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Abstract

Ectomycorrhizal (ECM) fungi form association with relatively small number of plants that dominate boreal, temperate, Mediterranean, and some subtropical forest ecosystems. These plant species have been able to acquire metabolic capabilities through symbioses with ECM fungi, thus improving their mineral nutrition and growth in several ecological niches. Mycorrhizal fungi can also play several other important ecological roles, including the protection of plants from abiotic and biotic stresses. Several “targeted” metagenomic projects have been carried out, or are now in progress, in order to identify the fungal communities in soil, including ECM fungi, which are present in various habitats (e.g., forest and truffle-ground soils, etc.). ECM fungi, which are important both because of their economic value as edible fungi (i.e., truffles, boletes) and because of their application in reforestation projects, are the subject of this chapter, in which the recent advances in ECM fungal communities are reviewed, focusing mainly on the applicative aspects related to the use of these fungi.

Introduction

Mycorrhizae are widespread symbiotic interactions between soil fungi and the roots of almost all land plants, including forest trees, grasses, and many crops (Smith and Read 2008). It has been estimated that about 90 % of terrestrial plant species undergo an improvement in mineral nutrient uptake, thanks to root symbiosis with mycorrhizal fungi (Brundrett 2009), which, in turn, provide the fungus with carbon compounds (i.e., sugars). Several mycorrhizal associations exist, and these are identified primarily on the basis of the taxonomic

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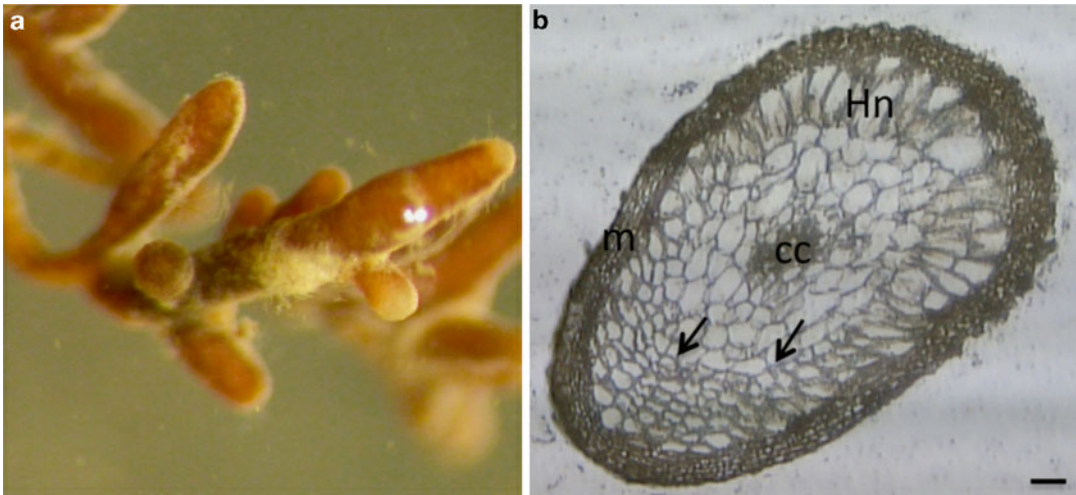


Fig. 16.1 (a) *Corylus avellana/Tuber melanosporum* ectomycorrhizae with the typical clavate aspect and the presence of external mycelium. (b) Paraffin oblique transverse section of a *C. avellana/T. melanosporum* ectomy-

corrhiza showing the mantle (m), which consists of several layers of hyphae, and the Hartig net proliferation (Hn and arrows). cc central cylinder. Bar corresponds to 25 μ m

identity of the hosts and the structural features of the symbiotic interfaces (Smith and Read 2008). According to the ability of the mycorrhizal fungus to penetrate the root cells, mycorrhizae can be divided into two main types: endomycorrhizae and ectomycorrhizae (Balestrini et al. 2012; Perotto et al. 2013).

