Chapter 6
Mycorrhization of Fagaceae Forests Within Mediterranean Ecosystems

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Abstract Mediterranean Fagaceae forests are valuable due to their ecological and socioeconomic aspects. Some profitable plant species, such as *Castanea* (timber and chestnut), *Quercus* (timber and cork), and *Fagus* (timber), encounter in this habitat the excellent edaphoclimatic conditions to develop. All Fagaceae plants are commonly associated to ECM fungal species, which are found in these forests in quite stable communities, mainly enriched in Russulaceae and Telephoraceae species. Currently, the Mediterranean Basin is considered as one of the global biodiversity hotspots, since many of their endemic plant species are not found elsewhere and are now under threat. Due to climate changing and introduction of disease agents, Fagaceae forests are facing an adaptation challenge to both biotic and abiotic threats. Although ECM communities are highly disturbed by climate factors and tree disease incidence, they could play an important role in increasing water availability to the plant and also improving plant tree defense against pathogens. Recent advances, namely, on genomics and transcriptomics, are providing tools for increasing the understanding of Fagaceae mycorrhization process and stress responses to biotic and abiotic stresses. Such studies can provide new information for the implementation of the most adequate management policies for protecting threaten Mediterranean forests.

6.1 Introduction

Plant nutrient acquisition is mainly performed by root symbionts in about 86% of land plant species (Brundrett 2009). From the two most common mycorrhizal associations, arbuscular mycorrhizal (AM) fungi colonize a diverse spectrum of plant species, whereas ectomycorrhizal (ECM) fungi become specialized in trees

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and shrubs colonization playing an essential role in forest sustainability. The physiology of colonization is also different. AM hyphae are capable of enter inside the root cells forming arbuscules, whereas ECM hyphal growth takes place in intercellular spaces of root cells forming an Hartig net, and the root tip is covered by a mantle (Bücking et al. 2012). Boreal, temperate forests (Mediterranean, Northern Hemisphere, South America), rain forests (Africa, India, and Indo-Malay), and seasonal woodlands of Australia are the most important habitats for ECM communities (Tedersoo et al. 2010). Both responsible for seedling establishment and tree growth, ECM are crucial for Pinaceae, Fagaceae, Betulaceae, Nothofagaceae, Leptospermoideae, Dipterocarpaceae, and Amhersteae families in woodland and forest communities (Tedersoo et al. 2010).

The Fagaceae family has a worldwide distribution and is well recognized for comprising the largely widespread beeches (*Fagus*), chestnuts (*Castanea*), and oaks (*Quercus*) species. However, this family comprises a total of about 900 plant species, which are included in nine genera of both deciduous and evergreen trees and shrubs (Kremer et al. 2012). Fagaceae family is currently divided into two subfamilies depending on their floral attributes, fruit morphology and germination: Castaneoideae (comprising *Chrysolepis*, *Castanea*, *Castanopsis*, and *Lithocarpus* genera) and the less consensual subfamily Fagoideae (Manos et al. 2001). The placement of *Fagus* together with *Quercus* and *Trigonobalanoid* genera (*Trigonobalanus*, *Formanodendron*, and *Colombobalanus*, which sometimes are collectively included under *Trigonobalanus*) in Fagoideae is still under debate (Nixon and Crepet 1989; Manos et al. 2001; Oh and Manos 2008; Kremer et al. 2012). Recently, a new genus, *Notholithocarpus*, has been isolated from *Lithocarpus*, since it is more closely related to *Quercus*, *Castanea*, and *Castanopsis* (Manos and Oh 2008). Presenting a high economic value (mostly *Castanea*, *Quercus*, and *Fagus* genera), due to their timber, fruits (chestnuts), and cork, the plantation areas of these plant species have been increasing in the past years (FAO 2013).

6.2 Fagaceae Forest Distribution

Fagaceae forests are mainly distributed in the northern temperate hemisphere, presenting also a biodiversity hotspot in Southeast Asia (reviewed by Kremer et al. 2012). While the temperate, subtropical, and semiarid floras are particularly rich in *Quercus*, *Castanea*, and *Fagus*, the warmer forests of Southeast Asia are comparably diverse in the castaneoid *Lithocarpus* and *Castanopsis* genera (Fig. 6.1). Northern Hemisphere temperate forests are all very similar, presenting high abundance of *Castanea*, *Fagus*, and *Quercus* genera. These temperate forests are characterized by well-defined seasons and moderate climate, comprising at least 4–6 frost-free months with regular rates of precipitation (Manos and Oh 2008). For this reason, European and North America ecosystems are the most closely related (Manos and Oh 2008), being both currently affected by a decrease of native beech

