

Chapter 2

The Ectomycorrhizal Symbiosis in South America: Morphology, Colonization, and Diversity

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2.1 Introduction

About 95% of the world's living species of vascular plants belong to families that are characteristically mycorrhizal (Trappe 1977). The symbiotic root–fungus associations result from the coevolution between plants and fungi, which determined mycorrhizae to be the norm in terrestrial plant nutrition, not the exception (Trappe 1977, 1987, Brundrett and Cairney 2002).

Among the seven types of mycorrhizae widely described (arbuscular, arbutoid, ectendo, ecto, ericoid, monotropoid, and orchidaceous), both arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM) are the most abundant and widespread in forest communities (Allen et al. 2003; Smith and Read 2008).

Forest communities cover approximately 33% of the world's land surface (Rumney 1968) being ECM the most frequent and widespread mycorrhizal type in forests and woodlands of cool temperate and boreal latitudes. Forests characterized by the dominance of ECM woody species would have extended both throughout the hemispheres and upwards in mountain areas at the expense of AM woodlands (Malloch et al. 1980). On the other hand, even though various tropical and subtropical trees throughout the world also form ECM (Moyersoen et al. 1998a, b,

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2001; Pérez-Moreno 1998; Founoune et al. 2002; Onguene and Kuyper 2002), most of them form AM (Alexander 1989). This AM are obligate symbionts belonging to the Glomeromycota phylum (Schüßler et al. 2001), which have been found in trees, shrubs, and herbs in all tropical regions (Janos 1980, 1985; Béreau et al. 1997; Smith and Read 2008).

According to Singer and Morello (1960), ECM forests in South America continue the important ectomycorrhizal complex of Central America into Colombia, where *Quercus* sp. (Fagaceae) appears. There is also a strip formed by *Alnus acuminata* Kunth (Betulaceae) extended from Venezuela to Argentina, while the largest and most important ectomycorrhizal area, the *Nothofagus* (Fagaceae) region extends from 33° to 50°S. Beyond these naturally occurring forests, human activity made possible the existence of many ECM forests of plant species naturally found in the Northern Hemisphere, such as *Pinus* sp., *Eucalyptus* sp., *Populus* sp., *Salix* sp., *Larix* sp., *Cedrus* sp., *Betula* sp., and *Quercus* sp. (Singer and Morello 1960) with their ECM fungi of European and North American origin.

On this basis, the general aim of the present chapter is to review the ECM symbiosis in South America with particular emphasis on its anatomical characteristics. This will provide an organized structure essential for the better understanding of the plant–fungus mutualism in ectomycorrhizal associations in South America, so adding new tools for the management and conservations of threatened ecosystems.

2.2 ECM Studies in South America

The tradition on ECM research in South America is important. The great diversity of available studies covers descriptions of mycorrhizal status, ECM fungi, inoculations, colonization, and morphological characterization. Unfortunately, and due in part to their abundance but often also to their inaccessibility, it is not possible to aim at describing the whole array of studies carried throughout the continent. Therefore, this chapter pretends to summarize the wide range of families and genera of Angiospermae and Gymnospermae forests growing in South America in which ectomycorrhizal studies have been carried.

Most ECM fungi can associate with various host plants, while the opposite is also true, being it possible for a single host to form ECM with a number of different fungi (Moyersoen 1993). Most studies analyzed (Table 2.1) present lists of ectomycorrhizal fungi (most of which belong to the Basidiomycota phylum) and taxonomic descriptions in exotic plants such as *Pinus* (*P. radiata*, *P. elliottii*), *Eucalyptus* (*E. citriodora*, *E. dunii*, *E. robusta*), and *Quercus*. Among endemic plants, most studies have been carried out in *Nothofagus* (*N. obliqua*, *N. dombeyi*, *N. alpina*) forests. Besides, some of the associations found in these forests are established with fungi species from exotic plantations (*P. radiata* en Chile) (Garrido 1986).

