Chapter 14
Mycorrhizas in the South American Mediterranean-Type Ecosystem: Chilean Matorral

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14.1 Introduction

The five Mediterranean-type ecosystems (MTEs, singular: MTE) in the world are climatically characterized with warm-dry summers and cool-wet winters (Rundel and Cowling 2013). These ecosystems are located in California, central Chile, the Mediterranean Basin, the Cape Region of South Africa, and southwestern and south Australia (Dallman 1998; Rundel and Cowling 2013). A remarkable feature of the MTEs is the fact that they occupy, in total, less than 3% of the Earth's surface and contain almost 50,000 species of vascular plants, which correspond to 20% of the world's known species (Cowling et al. 1996; Rundel and Cowling 2013). Also, many of the plant species are endemic (Cowling et al. 1996) and, at the same time,

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they are threatened by several human-related factors (Underwood et al. 2009). All these characteristics have placed the MTEs as biodiversity hotspots (Myers et al. 2000), which means that they are priorities for conservation. Due to this situation, much research has been done in MTEs, mostly in plants (Dallman 1998), but also some attention has been paid to animals (Rundel and Cowling 2013). However, the soil microbiological biodiversity has been overlooked, despite the fact that they are increasingly being recognized as key players in the restoration of degraded ecosystems (Harris 2009).

One of the most important microorganisms in the soil are the mycorrhizal fungi (MF) which form symbiotic relations with the roots of approximately 90% of known plant species (Brundrett and Tedersoo 2018). These mycorrhizal symbiotic relations occurs in almost all ecosystems (Read 1991; Read and Perez-Moreno 2003; Read et al. 2004) and as four main types: arbuscular mycorrhiza (AM), ectomycorrhiza (EcM), orchid mycorrhiza (OrM) and ericoid mycorrhiza (ErM) (Brundrett and Tedersoo 2018). The MF uptake nutrients from soil and supplies to the plant partner in return for carbohydrates (Smith and Read 2008) and lipids (Jiang et al. 2017; Keymer et al. 2017; Luginbuehl et al. 2017). Consequently, the mycorrhizal symbiosis, significantly influences plant fitness, as well as several ecosystem processes such as carbon, nitrogen and phosphorous cycles, regulation of plant diversity, soil aggregation and seedling survival (van der Heijden et al. 2015). Thus, because of the importance of MF to plants, they cannot be ignored in the efforts to preserve ecosystems as MTEs. However, regarding MF in the MTEs, scarce research has been performed. In fact, in an ISI Web of Knowledge search (status May 2018), it is possible to find only 512 publications in a 10 year span regarding this topic. Moreover, in the last XIV MEDECOS and XIII AEET Consortium Meeting held in Spain in February 2017 that gathered 538 participants (Arista et al. 2017), there were only fifteen investigations dealing with mycorrhiza in MTEs – most of them from the Mediterranean Basin (Álvarez-Garrido et al. 2017; Benito Matías et al. 2017; Parker et al. 2017; Pérez-Izquierdo et al. 2017; Rincón Herranz et al. 2017; Romero Munar et al. 2017; Verdú 2017; Calviño-Cancela et al. 2017; Dias et al. 2017; Gil-Martínez et al. 2017; Hernández-Rodríguez et al. 2017; López García et al. 2017; Marañón et al. 2017; Mediavilla et al. 2017; Navarro-Fernández et al. 2017). Recently, researchers have started to focus on MF in the central Chile MTE. Due to this, in this chapter we aim to highlight and compile the arising and existing knowledge on mycorrhizas of central Chile MTE. This chapter will focus on basic and applied research on different mycorrhizal types, as well as on the detection of knowledge gaps and proposals for future research directions.

14.2   Mycorrhizas in Central Chile Mediterranean-Type Ecosystem

The unique South American Mediterranean-type ecosystem is located from 30° to 36° South Latitude in the western portion of the continent (Armesto et al. 2007). It is surrounded by the Atacama Desert in the north, by the Pacific Ocean in the west,

by the Andes in the east and by the evergreen-deciduous temperate forests in the south. This topography, which in turn produces antagonistic radiation/moistness systems and a highly variable soil system, generates environmental gradients that have produced highly rich plant communities (Armesto et al. 2007). Also, several types of plant communities occur here, which altogether are known as **Chilean matorral** (Armesto et al. 2007).