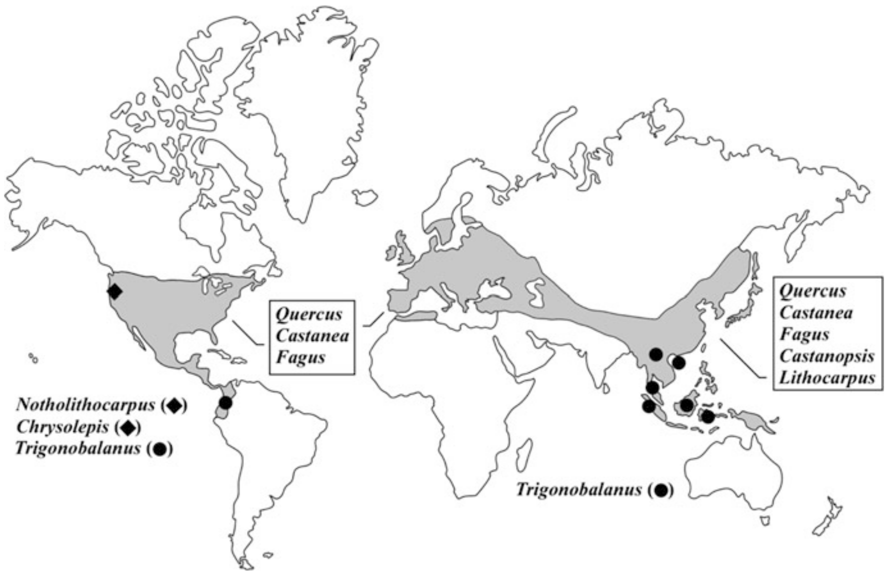

Fig. 6.1 World distribution of Fagaceae genera (adapted from Kremer et al. 2012). *Quercus*, *Castanea*, and *Fagus* genera are the most widespread genera and dominate broadleaf deciduous Mediterranean forests

and oak forests and natural reforestation (Brunet et al. 2010; Dulmer et al. 2014). Anthropogenic influence and disease incidence are two major threats. The Fagaceae forest cut down and forest clearing for activities like agriculture or natural products extraction (e.g., coal mining) has been a major source of income but is degrading forest ecosystems (Bauman et al. 2013). The population awareness for the need of appropriated reforestation programs is thus important to decrease forest erosion and desertification. The knowledge of ECM community of a particular geographic place could contribute for increasing tree adaptation and reforestation survival rate (Ding et al. 2011; Bauman et al. 2013; Dulmer et al. 2014).

Mediterranean climate features have provided unique conditions for the remarkable evolutionary adaptation and divergence of life. Mediterranean Basin only represents 1.5% of earth dry land but comprises about 10% of the total plant species identified (Blondel et al. 2010). From 22,500 plant species found in this region, 11,700 (52%) are endemic to Mediterranean Basin and cannot be found anywhere else in the world (Valavanidis and Vlachogianni 2011). However, the Mediterranean biodiversity has been currently threatened by the habitat loss and degradation, provided by the pollution levels, drought, alien invasive species spread, and overexploitation, among others. For example, from the original Mediterranean forests and shrubs lands, 70% have been destroyed by 1990 (Acácio et al. 2009). This resulted in the recognition of Mediterranean Basin as one of the first 25 Global Biodiversity Hotspots and a hyper-hot candidate for conservation due to the presence of exceptional totals of endemic plants (Myers et al. 2000). For these reasons, the European Union (EU) has classified the Mediterranean Basin as an area of European Community importance and established the “EU Habitats Directive” for the conservation of wild animal and plant species and natural habitats. From the 37 world habitat types identified as priority, 26 occur only in the Mediterranean region (Condé et al. 2005).

Mediterranean natural forests contain about 100 different tree species, whereas only 30 are present in forests of central Europe (four times larger; Valavanidis and Vlachogianni 2011). The Mediterranean forest is mainly composed by broadleaved evergreen tree species, such as oaks and mixed sclerophyllous trees, that alone present more than 20 species in the Mediterranean region (Valavanidis and Vlachogianni 2011). Conifers are also frequently found (Aleppo pine, *Pinus halepensis*; stone pine, *P. pinea*), being the rare conifer species of *Abies*, *Juniperus*, and *Taxus* commonly found in mountains. The most frequent oak species are the cork oak—*Quercus suber*—Fig. 6.2a; the holm oak, *Q. ilex* [considered as two subspecies, *Q. ilex* subsp. *ilex* and *Q. ilex* subsp. *rotundifolia* (Amaral Franco 1990), or as two different species: *Q. ilex* and *Q. rotundifolia* (Lumaret et al. 2002)]; or the Turkey oak, *Q. cerris*. While some oak species, like holm oak and kermes oak (*Q. coccifera*), encircle whole the Mediterranean Sea, others like cork oak and Mediterranean oak (*Q. canariensis*) exhibit a denser distribution in the western region (Condé et al. 2005). Although *Q. robur* is also found in Mediterranean countries, this tree species distribution is more evident in central and northern Europe (Fig. 6.2b), as also reported for *Fagus sylvatica* that has the preferable

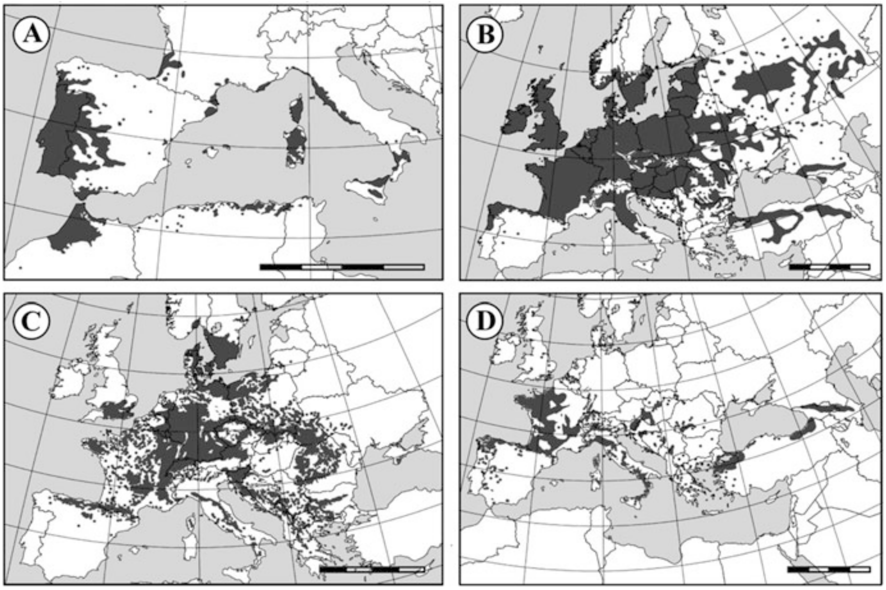

Fig. 6.2 European distribution of the most important Fagaceae species for the economy of Mediterranean Basin countries. *Quercus suber* (**a**), *Fagus sylvatica* (**b**), *Quercus robur* (**c**), and *Castanea sativa* (**d**) (www.euforgen.org)