In ECM symbiosis, which is the subject of this review, the fungus forms a hyphal sheath, called mantle, which is made of aggregated hyphae that surround the root surface, and the Hartig net, which is formed by the hyphae that penetrate between the root cells (Balestrini et al. 2012; Fig. 16.1). The mantle is thought to be responsible for the mineral nutrition and water uptake of the symbiotic tissues, while the Hartig net is considered the site in which metabolites are exchanged. A preliminary confirmation of the functional diversity of these two fungal compartments can be found in the study on *Amanita muscaria* ECMs by Nehls et al. (2001) in which the separation of the mantle from the ECM root, using only tweezers, underlined a differential expression for two hexose-regulated fungal genes. A specificity in the mantle and Hartig net transcriptomic profiles, which reflects a functional specificity, has recently been revealed by Hacquard et al. (2013) through a laser microdissection approach, in which the two fungal compartments

in truffle ECM were dissected, in combination with microarray gene expression analysis.

ECM fungi occur all over the world, and their host range includes most angiosperm and gymnosperm trees, as well as economically important timber-producing tree species. They play an important ecological role in woodland and forest communities in boreal, temperate, Mediterranean, and some subtropical forest ecosystems (Tedersoo et al. 2010a) that are dominated by hundreds of ECM fungal species (i.e., *Basidio-* and *Ascomycetes*), which form symbiotic associations with the lateral roots of trees and shrubs (Bonfante 2010). ECM symbiosis involves a relatively small number of plants, i.e., those belonging to Betulaceae, Dipterocarpaceae, Fagaceae, Nothofagaceae, Myrtaceae (e.g., *Eucalyptus*), Pinaceae, Salicaceae, and some genera of shrubs (e.g., Cistaceae), which are assisted by ECM fungi in the nutrition and protection against root diseases (Smith and Read 2008). As far as the fungal part is concerned, the majority of ECM fungi belong to *Basidiomycetes*, which can form macroscopic epigeous fruiting bodies that often grow next to tree trunks in woodlands, such as *Boletus edulis* and *Cantharellus cibarius*, while some others belong to *Ascomycetes* and form hypogeous fruiting bodies, such as truffles (Girlanda et al. 2007).

ECM fungi in the soil are highly competitive for nutrient acquisition (Bücking et al. 2012 and reference therein), and their colonization allows plant access to N forms that are not so easily available to non-mycorrhizal plants (Hobbie and Hogberg 2012 and reference therein). In line with these observations, Averill et al. (2014) and the relative commentary by Bradford (2014) have suggested that the presence of greater stores of organic matter in forest soils dominated by ECM fungi, than in those dominated by arbuscular mycorrhizal (AM) fungi, could be due to a reduced nitrogen availability for the free-living microbes that use organic matter. Interestingly, when a tripartite interaction is present, as in the *Alnus* host system (N-fixing bacteria, ECM fungi, *Alnus* roots), the ECM fungal activity seems to be shifted toward a greater capacity for organic P acquisition (Walker et al. 2013). A study about the impact of an ECM fungus (*Hebeloma cylindrosporum*) on the potassium (K⁺) nutrition of its host plant (*Pinus pinaster*) has recently been performed, and the involvement of a fungal K⁺ transporter has been investigated (Garcia et al. 2014). The results have shown that the K⁺ nutrition of mycorrhizal pine plants was significantly improved under potassium-limiting conditions (Garcia et al. 2014).

A positive correlation between ECM symbiosis and plant performance in drought conditions has been reported (Morte et al. 2001; Dunabeitia et al. 2004; Alvarez et al. 2009), although plant response to drought can vary depending on the ECM fungal species (Dosskey et al. 1991; Kennedy and Peay 2007). More recently, a pot experiment, using *Pinus sylvestris* seedlings inoculated with several ECM fungi (*Cenococcum geophilum*, *Paxillus involutus*, *Rhizopogon roseolus*, and *Suillus granulatus*), has shown that only *S. granulatus* has a positive effect on shoot growth. Two different watering regimes (moist versus dry) were considered, and it was shown that *S. granulatus* effect on shoot growth was more pronounced under moist conditions (threefold increase) than under dry conditions (twofold increase), thus suggesting that the considered ECM fungus did not provide any additional support during drought stress (Kipfer et al. 2012). Danielsen and Polle (2014) have instead investigated the

nutrient status and the physiological responses to drought of young poplar trees in the presence/absence of the ECM fungus *P. involutus*, and they have been shown that root tips from ECM plants have a higher vitality than those from non-mycorrhizal plants. Since this effect is evident in both the colonized and non-colonized tips of ECM plants, the authors have suggested that it could be due to a general improved water supply to the roots of the host plants.