From a recent study it was possible to extract the proportions of the mycorrhizal types from up to 1576 native plant species (from a total of 1591) of the Chilean matorral (Silva-Flores et al. unpublished work). On that study, the proportions of mycorrhizal types were calculated at three resolution levels (Fig. 14.1). The first one calculated the proportions using an empirical approach (Bueno et al. 2018), i.e. using published in peer-reviewed literature in where the mycorrhizal type of a plant species was assessed through empirical methods (Fig. 14.1a). With this approach it was possible to assess the mycorrhizal type of only 17.3% of the plant species in the Chilean matorral (Fig. 14.1a). The other two levels of resolution used to assess the mycorrhizal type of the plant species, calculated the proportions using a taxonomic approach (Bueno et al. 2018), i.e. extrapolating a certain plant species mycorrhizal type to a taxonomically and phylogenetically related plant species. Extrapolating information from plant species to plant genus (Fig. 14.1b) and subsequently to plant family (Fig. 14.1c), allowed to assess the mycorrhizal type of 78% and 99% (at genus and family level of resolution respectively) of the plant species of the Chilean matorral. From the results of that study was possible to extract that the AM type is in higher proportion relatively to the other mycorrhizal types, independent of the level of resolution (Fig. 14.1). The other mycorrhizal types proportions vary depending on the level of resolution. In order to learn the exact proportions of all mycorrhizal types in the Chilean matorral more empirical data are urgently needed, since
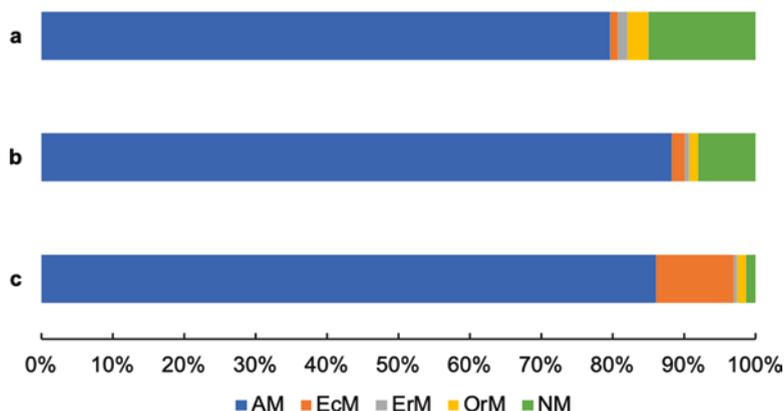
Fig. 14.1 Proportions of mycorrhizal types in the Chilean matorral. Proportions were calculated from: (**a**) empirical data of plant species, (**b**) extrapolation from plant species to genus, and (**c**) extrapolation from plant genus to family. AM: arbuscular mycorrhiza, EcM: ectomycorrhiza, ErM: ericoid mycorrhiza, OrM: orchid mycorrhiza and NM: non-mycorrhiza

it has been recently showed the inaccuracy of the taxonomic approach to describe plant mycorrhizal types (Bueno et al. 2018). To learn the mycorrhizal type distribution patterns in plant species can indicate the relationship strength between plant communities and mycorrhizas (Moora 2014), potentially regulating both the mycorrhizal and plant community (Neuenkamp et al. 2018). Consequently, this information might be useful in developing tools for restoration of degraded ecosystems as the Chilean MTE.

It is important to highlight from the above-mentioned research (Silva-Flores et al. unpublished work) that even with the extrapolation of mycorrhizal type data from plant species to plant families, there are still 17 plant species in the Chilean matorral where the mycorrhizal type is absolutely unknown. Two of these species are in the Chilean national regulation of classification of species according to their conservation status. The species *Berberidopsis corallina* Hook. f. (Berberidopsidaceae) and *Gomortega keule* (Molina) Baill. (Gomortegaceae) are both classified as endangered; thus, it would be essential to clarify their mycorrhizal type, mycorrhizal abundance and other aspects on mycorrhizal biology in order to assess the relative importance of the MF in the recovery of these plant species.