climate and soil properties in the central Europe (Fig. 6.2c; EUFORGEN 2016). *Castanea sativa* presents the smallest forest area in Europe (predominantly in north of Iberian Peninsula, France, and west of Italy), mainly due to widespread diseases and cultural practices (Fig. 6.2d; Condé et al. 2005). On the other hand, regions with increased water availability are more favorable for downy oak (*Q. pubescens*), Valonia oak (*Q. ithaburensis*), or golden oak (*Q. alnifolia*—Cyprus native) growth (Condé et al. 2005). In all Mediterranean region, the dominant shrubs present in Fagaceae forests are highly aromatic, namely, *Cistus*, *Genista*, *Calluna*, *Arbutus*, thyme, and sage (Condé et al. 2005).

6.3 Mycodiversity in Fagaceae Forest Ecosystems

The interaction between trees and ECM fungi is dependent on many factors, namely, tree species, environmental conditions, and belowground interactions, among others (Öpik et al. 2006). Even season variations have an important role in ECM fungal dynamics in the soil. According to Voříšková et al. (2014), seasonal changes have a significant impact on fungal activity, biomass content and composition, as well as in the relative abundance of different fungal groups in temperate oak forests. A recent work performed in *Castanopsis fargesii*, *Lithocarpus harlandii*, *Pinus armandii*, and *Pinus massoniana* forests revealed that ECM community is much more dependent on the host plant species (33.3%) than soil origin (4.6%) (Ding et al. 2011). This is an important result to take into consideration in reforestation programs, dictating that adequate tree species selection is essential due to ECM host preference.

Fagaceae forests present a quite stable ECM community, mainly consisting of Basidiomycota species, like Russulaceae (Russulales), Thelephoraceae (Thelephorales), *Boletus* (Boletales), Cortinariaceae, Inocybaceae, and Amanitaceae (all Agaricales) species. When analyzing the ECM community diversity of Japanese and Chinese Fagaceae forests, the fungal families Russulaceae and Thelephoraceae were indeed the most abundant, being *Russula*, *Tomentella*, and *Clavulina* the most common ECM fungi (Wang et al. 2011; Toju et al. 2014). Results also showed that these Fagaceae forests, comprising *Castanopsis sieboldii*, *Lithocarpus edulis*, and *Quercus salicina*, present threefold more abundant ECM fungi than non-Fagaceae forests (Lauraceae, e.g., *Machilus japonica* and *Neolitsea sericea*; Toju et al. 2014). A North-American *C. dentata* forest also revealed the same trend as Asian Fagaceae forests, with Russulaceae as the major fungal family identified either by fruit bodies collection (aboveground analysis) or by morphotyping ECM root tips followed by direct sequencing of corresponding rDNA-ITS region (belowground analysis) (Palmer et al. 2008). Although highly abundant, the relative abundance of Boletales, Cortinariaceae, and Thelephoraceae was different in both fungal community views.

The temperate forests from the Mediterranean Basin uncover highly diverse ECM fungal communities, in which several hundreds of fungal species coexist (e.g., Richard et al. 2005; Buée et al. 2009). In a meta-analysis study where fruit bodies surveys were compared in holm oak, cork oak, and mixed forests from Andaluzia (Spain) region, a common dominance of Agaricomycetes species (e.g., Boletales and Russulales) was found (Ortega and Lorite 2007). In this study, a higher diversity and number of exclusive species were reported for cork oak forests. The diversity and structure of other Mediterranean *Quercus*, *Fagus*, and *Castanea* ECM communities have also revealed a high dominance of Russulaceae, Cortinariaceae, Thelephoraceae, and Inocybaceae fruit bodies (Table 6.1).