Numerous *in situ* ¹³CO₂ pulse-labeling experiments have been conducted on annual crops or grasslands to demonstrate a rapid carbon flux pathway from the host to the roots and from the roots to the rhizosphere (Robin et al. 1990; Nguyen et al. 1999; Johnson et al. 2002; Leake et al. 2006). The studies on carbon allocation in trees using pulse labeling have usually been performed in microcosms or mesocosms (Norton et al. 1990; Ek 1997; Simard et al. 1997), and only a few studies have been conducted *in situ* with adult trees but have never considered the fruiting bodies of the associated fungi (Högberg et al. 2008; Plain et al. 2009; Subke et al. 2009; Epron et al. 2011). Recently, Le Tacon et al. (2013) have elegantly assessed the allocation of carbon by the host to *Tuber melanosporum* mycorrhizae and ascocarps via an *in situ* ¹³CO₂ pulse-labeling experiment performed on a 20-year-old hazel tree in a truffle orchard established in the northeast of France. Almost all of the carbon allocated to the truffle ascocarps came from the host; thus, the hypothesis that it was mainly supplied via saprotrophic pathways was excluded. The development of truffles requires that carbon is stored in the trunk or roots of the host, and the process takes several weeks/months unlike what happens in an ectomycorrhizal member of *Basidiomycotina* producing fruiting bodies over a number of days (Teramoto et al. 2012). This result, as expected, demonstrates that the processes involved in carbon acquisition and ascocarp development are different from those of basidiocarps, since *Tuber* ascocarps take at least 6 months to grow between the production of the primordia and full ascocarp development, unlike *Basidiomycota* sporocarps, which develop over a number of days directly from diploid mycorrhizae.

ECM symbiosis can therefore be considered a crucial component in nutrient cycling in sustainable forest ecosystem, and the current genome sequencing projects on ECM fungi are providing useful information to understand the functional and ecological roles for these fungi (Martin et al. 2008, 2010; Martin and Nehls 2009; Plett and Martin 2011; Martin and Bonito 2012; Balestrini et al. 2013; Marmeisse et al. 2013).

ECM fungi, which are therefore important for both their economic value (i.e., truffles, boletes) and their use in reforestation projects, are the subject of this chapter, in which the recent advances in ECM fungal communities are reviewed, focusing mainly on the applicative aspects related to the use of these fungi.

Research on ECM Fungi: From the Past to the Present

The study of ECM fungal diversity initially focused on the screening and molecular identification of fruiting bodies and, only later, on ECM tips, usually after sorting these in morphotypes (Horton and Bruns 2001; Mello et al. 2006a). As each ECM species is specialized in exploiting specific resources of the soil ecosystem, investigations have focused on the spatial distribution of the extraradical mycelium. Tracking the distribution of a given ECM fungus is considered difficult, since fruiting bodies do not reflect the distribution of ground networks (Dahlberg 2001). *H. cylindrosporum* was the first ECM fungus to be detected in soil (Guidot et al. 2002), and its presence was revealed within 50 cm from the fruiting bodies. Thanks to the use of the β -tubulin gene as a marker, Zampieri et al. (2010) were able to show that *T. magnatum* mycelium is more widespread than could be inferred from the distribution of its fruiting bodies and ECM and were able to identify a new haplotype that had never been described before from fruiting body material. The application of the denaturing gradient gel electrophoresis (DGGE) technique made it possible to discover that *T. melanosporum* is the dominant fungus in an area characterized by

scanty vegetation, known as brûlé, which is associated to this fungus, and that *Basidiomycota* ECM fungi decrease within the brûlé, thus indicating a competitive effect of *T. melanosporum* on other ECM fungi (Napoli et al. 2010).