14.3 Arbuscular Mycorrhiza in the Chilean Matorral

Arbuscular mycorrhizal fungi (AMF) are found as root symbionts in 72% of land plant species (Brundrett and Tedersoo 2018). This symbiosis, known as AM, occurs between the roots of certain plants and the hyphae of fungi from the Phylum Glomeromycota (Tedersoo et al. 2008). With the currently available research, it is known that the AM symbiosis is the more frequent across the plant species of the Chilean matorral (Fig. 14.1) and consequently probably a key component for this ecosystem. Despite this, there is scarce information on the topic, probably due the lack of awareness. In fact, to our knowledge, there are only five published studies regarding basic research on AM symbiosis related to the Chilean matorral (Casanova-Katny et al. 2011; Torres-Mellado et al. 2012; Marín et al. 2017; Benedetti et al. 2018; Silva-Flores et al. 2019) and two on applied research (Curaqueo et al. 2010, 2011).

14.3.1 Basic Research on AM Symbiosis in the Chilean Matorral

One study explored the unknown mycorrhizal type of 10 plant species of the Amaryllidaceae family: *Gilliesia curicana*, *G. graminea*, *G. montana*, *Miersia chilensis*, *M. leporina*, *M. myodes*, *M. tenuiseta*, *Solaria atropurpurea*, *S. miersioides* and *Speea humilis* (Torres-Mellado et al. 2012). The study found that all the plant species had an association with the AM type with a mean colonization

percentage of 45%. The study has an impact for conservation strategies of those plant species since all of them are either vulnerable or endangered. The authors concluded that because the plants have a high mean mycorrhization level, they should be highly AM dependent and thus the associated AMF should be considered in conservation strategies as plant propagation. The study also suggests that the next step should be the identification of AMF species associated to the plant species in order to successfully use it in conservation programs.

In the same line, another investigation also explored the mycorrhizal type of 23 Andean plant species, 18 of which belonged to the AM type (Casanova-Katny et al. 2011). This was done in order to show that cushion-associated plants had a higher AM colonization in comparison with the same plant species growing in bare soil.

One study explored the factors affecting AMF communities in ten Chilean *Nothofagus* forests (Marín et al. 2017), included three sampling plots that according to Armesto et al. (2007) can be considered as part of the Chilean matorral. One plot was from *Reserva Natural Los Ruiles* and was dominated by *N. alesandrii* (P1). The other two plots were from *Parque Nacional La Campana*, one plot dominated by *N. macrocarpa* (P2) and the second by *Luma apiculata* and *Peumus boldus* (P3). In that study, AMF communities were studied through the analysis of spores extracted from soil samples. Only *Glomus* sp. was found in P1 and P2, whilst in P3 was also present together with *G. diaphanum.* Consequently, P3 resulted to have a higher diversity than P1 and P2, whilst the community composition of P1 and P2 were similar, but also different from P3. The content in the soil of plant available phosphorus and magnesium were the main edaphic variables affecting the AM fungal community composition in those three plots. The higher spore abundance was in P2, followed by P3 and P1.

A recent published study, quantified and morphologically identified the AMF spores associated to nine sites of *P. boldus* forests (Benedetti et al. 2018). They reported a total of 23 AM fungal species considering all sites. *Funneliformis badium* was present in all sites and with a high abundance relative to the other AM fungal species. In contrast, *Septoglomus constrictum* was also present in all sites but with a low abundance. *F. mosseae, Acaulospora spinosa* and *Rhizophagus irregularis* were also frequent species considering all sites.Finally, in the VI Region of Libertador Bernardo O'Higgins, the role of biotic and abiotic factors in regulating soil AMF spore density in two sclerophyllous shrublands were explored. The results showed a strong regulation of climatic seasons on spore density in both shrublands, in contrast to plant host species that did not have an effect on soil spore density in any of the shrublands. Soil factors as clay content, electrical conductivity, soil organic matter and available phosphorus and nitrogen also affected AMF spore density (Silva-Flores et al. 2019).