DNA technologies have improved fungal ecology studies during the recent past years. Fruit bodies as well as root tip descriptions have been greatly enriched by soil-based metabarcoding DNA sequencing (Shokralla et al. 2012). Even though this recent approach revealed a high potential for microbial diversity identification in every ecological guilds, there are still some issues remaining when applying next-generation sequencing (NGS) methods for assessing fungal diversity (Orgiazzi et al. 2015). When studying Fagaceae ECM communities recurring to molecular methods, such as ITS barcoding of ECM tips (e.g., Richard et al. 2005) or ITS metabarcoding of soil sample approaches (Buée et al. 2009), which are methods not dependent on the ability of fungi to produce conspicuous fruit bodies, a different picture of ECM community is obtained. While ECM surveys based exclusively on fruit bodies identification (aboveground approaches) have been hyper-dominant in Basidiomycetes species (mainly Agaricomycetes), a high diversity of Ascomycetes has been detected using belowground approaches based on molecular methods (Peintner et al. 2007; Orgiazzi et al. 2012; Baptista et al. 2015). In spite of that, a higher abundance of Basidiomycota operational taxonomic units (OTUs) has been consistently found. However, from 140 identified taxa among 558 ECM *Q. ilex* root tips, the Ascomycota *Cenococcum geophilum* dominated (35% of ECMs), together with Russulaceae (21.4%), Cortinariaceae (7.1%), and Thelephoraceae (25%) (Richard et al. 2005). The same trend was detected by Azul et al. (2010) when studying the influence of managed oak woodlands dominated by *Q. suber*, under different land use practices, by using the same ECM root tip surveys complemented with ITS rDNA analysis. In this study, the Ascomycota *C. geophilum*, together with Russulaceae and Thelephoraceae, represented 56% of whole ECM fungal community. A positive correlation between ECM fungal richness and silvo-pastoral exploitation regime and low mortality of cork was detected in this study (Azul et al. 2010). In addition, the use of NGS DNA sequencing methods on *Fagus sylvatica* forest soils revealed that the most abundant fungal genera were *Russula*, *Boletus*, but also *C. geophilum* (Coince et al. 2013). Moreover, *C. geophilum* was the main ECM fungus reported in root tip assessment in *Q. rubra* forests, although its abundance has oscillated significantly with tree age (Gebhardt et al. 2007).

Although the ECM association is the dominant symbiotic relationship, Mediterranean Fagaceae species can also be simultaneously colonized by different mycorrhizal fungal types, such as AM and ericoid fungi, among others (Bergero et al. 2000). Accordingly, in oak forests, a higher number of AM fungal spores (mainly *Ambispora gerdemannii*) have been found when compared to other landscapes, such as pine forests, combined forests of pines and oaks, or in several

Table 6.1 ECM communities present in Fagaceae forests in Mediterranean Basin ecosystems. Revision of published studies since 2000

Fagaceae species	Ecosystem	ECM taxa	Approach	Reference
Q. ilex	Corsica Island, France	*Russula*, *Amanita*, *Tricholoma*, *Cortinarius*	Root tips	Richard et al. (2004)
Q. ilex	Mediterranean forests	*Cenococcum geophilum*	Root tips	De Román and De Miguel (2005)
Q. ilex	Mediterranean forests	*Cenococcum geophilum*, Russulaceae, Cortinariaceae, Thelephoraceae	Root tips	Richard et al. (2005)
Q. ilex	Mediterranean forests	Thelephoraceae, Russulaceae, Cortinariaceae	Root tips	Richard et al. (2011)
Q. ilex	Southern France	Thelephoraceae, Pyrenomataceae	Root tips	Taschen et al. (2015)
Q. suber	Moroccan woodlands	*Pisolithus*, *Boletus aureus*	Fruit bodies survey	Yakhlef et al. (2009)
Q. suber	Portuguese montados (savanna-type forests)	*Cenococcum geophilum,* Russulaceae, Thelephoraceae	Root tips	Azul et al. (2010)
Q. suber	Declining forest in northwestern Sardinia, France	Pyronemataceae, Thelephoraceae, Russulaceae, Inocybaceae, Cortinariaceae	Root tips	Lancellotti and Franceschini (2013)
Q. suber	Portuguese forests and landscapes	*Russula*, *Tomentella*, *Cenoccoccum*	Root tips	Reis et al., unpublished results
Q. suber and *Q. canariensis*	South of Spain	*Lactarius chrysorrheus*, *Cenococcum geophilum*	NGS	Aponte et al. (2010)
Q. petraea	Czech Republic	*Russula*, *Lactarius*	NGS	Voříšková et al. (2014)
Q. petraea and *Q. robur*	100-year-old forest in northeastern France	*Tomentella*, *Lactarius*, *Cenococcum*	Root tips	Courty et al. (2008)
C. sativa	Greece	*Amanita caesarea*, *A. rubescens*, *Boletus edulis*, *B. aereus*, *Cantharellus cibarius*, *Craterellus cornucopioides*, *Hydnum repandum*, *H. rufescens*	Fruit bodies surveys	Diamandis and Perlerou (2001)
C. sativa	Italy	*Russula*, *Inocybe*, *Lactarius*, *Tricholoma*, *Cortinarius* and *Amanita*	Fruit bodies surveys	Laganà et al. (2002)
C. sativa	Italy	*Cenococcum geophilum*, *Boletus aestivalis*, *Lactarius chrysorrheus*	Root tips and fruit bodies survey	Peintner et al. (2007)

(continued)

Table 6.1 (continued)

Fagaceae species	Ecosystem	ECM taxa	Approach	Reference
C. sativa	Healthy and *Phytophthora*-infected forests in central Italy	*Cenococcum geophilum*, *Oidiodendron maius*	Root tips	Blom et al. (2009)
C. sativa	Portuguese orchards	*Russula*, *Inocybe*, *Lactarius*, *Tricholoma*, *Boletus*, *Cortinarius*, *Amanita*	Fruit bodies survey	Baptista et al. (2010)
C. sativa	Portuguese orchards	*Inocybe*, *Amanita* (above) and *Inocybe*, *Amanita*, *Sistotrema* (below)	Fruit bodies survey and NGS	Baptista et al. (2015)

agroecosystems (Chaturvedi et al. 2012). In addition, the symbiotic relationship between plant and ECM fungi can be mediated by other microorganisms or plants (Herrmann 2007; Toju et al. 2014). For example, recent studies on red oak (*Q. rubra*) have showed that soil bacteria can help plants to establish ECM symbiosis by maintaining adequate plant signaling gene levels that will promote mycorrhization (Kurth et al. 2015). Accordingly, as obligatory ECM hosts, *Quercus* are usually sensitive to shifts on microbial communities (Smith et al. 2007).