Since each individual within a species has its own functional traits, the next step toward a better understanding of the role of biodiversity in ecosystem functioning will need to consider the intraspecific diversity of mycorrhizal plants and fungi (Johnson et al. 2012).

The possibility of studying (micro)organisms directly in the field (metagenomics or environmental genomics, Chivian et al. 2008) thanks to the introduction of high-throughput sequencing techniques (i.e., 454 pyrosequencing) has given a strong impulse to the development of projects devoted to the study of fungal communities in different environments, including soils. The first studies on fungal diversity, which used a metagenomic approach in combination with high-throughput technology, appeared in 2009 (Buée et al. 2009; Jumpponen and Jones 2009). Buée and colleagues investigated fungal diversity in six different forest soils from a temperate French site using tag-encoded 454 pyrosequencing of the ITS-1 (nuclear ribosomal internal transcribed spacer-1), while Jumpponen and Jones (2009) studied the fungal communities in leaves of *Quercus macrocarpa* of trees located inside and outside a small urban center using the same molecular target. These authors have demonstrated that 454 pyrosequencing can be used successfully to study fungal communities in forest soil and phyllosphere. Starting from these first works, an approach based on 454 GS-FLX pyrosequencing has been widely used to investigate fungal communities in soils and has allowed new information to be provided on ECM fungal communities in several biomes/ecosystems, e.g., Swedish spruce plantations (Wallander et al. 2010); tropical African forests (Tedersoo et al. 2010b); truffle grounds (Mello et al. 2011); transgenic poplar plantations (soils and roots; Danielsen et al. 2012); ECM herb *Bistorta vivipara* roots on the Arctic archipelago of Svalbard (Blaalid et al. 2012, 2014); an urban landscape

(Lothamer et al. 2013); a boreal forest (Clemmensen et al. 2013); boreal and tropical forests (McGuire et al. 2013); truffle grounds, a Mediterranean agro-silvo-pastoral system, serpentine substrates, and a contaminated industrial area (Orgiazzi et al. 2013); an oak-dominated forest in Japan (Toju et al. 2013); and three microsites (decayed wood, mineral soil adjacent to intact logs, control mineral soil) in mature spruce forests in British Columbia (Walker et al. 2014).

Global climate change is supposed to influence soil fungal communities, including ECM fungal communities. It has already been demonstrated that several ecological factors, disturbances (e.g., fire; Kipfer et al. 2011), and management practices (e.g., nitrogen deposition; Peter et al. 2001) affect the composition of ECM fungal communities and can lead to a reduction in the number of ECM fungal species (Koide et al. 2011). Changes in ECM fungal communities have recently been investigated using 454 pyrosequencing. Voříšková et al. (2014) have shown that seasonality and soil depth can influence ECM fungal communities in a temperate oak forest soil. A decrease in ECM fungi abundance has been verified in buried soils in the Siberian tundra (Gittel et al. 2013), where the abiotic conditions (low temperature and anoxia) seem to favor an abundance of bacteria, facultative anaerobic decomposers of soil organic matter (SOM) such as *Actinobacteria*, which increase compared to unburied soils. Hui et al. (2011) have observed, in a boreal coniferous forest site in Southern Finland, that a long-term exposition to Pb contamination can lead to a shift in the composition of the ECM community associated with the dominant pine (*P. sylvestris* L.), as well as an increase in the abundance of the OTUs (operation taxonomic units) assigned to the *Thelephora* genus and a decrease in the frequency of OTUs corresponding to *Pseudotomentella*, *Suillus*, and *Tylospora* in the contaminated zone (Hui et al. 2011).