There are also several ongoing studies with unpublished data or submitted results regarding AM symbiosis on the Chilean matorral. In this respect, a study performed in the *Reserva Río Los Cipreses* ecosystem (34°27′54″S 70°27′18″W) allowed scientists to have a first screening of the diversity of AMF in the upper part of the *Cachapoal* river (Aguilar et al. unpublished data). Three plant formations were studied in this ecosystem: the *Austrocedrus chilensis,* the Matorral and the Espinal.

The main AMF genera found in all three plant formations were *Glomus, Acaulospora* and *Archeospora* (Fig. 14.2). Moreover, the Matorral plant formation showed a higher species richness relative to the Espinal and *Austrocedrus chilensis* (Fig. 14.2). The tree plant formations had different species composition (Fig. 14.2). Also, a high level of AMF colonization was observed in the roots of all three plant formations; *Austrocedrus chilensis* (90%), the Matorral (75%) and the Espinal (65%). Finally, a positive correlation was observed between the diversity of AMF and edaphic factors, such as nitrogen and phosphorus concentration, available and exchangeable potassium and soil organic matter percentage.

Another study performed in the VI Region of *Libertador Bernardo O'Higgins* in central Chile, aimed to assess the mycorrhizal type of the dominant plant species of the sclerophyllous shrubland plant formation (Silva-Flores et al. submitted). It was possible to stablish that *P. boldus*, *Kageneckia oblonga*, *Escallonia pulverulenta*, *Quillaja saponaria* and *Cryptocarya alba* were all AM plant species. In *Lithrea caustica* it was possible to observe AMF hyphae only in the surface of roots thus further analyses are recommended to accurately assess whether is an AM plant.

Finally, another study explored the variation of the molecular AMF community of the sclerophyllous shrubland in relation with host plant species, compartment (root or soil), physico-chemical soil factors and seasons (Silva-Flores et al. unpublished data). So far, a richness of 153 virtual taxa (VT) has been found. Also, the main AMF genera found were *Glomus, Claroideoglomus* and *Paraglomus.* AMF richness was regulated by host plant species, while AMF community composition was regulated by seasons, host plant species, soil compartment (root or soil) and some physico-chemical soil factors.

All the studies above described indicate that AMF are highly present in the Chilean matorral and consequently playing an important role on this MTE. However, all this research is in a descriptive stage and further studies quantifying the AMF
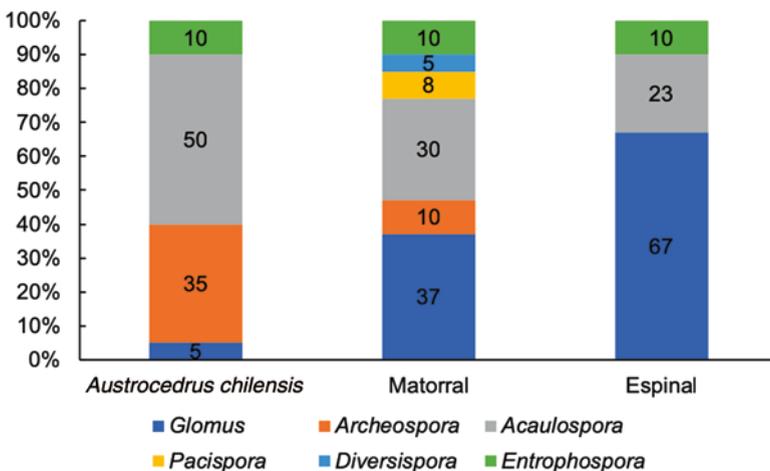

Fig. 14.2 Percentage of AMF spore genera in 100 g of soil in each plant formation studied

contribution to ecosystem processes should be performed, in order to develop efficient conservation strategies for this MTE.