To conclude, the enriched decaying litter soil from Fagaceae forests is an excellent habitat for fungal development and has been a natural source of many economically important mushrooms (Boa 2004). Those edible ECM fungi naturally associated with Fagaceae trees, mainly in *Castanea* or *Quercus* forests, comprise a main forest subproduct for population food supply, as well as for the production of natural medicines (Boa 2004; Savoie and Largeteau 2011). However, ECM mushroom harvesting has been dramatically decreasing in the past century (Yun and Hall 2004), mainly due to air pollution and litter accumulation in soil surface (Smit et al. 2003). For all these reasons, the preservation of forests including Fagaceae forests has become not only ecologically important but also necessary for maintaining an ECM edible mushroom repository.

6.4 Disturbance and Protection of Fagaceae Forests from Biotic Threats

Beyond ecological and physiological importance to the forests, ECM community is essential for plant tree disease prevention and incidence (Smith and Read 2008). The most devastating diseases of Fagaceae family are caused by *Phytophthora* spp. (ink disease and oaks decline) and *Cryphonectria parasitica* (blight disease). The sudden oak disease caused by *Phytophthora ramorum* has been responsible for the rapid mortality of native oak trees (*Quercus* spp. and *Lithocarpus densiflorus*) in central and northern California (USA) since its first observation in 1995 (DiLeo et al. 2009). More recently, surveys revealed that *P. ramorum* was introduced into Pacific northwest nurseries and into at least eight European countries by movement of stock plants (Brasier et al. 2004). Also, the introduction of the causal agent of chestnut blight disease (*C. parasitica*) by the importation of infected Asian chestnut trees to the USA east coast in the early twentieth century almost led to the extinction of American chestnuts (*C. dentata*; Milgroom et al. 1996). Indeed, this later epidemic has been considered as one of the greatest ecological disasters in US history (Wheeler and Sederoff 2009) and one of the most devastating plant disease epidemics caused by fungi or fungal-like oomycetes (Fisher et al. 2012). Although pedunculate oaks (*Quercus petraea* and *Q. robur*), holm oak (*Q. ilex*), and *Castanopsis* have been also classified as *C. parasitica* host species by the European Plant Protection Organization (EPPO), corresponding plant damages are relatively less when compared with chestnut species. Although susceptible to this fungus, the relatively higher tolerance of European chestnut (*C. sativa*) in comparison to the American chestnut prevented the heavy mortality levels previously observed in the USA (Heiniger and Rigling 1994). However, when *C. parasitica* was first observed in Europe (Genova, Italy, in 1938; reviewed by Anagnostakis 1987), the blight disease rapidly spread all over France, Spain, and Portugal chestnut orchards (Robin and Heiniger 2001).

Within the Mediterranean region, oomycetes from *Phytophtora* spp. are serious threats to Fagaceae forests. Between 1900 and 1950, the main *C. sativa* growing areas of southern Europe, especially Italy, France, and Iberia, suffered heavy mortality due to the chestnut ink disease caused by *Phytophthora cambivora* and *P. cinnamomi* (reviewed by Brasier 2000). After introduction in the late eighteenth century from a center of origin in the Papua New Guinea-Celebes, this disease rapidly spread in France and in all chestnut-growing areas (Vettraino et al. 2002), being the main reason for abandonment of several chestnut orchards. In addition, *P. cinnamomi* has been reported as the agent responsible of ink disease of red oak (*Quercus rubra*; Robin et al. 2012) and as the primary factor of root infection resulting in oak decline and mortality in Mediterranean countries (Brasier et al. 1993). Although cork and holm oak decline have occurred in the Mediterranean Basin since the beginning of the twentieth century, only in the early 1980s, a severe oak decline was reported across the Mediterranean region (Brasier 1996). Oak decline has been described as a complex disease triggered by several interacting environmental constraints, including pathogens (*P. cinnamomi*), as well as drought and other site factors (soil texture and fertility, slope) (Camilo-Alves et al. 2013). The affected oak trees face a progressive defoliation that can go over 75% (Franceschini et al. 2002). Typical symptoms of *Phytophthora* diseases have also been observed in *Fagus* stands of several European countries in the last two decades, which are caused by *P. citricola*, *P. cambivora*, and *P. cactorum* (Schmitz et al. 2006), and in Swedish *Q. robur* stands caused by *P. quercina* (Jönsson-Belyazio and Rosengren 2006).