However, although several factors influence the composition of an ECM community and species richness of ECM fungi, the functional consequences of these shifts on the aboveground

communities (e.g., for tree performance), as well as for the soil ecosystems, still require further investigation (Kipfer et al. 2012). An extensive metabolic reprogramming during the colonization between *Laccaria bicolor* and its compatible host *Populus trichocarpa* has recently been demonstrated. However, this extensive metabolic reprogramming is repressed in incompatible interactions where more defensive compounds are produced or retained (Tschaplinski et al. 2014). Moreover, Pena and Polle (2014) have demonstrated, using ¹⁵N isotope enrichment, that ECM assemblages provide advantages for inorganic N uptake mainly under environmental constraints with respect to unstressed plants, thus suggesting a stress activation of specific ECM taxa.

In addition to their ecological role, some ECM fungi such as *Tricholoma matsutake*, the so-called pine mushroom, have great value as commercial food. This mushroom is popular in Asia because of its aromatic odor and particular taste, as well as its high nutritional and medicinal value (Ohnuma et al. 2000; Kim et al. 2008; Ding et al. 2010). However, its annual production is limited, and several abiotic factors (e.g., rainfall and temperature) can affect it; moreover, attempts to cultivate it artificially have been unsuccessful. Kim and colleagues (2013) have investigated, through a 454 GS-FLX pyrosequencing platform, the fungal communities in soil where fruiting bodies develop. Several zones have been considered (inside, beneath, and outside the fairy ring zone of *T. matsutake*), with the aim of obtaining information on the fungal communities that could influence the development of the fruiting bodies. Mello et al. (2011) have used a similar approach to verify the fungal populations inside and outside the brûlé (burnt area), in which *T. melanosporum* fruiting bodies (the black truffles) are usually collected. The results show that *Ascomycota*, which was the most dominant phylum in the investigated French truffle ground, are more abundant inside than outside the brûlé, while *Basidiomycota* increase outside the brûlé in agreement with previous results reported by Napoli et al. (2010) using the DDGE technique.

The Application of ECM Fungi to Field Projects

ECM fungi provide trees with several benefits, such as the enhanced ability to absorb water, phosphorus, and nitrogen and protection from soilborne root pathogens such as *Fusarium oxysporum*. Evidence of the positive role of ECM *Pisolithus albus* in enhancing the growth of plants, such as *Acacia spirorbis* and *Eucalyptus globulus*, has been observed by significant increases in shoot and root biomass and mineral nutrition (P, K, and Ca), as well as a limited metal uptake, acting as a protective barrier, in nickel-rich ultramafic topsoils in New Caledonia (Jourand et al. 2014). In the restoration of ultramafic ecosystems degraded by mining activities, it could be convenient to isolate indigenous and stress-adapted beneficial ECM fungi in order to inoculate endemic plants (Jourand et al. 2014). ECM fungi have already been proposed for the ecological restoration of mine sites (in particular chromium and nickel mines) in Australia by Reddell et al. (1999) and in New Caledonia by Perrier et al. (2006) as well as in the post-mining of bauxite in Brazil by Khosla and Reddy (2008). ECM fungi are also expected to play a key role in forest regeneration after major disturbance events such as stand-replacing forest fires. Kipfer et al. (2010) investigated the heat tolerance of ECM fungi of Scots pine. They verified that 60 and 70 °C reduced the mean of the species, but not 45 °C. The composition changed because of heat, but most of the ECM fungi, such as *R. roseolus*, *C. geophilum*, and several unidentified species, survived.

Sustainable soil ecosystem services require the management of the beneficial soil organisms that are considered of economic value and which are available in the market for their application. Reforestation using container-grown seedlings of *P. pinaster* produced in nurseries is a common practice in many countries. Fertilizers are often used in nurseries. However, the use of chemical fertilizers can constitute a threat to the environment, in addition to modifying nutrient availability of the fertilized seedlings, which may not be able to adapt to forest soil conditions when transplanted.