14.3.2   Applied Research on AMF in the Chilean Matorral

Two studies related to AMF and applications of it have been performed in the Chilean Mediterranean agroecosystems. The first one evaluated the effect of no tillage and conventional tillage on soil organic matter, arbuscular mycorrhizal hyphae and soil aggregates (Curaqueo et al. 2010). Tillage affected the quantity and quality of soil organic matter, as well as AMF activity, glomalin content, and soil aggregation. No tillage produced higher values of hyphal length and glomalin production in contrast to conventional tillage. Thus, no tillage favors soil aggregation and consequently contribute to the stability of organic matter of the Mediterranean agroecosystems. The second study explored the effect of conventional tillage and no tillage for 6 and 10 years on AMF propagules (spore density and total and active fungal hyphae) and glomalin content (Curaqueo et al. 2011). AMF propagules and glomalin content resulted to be higher in a 6 year no tillage system compared with a conventional tillage system and 10 years no tillage system, suggesting that the positive effects of no tillage system for 6 year vanished after certain time.

Finally, Aguilar et al. (unpublished data) studied the effect of two different agricultural managements (organic vs conventional) on the diversity of AMF present in the soil of Mediterranean Chilean vineyards. The morphological analysis from spores of grapevine rhizospheric soil resulted in a total of twelve morphospecies of AMF (Fig. 14.3). Organic management had a higher species richness (11) compared to conventional management (10). Also, the species composition was different between managements. The organic management was composed by 2 exclusive species (*Acaulospora* sp. and *Pacispora scintillans*) and 9 shared with conventional management, while conventional had 1 exclusive (*Claroideoglomus etunicatum*) (Fig. 14.3). Finally, a molecular analysis showed that the three most common colonizers of grapevine roots, independent of the management, were *Funneliformis verruculosum*, *Septoglomus constrictum* and an unknown *Septoglomus* sp. This study provides valuable information since identification of AMF species have the potential for being used in sustainable management practices to improve grapevine production in the Mediterranean region.

The investigation on AMF in Mediterranean agroecosystems shows that AM symbiosis is also important and contributes to a better performance of the productive systems (Curaqueo et al. 2010, 2011). However, more detailed studies are needed in order to assess their role as a provider of ecological services in, for instance, sustainable agriculture (Johansson et al. 2004).

Finally, the recognition of the crucial role of AMF in the central Chilean MTE is needed in order to protect the diversity of AMF populations as well as the vegetation diversity. Additionally, it is also important to considerer the relationships between AMF and other microorganisms (e.g. PGPR and rhizobia).
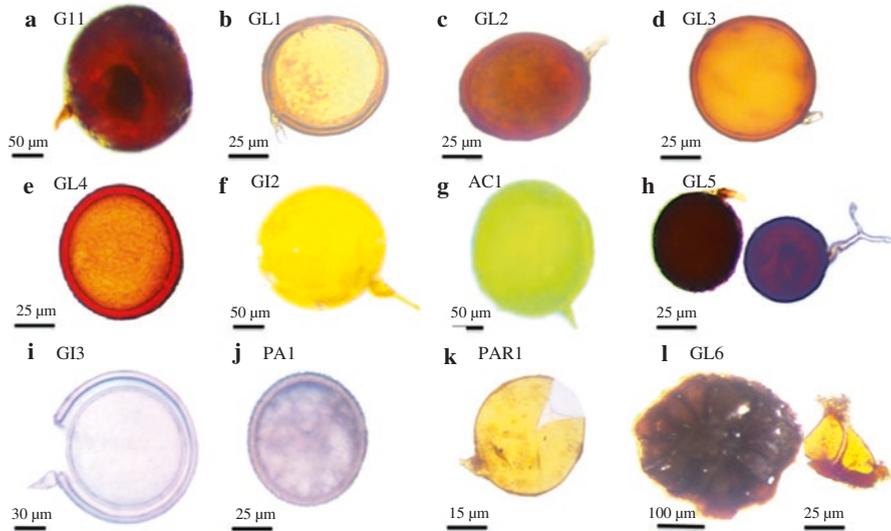
Fig. 14.3 AMF spore morphotypes from soil of ten Chilean grapevine valleys. (**a**) GI1 *Scutellospora* sp., (**b**) GL1 *Funeliformis verruculosum*, (**c**) GL2 Uncultured *Septoglomus,* (**d**) GL3, *Claroideoglomus etunicatum***, (**e**) GL4 Uncultured *Septoglomus,* (**f**) GI2 *Gigaspora* sp., (**g**) AC1 *Acaulospora* sp.*,* (**h**) GL5 *Septoglomus constrictum,* (**i**) GI3 *Cetrospora gilmorei,* (**j**) PA1 *Pacispora scintillans*,* (**k**) PAR1 *Paraglomus* sp. and (**l**) GL6 *Sclerocystis* sp. *species exclusively from soils with organic management, ** species exclusively from soils with conventional management