All *Phytophthora* diseases result in severe leaf loss, which would lead to the reduction of root sugar content and would alter the ECM community of diseased plants. Accordingly, tree crown defoliation has been shown to modify ECM community structure in Scots pine (Kuikka et al. 2003) and increase the frequency of thin mantled ECM morphotypes (Saravesi et al. 2008). Even artificial defoliation has been reported to negatively affect ECM symbionts by reducing the production of fungal biomass in interacting roots (Markkola et al. 2004; Stark and Kytöviita 2005). Comparing healthy and ink-diseased chestnut stands, Blom et al. (2009) found differences in the richness of ECM communities and relative abundance of most important ECM fungi. *C. geophilum* was dominant on both stands, but its relative abundance was 1.5-fold higher in the infected orchard. Also, other Basidiomycota, such as Boletaceae, Paxillaceae, Sistotremataceae, Hydnaceae, and Atheliaceae, showed significantly higher values in infected soils, whereas Thelephoraceae, Cortinariaceae, and Sebacinaceae showed an opposite trend (Blom et al. 2009). As a result of oak decline disease, a reduction of ECM diversity and ECM root colonization has been detected in *Q. ilex* trees (Causin 1996; Montecchio et al. 2004). In contrast, *Q. suber* declined trees do not present differences in ECM community when compared to healthy trees (Lancellotti and Franceschini 2013). But, although no differences in ECM community have been detected in Spanish *Q. ilex* forest trees infected or not with *P. cinnamomi*, non-mycorrhizal root tips seem to be more susceptible to infection than mycorrhizal ones (Corcobado et al. 2014). Although these results indicate that ECM communities are strongly affected in diseased Fagaceae plants, ECM fungal species could also contribute for disease protection. This feature could be provided by the formation of a mantle that serves as a physical barrier to the pathogen, by the production of antibiotics that inhibit pathogen growth and reproduction, by diverging plant exudates that could act as biochemical signals to the disease agent, by providing habitat for antagonistic rhizosphere microorganisms, or by improving plant vigor and protection potential (reviewed by Keen and Vancov 2010). Accordingly, a number of ECM fungi have been already related to *P. cinnamomi* suppression in conifers and eucalyptus forests (Marx 1972; Malajczuk 1979; Malajczuk and McComb 1979), and several ECM fungal isolates (mainly *Suillus brevipes*) have revealed high antagonistic potential against *Phytophtora* sp. (Mohan et al. 2015). The direct protection of ECM fungi against both *P. cambivora* and *P. cinnamomi* infection was achieved after inoculation of *C. sativa* seedlings with *Laccaria laccata*, *Hebeloma crustuliniforme*, *H. sinapizans*, and *Paxillus involutus* (Branzanti et al. 1999). Biocontrol and bioprotection strategies by using ECM could then be the future key for Fagaceae disease prevention and treatment. This kind of information would be important for advising tree nurseries involved in reforestation programs, even though artificial inoculation of *Q. garryana* and *F. sylvatica* seedlings has not been considered necessary in nursery practices (Southworth et al. 2009; Pietras et al. 2013). In any case, the inoculation of *Q. ilex* seedlings with *Hebeloma mesophaeum* revealed to increase the mycorrhizal colonization and plant growth while reducing the need for fertilizers (Oliveira et al. 2010). Also, *Q. ilex* and *Q. faginea* artificial mycorrhization with *Tuber melanosporum* improved seedling growth, water, and phosphorous acquisition (Núñez et al. 2006). Although the growth of cork oak nursery seedlings has not increased by artificial inoculation with

Pisolithus tinctorius, several physiological parameters, such as higher photosynthetic capacity, water use efficiency, and N uptake capacity, benefit from mycorrhization (Sebastiana et al. 2013).

In the recent past years, asymptomatic endophytic fungi have been also regarded as potential biocontrol agents for tree diseases (e.g., Arnold et al. 2003; Blumenstein et al. 2015). The oak decline has been correlated with the diversity and amount of fungal endophytes present on different tissues of *Quercus* spp., and many oak-specific endophytes are specifically described to accelerate the decline of oaks stand (Ragazzi et al. 2001, 2003, 2004). *Q. cerris* exhibited a more diverse endophytic assemblage, but greater infection levels, than *Q. pubescens* suggesting a role of some pathogenic fungal endophytes in Mediterranean oak forests (Moricca et al. 2012).

Other biocontrol agents against Fagaceae diseases are now arising. Strains of the chestnut blight fungus, *C. parasitica*, harboring asymptomatic mycoviruses (CHV1-4; reviewed by Xie and Jiang 2014) are described to induce hypovirulence (virulence attenuation) (Dawe and Nuss 2001). The use of the complex triple interaction (hypovirus, fungal pathogen, and chestnut tree) for controlling chestnut blight in orchards remains a possibility (Xie and Jiang 2014). Antagonistic microbes or metabolites produced by them have been also studied as potential biocontrol agents against *Phytophthora* spp. causing chestnut ink disease (reviewed by Choupina et al. 2014). Most promising results were obtained with *Trichoderma* sp., *Gliocladium* sp., and *Pseudomonas* sp. (Aryantha et al. 2000).

6.5 Fagaceae Mycorrhization in a Mediterranean Changing Climate

The sustainability of forests is extremely dependent on both biotic and abiotic factors, and worldwide climate changes are affecting forests all over the world (Keenan 2015). The effects of drought can be minimized by increasing water uptake through fine root growth, by deep taproot formation, and by osmotic adjustment in water-stressed roots through the accumulation of osmolytes (reviewed in Brunner et al. 2015). Due to their long-term evolutionary adaptation to long periods without rain and high temperatures, typical Mediterranean tree species, particularly evergreen oaks, are particularly adapted to cope with moderate drought without significant losses of production and survival (Ramirez-Valiente et al. 2009, 2011). For example, although not so drought tolerant as *Q. ilex* (described as one of the most drought-resistant oaks), cork oak presents rather drought-tolerant traits such as deep roots (Kurz-Besson et al. 2006). However, Mediterranean forests are now facing problems due to the rapid environmental changes (Lindner et al. 2014). Forests become more likely to be exposed to extreme events, such as the increased risk of fire, extreme drought events, or severe heat waves, which could even lead to the spread of pests and diseases (reviewed by

Bussotti et al. 2013; Moricca and Ragazzi 2008; Moricca et al. 2014). Recurrent episodes of extreme water stress can greatly increase the number of declined trees (also with the contribution of pathogens) and represent a major threat to the survival of Mediterranean plant species (Nardini et al. 2014). Tree plasticity and adaptation to drought is now slower than the increase of stress severity. In *Q. faginea*, a typical Mediterranean tree, the rate of plant adaptive response in xeric environment is significantly lower than drought increase occurring in Spain (Nuche et al. 2014).