Sousa et al. (2012) showed that selected ECM fungi could be used as a beneficial biotechnological tool in the nursery production of *P. pinaster*, without the need of fertilizers. Oliveira et al. (2012) found that inoculation with selected ECM fungi can be an advantageous ecotechnological approach that can be used to improve the nursery production of *P. pinaster*. The inoculation of Chinese pine (*Pinus tabulaeformis* Carr.) seedlings with *Boletus luridus*, under field experimental conditions, has shown to significantly influence bacterial functional diversity in the rhizosphere of *P. tabulaeformis* seedlings, thus highlighting the importance of the application of ECM fungal inoculum in order to promote microbial community diversity of soil in forest restoration projects (Zhang et al. 2010).

The fast growth rate of American chestnut, coupled with its quality timber, makes it a desired species for use in reforestation projects. Bauman et al. (2013) have evaluated various soil preparation methods that promote ECM colonization and American chestnut *Castanea dentata* establishment in coal mine restoration projects. *Quercus ilex* forests play ecological and socioeconomic roles by protecting the environment and providing wood, forage resources, and tourism. Oliveira et al. (2010) considered the management of nursery practices for efficient ECM fungi application in order to establish *Q. ilex* plantations. The ECM inoculants could be rhizosphere soil from forests, spores, or vegetative mycelia, although the soil from forests has the disadvantage of perhaps containing both beneficial (e.g., mycorrhizal fungi) and harmful (pathogenic fungi) microorganisms. The use of spores or vegetative mycelia of ECM fungi seems to be the most convenient and practical technique although the supply of spores is limited by the onset of the rainy season and the maturing of the fruiting bodies. Aggangan et al. (2012) have developed a protocol for the production of quality rooted cuttings for plantation establishment or enrichment planting in the red soil of Caliraya, Philippines, of *Anisoptera thurifera* (Blanco) Blume and *Shorea guiso* (Blanco) Blume, which belong to the *Dipterocarpaceae*, the most important tree family in the tropical forests of southeast Asia, and are considered as endangered species. These authors have shown

that ECM mycelia entrapped in alginate beads are effective in promoting the growth and P uptake of *A. thurifera* and *S. guiso*. Immobilized mycelium offers more advantages than non-immobilized inoculum such as longer survival in the soil, easy storage, and greater viability. However, the cultivation in fermenters or in bioreactors for the large-scale production of mycelial inoculum may compromise the quality of the inoculum and thus limit the application of this technique. Forecasting the response of ECM fungi to environmental changes represents an important step in maintaining forest productivity for the future. Jarvis et al. (2013) have analyzed and identified fungal communities from 15 semi-natural Scots pine (*P. sylvestris* L.) forests through ITS sequencing. Their data have demonstrated an important effect of rainfall and soil moisture on community composition at the species level and less influence of temperature on the abundance of ECM exploration types. Valdés et al. (2006) observed that a severe drought had an important effect on both total fine-root biomass and the ECM-root biomass in a tropical pine forest and suggested that forest management practices should consider the effects of drought in reducing the capacity of *Pinus oaxacana* to form ECM.

Food Applications and Toxicity of ECM Fungi

Fungi are the most productive biological sources of primary and secondary metabolites that have long been exploited by the pharmaceutical and food industries. Some of them, such as *Boletus* species, are also an important source of proteins, carbohydrates, fatty acids (mainly linoleic acid), sugars (mainly mannitol and trehalose), and vitamins (tocopherols and ascorbic acid), as well as phenolic acids (Heleno et al. 2011). Since phenolic acids have antioxidative properties, they are currently being exploited by food and pharmaceutical industries. Important antioxidative properties have been found for polysaccharides extracted from *B. edulis*, and these could be employed as ingredients in healthy food to alleviate oxidative stress (Zhang et al. 2011). A lectin with antitumoral properties has also been found,