14.4 Ectomycorrhiza in the Chilean Matorral

In Chile, *Nothofagus* is the only native plant genus documented as EcM (Garrido 1988). It has 10 species, where six of them can be found in the Chilean matorral through altitudinal gradient replacement. *N. macrocarpa* inhabits in small, relictual and disjunct populations in the top of Coastal Mountain range, forming the northern limit of genus distribution (Alcaras 2010). In contrast, *N. obliqua*, *N. glauca*, *N. alessandri, N. alpina*, and *N. dombeyi* inhabit the altitudinal intermediate zones.

Several studies on *Nothofagus* forests in central Chile revealed the presence of 43 species of ectomycorrhizal fungi (Fig. 14.4), divided in 3 Orders, 9 Families, and 13 Genera (Singer 1969; Moser and Horak 1975; Horak 1980; Garrido 1985, 1988). *Cortinarius* is the dominant fungal genus, comprising 56% of the total species richness (Table 14.1). In addition, these forests are characterized by a high degree of fungal endemism, being 44% of the fungal species endemic to Chile, and 42% are endemic of the South American *Nothofagus* forest, comprising central-south of Chile and southwest of Argentina (Niveiro and Albertó 2012, 2013, 2014; Romano and Lechner 2013; Romano et al. 2017). Thus, a total of 86% of EcM fungal species found in the Chilean matorral are endemic of Nothofagus forests in southern South America (Table 14.1).

Fig. 14.4 Some native EcM species: (**a**) *Austropaxillus statuum*, (**b**) *Cortinarius austroturmalis*, (**c**) *C. magellanicus*, and (**d**) *Descolea antarctica*

Currently, macromycetes are being studied in forests dominated by *N. macrocarpa* in two locations: *Cerro El Roble* (33°00′S, 71°00′W) and *Reserva Natural Altos de Cantillana* (33°52′S, 71°00′W). We have found 17 ectomycorrhizal fungi corresponding to 10 species of the genus *Cortinarius*, two species of *Inocybe*, two species of *Laccaria*, one *Hebeloma* species, one *Amanita* species and one *Paxillus* species (Dibán et al. unpublished work). Although they are in the process of taxonomic determination, none of them coincide with those described in the literature for *N. macrocarpa* (Singer 1969; Moser and Horak 1975; Garrido 1985). Thereby, this study increases documented EcM fungal richness for *N. macrocarpa* to 28 species in total.

Most of the species records previously mentioned are based on the presence of ectomycorrhizal species through fruiting bodies (Singer 1969; Moser and Horak 1975; Garrido 1985), with few studies confirming the presence of the species in the roots (Garrido 1988). Thus, in mixed forests with the presence of two or more *Nothofagus* species, it makes it difficult to interpret which ectomycorrhizal species is associated with which host species. In addition, some fungal genera are both, ectomycorrhizal and saprotrophs (e.g. *Ramaria* spp.) (Tedersoo et al. 2008). Thus, in studies based only on fruiting bodies, there is no certainty whether *Ramaria* spp. are forming EcM associations or not. Consequently, one of the challenges in the

Table 14.1 List of ectomycorrhizal fungal species in four localities of the Chilean matorral, and its distribution. En = endemic, Ch = Chile, Ar = Argentina. S1: *Cerro El Roble* (33°00′S, 71°00′W), S2: *Altos de Vilches* (35°36′S, 71°12′W), S3: *Reserva Forestal El Maule* (35°50′S, 72°31′W) and S4: *Pilén* (35°57′S, 72°25′W)