As individual plant responses to environmental changes are largely dependent on fungal symbionts (reviewed by Kivlin et al. 2013), the microbial community present in the forest soil is suggested to play an essential role in plant drought stress resistance. The changing environmental conditions are likely to induce changes in plant physiology and root exudation, altering the composition of root exudates in chemoattractants or signal compounds (Kandeler et al. 2006) and thus changing the structure of ECM communities associated with stressed plants (reviewed by Compant et al. 2010). Accordingly, the increased drought imposed by reduction of rainfall induced significant shifts in *Q. ilex* ECM community composition (Richard et al. 2011). The most common taxa identified in these forests are Thelephoraceae, Russulaceae, and Cortinariaceae, but five consecutive years of increased drought have induced a positive response of Cortinariaceae species. In addition, when *F. sylvatica* plants were subjected to drought, no effect was detected in *Lactarius subdulcis* and *Byssocorticium atrovirens* mycorrhizae abundance, but *Xerocomus chrysenteron* mycorrhizae occurrence increased almost twofold (Shi et al. 2002). Furthermore, beech plants mycorrhized with *X. chrysenteron* and *L. subdulcis* were able to better cope with drought stress than others. These observations suggested that distinct ECM taxa differently respond to drought by specifically changing their occurrence/abundance in mycorrhized plants and each plant could be differently affected by drought according to the associated mycorrhizal community. Furthermore, the structure of *F. sylvatica* ECM communities and metabolic activity of each morphotype was reported to be dependent on the season, temperature, and soil moisture, being certain morphotypes more abundant and active in winter than in summer (Buée et al. 2005). The same authors described *C. geophilum* morphotype as being more active during summer, when the increase in temperature and drought could influence its abundance and enzyme activity as reported in oak ecosystems (*Q. robur*, *Q. petraea*, and *Q. pubescens*) (Herzog et al. 2012). Therefore, the overall function of ECM community would result from the occurrence and functional feature of each morphotype. In a complex ecosystem as Fagaceae forests, more than one variable could be influencing ECM communities. European *Q. robur* and *Q. petrea* forests ECM community are influenced by precipitation, pH, and N deposition (Suz et al. 2014).

Diverse drought tolerance levels exhibited by mycorrhized plants are most probably due to the well-recognized differences in drought resistance of specific ECM fungi. *Rhizopogon vinicolor* and *C. geophilum* have been reported as drought-tolerant species, being *C. geophilum* also particularly efficient in protecting forest trees against drought damage, while *L. laccata* is described as a drought-sensitive fungus unable to grow at very low water potentials (Coleman et al. 1989; di Pietro et al. 2007). Since the respiration activity of *C. geophilum* ectomycorrhizae has been reported to be significantly less altered than that of *Lactarius* sp., *C. geophilum* was suggested to better maintain the physiological integrity of beech roots facing drought stress (Jany et al. 2002). In contrast, under high temperatures, a decreased colonization with *C. geophilum* has been detected in *Quercus myrsinaefolia* (Kasai et al. 2000), agreeing with the observation of its reduced respiration under increasing temperature (Malcolm et al. 2008). In any case, *C. geophilum* being a hydrophilic and short-distance exploration fungus has been suggested as a potential indicator of environmental changes (reviewed by Lehto and Zwiazek 2011). However, several problems have been discussed about its use in environmental assessments, including its resistance to other stress factors besides drought and its inability of forming fruit bodies.

The ability for water uptaking in a typical Mediterranean climate is essential for tree resistance to drought scenarios, and ECMs have been recognized as crucial for drought resistance improvement (Kivlin et al. 2013; Brunner et al. 2015). The water status of drought-stressed trees is highly improved by the increased absorbing surface provided by the ECM fungi, through a higher efficient water conduction by mycelial strands, enhanced soil-root hydraulic conductivity, and other hormonal and nutritional effects that modify plant physiology (reviewed by Breda et al. 2006). Moreover, ECM networks can redistribute water from deep soils to roots or move water among roots of drought-stressed plants (Egerton-Warburton et al. 2007; Querejeta et al. 2007). Accordingly, studies performed in *Q. alba* inoculated with *P. tinctorius* revealed higher water potentials and larger root systems than non-inoculated plants (Dixon et al. 1980). Also, *Q. ilex* seedlings inoculated with *T. melanosporum* exhibited half of root hydraulic conductance than non-mycorrhized roots but presented 2.5-fold more fine root surface area (Nardini et al. 2000). The best ECM inoculum for improving drought tolerance is difficult to establish, but their choice should be based on fungal water uptake ability and exploration type. Hydrophilic fungi, such as *Russula*, *Hebeloma*, *Lactarius*, and *Laccaria*, are able to transport water in the apoplast, whereas hydrophobic fungi, like *P. involutus* and *Suillus* spp., need to form mycelia cords to transport water in the symplast (reviewed in Lehto and Zwiazek 2011). On the other hand, contact mycelia or short-distance exploration mycorrhizae are mainly hydrophilic, whereas long-distance exploration are hydrophobic fungal ECMs (Agerer 2001). This particular information would be essential in further research on ECM behavior in drought scenarios or on ECM fungal selection for in vitro and field assays.

