz et al., 2007).

Microbial taxonomic microarrays, or 'phylochips', represent a powerful tool for high-throughput identification of many organisms. These taxonomic arrays may comprise up to several thousand probes, based on neutral markers, such as microbial ribosomal DNA regions (ITS) or protein-coding genes, which are specific of strains, species or genera (Sessitsch et al., 2006). A similar technology, applied to ECM fungal communities, has been reported by Bruns and Gardes (1993) who developed specific arrays on nylon membranes to describe suilloid fungi. Recently, this same approach has also been used for identification of truffles (El-Karkouri et al., 2007). Nevertheless, despite the richness of sequences available *in silico* for the identification of fungal species (Nilsson et al., 2008), no study has reported the development and validation of ECM fungal taxonomic microarrays to detect a large number of ECM fungal species from soil or roots samples.

From a more general point of view, it is now possible to assess the total microbial diversity of a soil sample by meta-genomics (Rondon et al., 2000; Edwards et al., 2006) by random shotgun sequencing the

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