Species	Distribution	S1	S2	S3	S4
Amanita diemii Singer	Ch, Ar	0	1	1	0
Amanita merxmuelleri Bresinsky & Garrido	En Ch	0	0	1	0
Amanita umbrinella Gilb. Et Clel.	Gondwanic	0	1	0	0
Austropaxillus boletinoides (sing.) Bresinsky & Jarosch	En Ch, Ar	0	0	1	0
Austropaxillus statuum (Speg.) Bresinsky & Jarosch	En Ch, Ar	0	1	1	0
Boletus araucarianus Garrido	En Ch	0	0	1	0
Boletus putidus Horak	En Ch	0	1	0	0
Butyriboletus loyo Philippi	En Ch	0	1	0	0
Cortinarius albocanus (Horak & Moser) Peintner & Moser	Gondwanic	0	1	1	0
Cortinarius albocinctus Moser	En Ch, Ar	1	0	0	0
Cortinarius amoenus (Moser & Horak) Garnier	En Ch, Ar	0	0	1	0
Cortinarius argillohygrophanicus Moser & Horak	En Ch, Ar	1	0	0	0
Cortinarius aridus Moser	En Ch	1	0	0	0
Cortinarius austroturmalis Moser & Horak	En Ch, Ar	0	1	1	1
Cortinarius austroturmalis var. austroturmalis	En Ch	1	0	0	0
Cortinarius brevisporus Moser	En Ch	1	0	0	0
Cortinarius cauquenensis Garrido	En Ch	0	0	1	0
Cortinarius coigue Garrido	En Ch	0	0	1	0
Cortinarius columbinus Moser & Horak	En Ch, Ar	1	0	0	1
Cortinarius darwinii Spegazzini	En Ch, Ar	0	1	0	0
Cortinarius elaiotus Moser & Horak	En Ch	0	0	0	1
Cortinarius gracilipes Moser	En Ch	0	0	0	1
Cortinarius hualo Garrido	En Ch	0	0	1	0
Cortinarius magellanicus Spegazzini	Native	0	0	1	0
Cortinarius maulensis Moser	En Ch, Ar	0	0	0	1
Cortinarius pachynemeus Moser	En Ch	1	0	0	0
Cortinarius paguentus Garrido & Horak	En Ch	0	0	1	0
Cortinarius roblemaulicola Garrido & Horak	En Ch, Ar	0	0	1	0
Cortinarius teraturgus Moser	Gondwanic	1	0	0	0
Cortinarius teresae (Garrido) Garnier	En Ch	0	0	1	0
Cortinarius tumidipes Moser	En Ch, Ar	0	1	0	0
Cortinarius viridurifolius Moser	En Ch	0	0	0	1
Descolea antarctica Singer	En Ch, Ar	1	1	1	0
Inocybe neuquenensis Singer	En Ch, Ar	0	0	1	0
Laccaria ohiensis (Mont.) Singer	Broad	0	0	1	0
Paxillus aff involutus (Batsch ex Fr.) Fr.	Broad	1	0	0	0

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Table 14.1 (continued)

Species	Distribution	S1	S2	S3	S4
Russula austrodelica Singer	En Ch	0	1	1	0
Russula nothofaginea Singer	En Ch, Ar	0	0	1	0
Stephanopus vilchensis Garrido & Horak	En Ch	0	1	0	0
Tricholoma cortinatellum Singer	En Ch, Ar	0	1	1	0
Tricholoma fagnani Singer	En Ch, Ar	0	0	1	0
Tricholoma fusipes Singer	En Ch, Ar	0	0	1	0
Zelleromyces alveolatus (sing. & Sm.) Trappe, Lebel & Castellano	En Ch	1	0	0	0
	TOTAL	**11**	**12**	**20**	**6**

study of EcM in the Chilean matorral is to combine the taxonomy of fruiting bodies together with direct observation of the roots, and to sequence the described species to extend the genetic database. Another challenge is to increase sampling locations, especially in forests of *N. alessandri* and *N. macrocarpa*, that are scarcely sampled and they are both classified as endangered species (Benoit 1989).