Forest fires are common in Mediterranean region during summer period, but fire risk is clearly increasing due to extreme environmental conditions. Indeed, during the last decade, Mediterranean forest fires (especially in Portugal and Greece) have been associated with extreme weather, in particular to extremely long dry periods with hot temperatures and high wind speeds (reviewed by Lindner et al. 2014). Fire events could have significant effects on fungal communities of Mediterranean forests. After a fire event, the complexity of ECM communities tends to be reduced and replaced by a less diverse community, usually composed by resilient fungal species and previously rare species (Pezizales and *Rhizopogon* spp.; reviewed by

Buscardo et al. 2010). Colonization by new fungal species can benefit from a competition decrease, being spores the main structures for postfire natural recolonization. While *Telephora* spp. distribution was strongly affected by fire events in an oak forest, *Tomentella* spp. rapidly raised (Buscardo et al. 2010). When studying the ECM root tips of a *Q. ilex* forest over a 3-year postfire period, the richness of ECM community and the percentage of root tips were also significantly decreased (De Román and De Miguel 2005). *C. geophilum* was the most resilient ECM fungi and maintained its abundance all over the period.

6.6 Advances for Mediterranean Fagaceae ECM Studies

To better understand the symbiotic relationship that occurs between Fagaceae roots and ECM fungi, new molecular tools have been created. Several efforts have been made in order to know the genetic patrimony of several Fagaceae species. To the best of our knowledge, 18 Fagaceae genomes have already been sequenced, eight *Castanea* species and ten *Fagus* species, six of which considered as subspecies (http://www.fagaceae.org/). Other species, such as *Q. alba*, *Q. rubra*, and *Q. suber*, have their genome sequencing ongoing (The Fagaceae Genome Web, http://www.fagaceae.org/home; Genosuber Project—http://www.genosuber.com/). Furthermore, several transcriptomic studies are now allowing the generation of a comprehensive catalog of transcripts from Fagaceae. Recently, a number of transcriptomic studies have been successful at generating expressed sequence tags (ESTs) libraries, mainly from oaks and chestnuts, recurring to NGS approaches (e.g., *Q. robur* and *Q. petraea*, Lesur et al. 2015; *C. sativa* and *C. crenata*, Serrazina et al. 2015). The use of a *Q. robur* gene catalog allowed the discovery of specific molecular mechanisms involved in the regulation of oak ECM symbiosis and the identification of key molecular players involved in ECM formation (Tarkka et al. 2013). Their main findings concern the plant defense gene attenuation and ethylene signaling enhancement during mycorrhization, cell wall remodeling mechanisms, and alteration in several metabolic pathways (e.g., nitrogen, phosphorus, and sugar transporters). Within a national initiative, a Portuguese consortium was created to study cork oak ESTs and thus develop a new genomic resource for studying *Q. suber* (Pereira-Leal et al. 2014). This achievement has been used to better understand processes related with plant development (Rocheta et al. 2014; Teixeira et al. 2014) and adaptation responses to both biotic (Sebastiana et al. 2014) and abiotic factors (Magalhães et al. 2016). The global overview of up- and downregulated genes in cork oak roots following inoculation with the *P. tinctorius* resulted in a better insight of those molecular events that control ECM symbiosis (Sebastiana et al. 2014). ECM colonization resulted in extensive cell wall remodeling, activation of the secretory pathway, alterations in flavonoid biosynthesis, and expression of genes involved in the recognition of fungal effectors. Other identified genes could have putative roles in symbiotic processes such as nutrient exchange with the fungal partner, lateral root formation, or root hair decay (Sebastiana et al. 2014). The transcriptional response of *C. sativa* during the early contact with *P. tinctorius* revealed that gene expression alterations occur a few hours after contact, long before the development of a functional mycorrhiza (Sebastiana et al. 2009). Host plant rapidly reacts by eliciting a defense program similar to that described for pathogenic interactions and represses genes normally implicated in water stress. All these identified processes are consistent with the idea that ECM fungi alter plant-specific cellular processes, such as development, metabolism, or responses to abiotic and biotic stresses.

In addition to these plant-based tools, recent research has been made by the Mycorrhizal Genomics Initiative to sequence nuclear and mitochondrial genomes of 50 fungal species able to establish mycorrhizal symbiosis. Among them, 33 are already concluded, including 26 ECM, four ericoid, two orchidoid, and one AM fungal species (reviewed by van der Heijden et al. 2015). Genome sequencing of some ectomycorrhizal fungal species, such as *Laccaria bicolor*, *T. melanosporum*, and *P. tinctorius*, opens a window to better understand these processes (Martin et al. 2008, 2010).

Advances in Fagaceae genomics are providing new tools and methodologies for understanding the molecular processes of tree species adaptation to the main challenges (reviewed by Plomion et al. 2015). The climate changes and associated threats, as well as the introduction and spread of new disease agents, could rapidly deteriorate Mediterranean Fagaceae forests. The understanding of those mechanisms underlying tree adaptation to long-term defense strategies, for both biotic and abiotic stresses, and processes leading to the association with beneficial organisms like ECM fungi, could have a major role in devising new strategies for forest sustainability. Innovative management practices and policy actions could be planned to preserve forest adaptation to a changing climate and new threats. Yet, the fundamental knowledge provided by all available genetic resources will not be sufficient for getting immediate effects on forest management. Reforestation programs will be essential to forest sustainability maintenance, where natural ECM communities would play an important role.

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