thus opening new perspectives in research, with the aim of developing new drugs for cancer therapies (Bovi et al. 2011). A homologous of the sugar-binding antiviral protein cyanovirin-N (CVN), previously identified in the cyanobacterium *Nostoc ellipsosporum*, has been found by analysis of transcript sequences deriving from a gene expression profiling study conducted in the truffle *Tuber borchii*, and a novel protein family has been described in filamentous fungi and in the fern *Ceratopteris richardii* (Percudani et al. 2005). It has been proposed that these findings provide candidate polypeptides to be tested as antiviral agents (Percudani et al. 2005). Two genes coding for putative lectins belonging to the CVNH (CyanoVirin-N Homolog) family have also been found in *T. melanosporum* genome (<http://mycor.nancy.inra.fr/IMG/CTuberGenome/index.html>). However, preliminary results have shown that TbCVNH (the CVNH discovered in *T. borchii*) seems to be completely inactive in the antiviral activity test (Koharudin et al. 2008). Mushrooms produce particular aroma compounds that are of interest for industrial applications, such as 1-octen-3-ol, which is often added as flavoring to processed products in order to reintegrate its loss which occurs during the preparation of these food products (Zawirska-Wojtasiak 2004). Long-chain unsaturated fatty acids, such as palmitoleic acid and linoleic acid, show antibacterial activity and are used as antimicrobial food additives (Zheng et al. 2005). To date, more than 200 volatile organic compounds have been described from various truffle species, and the biosynthetic pathways involved in volatile biosynthesis have been traced in the genome of a mushroom that is highly appreciated for its special taste and aroma, the black truffle *T. melanosporum* (Martin et al. 2010). From the ecological point of view, truffle volatiles are used to attract mammals and insects, which are thus able to locate the precious hypogeous fungi, feed on them, and spread their spores. In addition, truffle volatiles diffuse in the soil and mediate complex interactions with microorganisms and plant roots (Splivallo et al. 2011; Mello et al. 2013). Truffles and porcini are greatly appreciated throughout the world, both as fresh fruiting bodies and as ingredients in processed products (Mello 2012).

A qPCR assay has been developed to authenticate and quantify *T. magnatum* and *T. melanosporum* in food matrices that have undergone intensive transformation processes, such as cream and butter (Rizzello et al. 2012). This method is promising in detecting the incorrect labeling of processed products and can therefore be used to protect the consumer and to assess food quality. The rapid identification of mushroom poisoning, which continues to be a public health concern in Europe, the USA, and several other parts of the world, is particularly important. The majority of reported fatal intoxications have been attributed to a few species of the *Amanita* genus and in particular to the death cap *Amanita phalloides*, which can cause a high mortality rate (10–30 % in adults). *A. phalloides* are often mistaken in appearance for nonpoisonous species, and the ingestion of one single mushroom cap may be sufficient to cause death within 2–8 days (Gausterer et al. 2014). Besides the previous publications that have reported the use of conventional and real-time PCR in the cases of suspected mushroom poisoning as an alternative to morphological investigations and as a complementary approach to toxicological analyses, an article on a rapid and sensitive detection of genetic traces from poisonous mushrooms in a variety of matrices, including raw, fried, and digested mushroom homogenates, spiked feces, and clinical samples (vomit, stool), has just been published by Gausterer et al. (2014). Mushrooms belonging to the *Boletus edulis* sensu lato group, a complex of at least four species of ECM fungi in the genus *Boletus* section *Boletus* (Singer 1986), constitute an interesting example of contrasting fungal features. These fruiting bodies are in fact in high demand as mushrooms because of their pleasant flavor and texture, but at the same time, they have been shown to induce allergic symptoms either through inhalation, ingestion, or contact (Helbling et al. 2002). In order to guarantee safe naturally derived food, Mello et al. (2006b) developed specific primers for the unambiguous detection of *B. edulis* sensu stricto, *B. aereus*, *B. pinophilus*, and *B. aestivalis*. In addition, the relationships of *B. violaceofuscus* with the members of *B. edulis* s.l. have been examined.

The data that will be obtained from the *B. edulis* genome sequencing project, which is currently in progress, will surely allow our knowledge on its allergenic potential and the presence of allergen orthologues to be improved. Thanks to the availability of the genome sequence, an extremely low allergenic potential and the lack of key mycotoxin biosynthetic enzymes have been found in the black truffle *T. melanosporum* (Martin et al. 2010).

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