14.5   Orchid Mycorrhiza in the Chilean Matorral

The Orchidaceae family forms an exclusive type of mycorrhiza, called the orchid mycorrhiza (OrM). In this association, orchids interact with a polyphyletic group of life-free saprophytic fungi called *Rhizoctonia* that includes fungi from three basidiomycetes families: Tulasnellaceae, Ceratobasidiaceae and Sebacinaceae (Dearnaley et al. 2012). In addition to the exchange of nutrients and carbon between fungi and adult plants (Cameron et al. 2006), OrM are crucial for orchid germination and seedling development. Orchid seeds are extremely small and lack of energy reserves (Arditti and Ghani 2000), so they require associating with MF that provide the nutrients and carbon needed to germinate (Rasmussen 2002). This process, known as symbiotic germination, is one of the defining characteristics of Orchidaceae (Givnish et al. 2016) and it means that all orchids are mycoheterotrophic (MHT) at least in one stage of their life. Most orchids are autotrophic at adulthood, but there are some species that remain fully MHT throughout life (Leake 1994). Furthermore, some green orchids species present a third nutrition mode called partial MHT or mixotrophy, in which they obtain carbon from MF and from photosynthesis (Selosse and Roy 2009; Hynson et al. 2013).

Although Orchidaceae has a tropical center of diversity, it shows a considerable secondary diversity outside tropical regions (Dressler 1981). This is the case of Mediterranean ecosystems, where the scarce orchid flora of Southern California is an exception compared to Mediterranean Australia, Chile, south Africa and southern Europe (Bernhardt 1995).

There are 42 orchid species that show continuous or partial distribution through the Chilean matorral (Novoa et al. 2015), all of them terrestrial and photosynthetic. Little is known about OrM associations in Chile (Herrera et al. 2019), and even less in the Chilean matorral, however the evidence available shows these orchids form associations mainly with fungi form the families Tulasnellaceae and Ceratobasidiaceae (Herrera et al. 2017). These findings support observations from other Mediterranean zones that show that Tulasnellaceae and Ceratobasidiaceae fungi are the main associates in a high number of orchid species (Girlanda et al. 2011; Jacquemyn et al. 2015). Interestingly, there is no record of Sebacinaceae forming OrM in Chilean matorral. This result agrees with other studies in Southern South America (Fracchia et al. 2014a, b) but differs from observations in Mediterranean Basin (Girlanda et al. 2011). Further studies assessing the distribution of OrM fungi in soils would help to elucidate the causes of the lack of Sebacinaceae. Nevertheless, more research on other orchid species including more populations is needed to confirm this pattern.

Another exciting observation is the variation in the degree of specificity among orchid species of Chilean matorral. Specificity ranges from generalist associations like in *Chloraea longipetala* (Herrera et al. 2017) and *Bipinnula fimbriata* (Steinfort et al. 2010) to more specialists, as observed in *Chloraea gavilu* (Herrera et al. 2017). This agrees with variation on mycorrhizal specificity observed among orchids species from Mediterranean Australia (Bonnardeaux et al. 2007; Swarts and Dixon 2009). Additionally, variation in specificity among populations of the same species was observed in *Bipinnula fimbriata* and *B. plumosa*, which was related to changes in soil nutrient availability (Mujica et al. 2016). In the last decade, it has been an increasing effort to identify OrM in Chilean matorral (Herrera et al. 2019). However, further studies are required to expand this knowledge and to allow comparisons between Mediterranean climates. For example, to our knowledge, there is no evaluation of nutritional modes of Chilean matorral orchids, while mixotrophy has been detected in Mediterranean Basin orchids (Liebel et al. 2010; Girlanda et al. 2011). This is particularly interesting considering that this nutritional mode might be more frequent in green orchids than previously thought (Gebauer et al. 2016). There is a lot to be done in the study of Chilean matorral OrM, especially bearing in mind that most of Chilean orchids are endemic and insufficiently known or in some degree of threat (Novoa et al. 2015; Herrera et al. 2019); and mainly considering that knowledge on OrM is crucial for successful strategies in orchid conservation (Batty et al. 2002; Swarts and Dixon 2009).

14.6   Final Considerations

Mycorrhizal research in the Chilean matorral is evidently scarce. However, an emerging interest is arising from several researchers – mainly in AM, EcM and OrM. South America, in general, with their contrasting mycorrhizal patterns in comparison with the northern hemisphere, climatic conditions and other features