Table 2.1 Description of 103 studies on ectomycorrhizal status in South America

Family	Species	Publication with country ^a and ECM characteristics ^b indication
<i>Native plants</i>		
Betulaceae	<i>Alnus acuminata</i>	1(A;2) 2(A;2) 3(A;1) 4(A;1) 5(A;1) 6(A;1) 7(A;1,4) 8(A;1,3,4) 9(A;1,3,4) 10(A;2)
Caesalpinaceae	<i>Dicymbe corymbosa</i>	11(FG;2,4) 12(FG;2) 13(FG;4) 14(FG;2)
	<i>D. alisonii</i>	11(FG;2,4) 12(FG;2) 13 (FG; 4) 15(FG;1,2)
	<i>D. jennmanii</i>	11(FG;4)
	<i>Dicymbe</i> sp.	14(FG;2)
Dipterocarpaceae	<i>Pakaraimaea dipterocarpacea</i>	17(V;1) 18(V;2)
Fabaceae	<i>Acacia bonaerensis</i>	19(U;4)
	<i>Aldinia heterophylla</i>	20(B;2)
	<i>A. insignis</i>	11(G;4) 13(G;4)
	<i>A. kunhardtiana</i>	21(V;1,4)
	<i>A. latifolia</i>	21(V;1,4)
	<i>Calliandra selloi</i>	19(U;4)
	<i>C. tweedii</i>	19(U;4)
	<i>Gleditsia amorphoides</i>	19(U;4)
	<i>Lonchocarpus nitidus</i>	19(U;4)
	<i>Prosopis</i> spp.	19(U;4)
Fagaceae	<i>Nothofagus alpina</i>	22(C;1) 23(C;1) 24(C;3) 25(C;2) 26(C;2) 27(C;1,4) 28(C;4)
	<i>N. alessandrii</i>	29(C;3)
	<i>N. antarctica</i>	25(C;2) 26(C;2) 30(C;4) 31(C;4) 32(A;4)
	<i>N. betuloides</i>	23(C;1) 25(C;2)
	<i>N. dombevi</i>	23(C;1) 24(C;3) 25(C;2) 26(C;2) 28(C;4) 30(C;4) 31(C;4) 32(A;4) 34(A;1) 35(C;1) 36(C;2)
	<i>N. glauca</i>	25(C;2) 38(C;3)
	<i>N. leonii</i>	25(C;2)
	<i>N. nervosa</i>	32(A;4)
	<i>N. nitida</i>	25(C;2) 39(C;1)
	<i>N. obliqua</i>	23(C;1) 25(C;2) 26(C;2) 30(C;4) 32(A;4) 37(C;4) 38(C;3)
	<i>N. obliqua</i> var. <i>macrocarpa</i>	25(C;2)
	<i>N. pumilio</i>	

(continued)

Table 2.1 (continued)

Family	Species	Publication with country ^a and ECM characteristics ^b indication
Gnetaceae	<i>Nothofagus</i> spp.	23(C;1) 25(C;2) 26(C;2) 32(A;4) 33(C;1) 40(C;1) 41(C;1) 42(C;1) 43(C;1) 44(C;2,4)
Melastomataceae	<i>Gnetum</i> sp.	1(C;2) 25(C;2) 26(C;2) 45(A-C;2)
Nyctaginaceae	<i>Graffenrieda emarginata</i>	46(B;4) 47(B;4)
	<i>Neea altissima</i>	48(E;1) 49(E;4)
	<i>N. divaricata</i>	48(B;4)
	<i>N. laetivirens</i>	50(E;2,4)
	<i>N. obovata</i> , <i>N. robusta</i>	52(B;4)
	<i>N. tristsis</i>	21(V;1,4)
	<i>Neea</i> sp. 1, <i>Neea</i> sp. 2	53(FG;4)
	<i>Neea</i> sp. 3, <i>Neea</i> sp. 5	49(E;4) 51(E;1)
	<i>Neea</i> sp.	50(E;2,4)
	<i>Guapira sancarlosiana</i>	46(B;4) 47(B;4) 54(P;4)
	<i>Guapira</i> sp.	21(V;1,4) 49(E;4)
Polygonaceae	<i>Coccoloba excelsa</i>	51(E;1)
	<i>C. latifolia</i>	21(V;1,4)
	<i>C. molitis</i>	53(FG;4)
	<i>C. rosea</i>	53(FG;4)
	<i>Coccoloba</i> sp.	55(B;1)
Salicaceae	<i>Salix humboldtiana</i>	53(FG;4)
Sapotaceae	<i>Glycoxylon inphyllum</i>	1(A;2) 56(A;1,2) 57(A;4)
Introduced plants		47(B;4)
Betulaceae	<i>Betula pendula</i>	25(C;2) 58(A;1)
	<i>Betula</i> sp.	59(A;2)
Myrtaceae	<i>Eucalyptus camaldulensis</i>	60(B;4) 61(B;3)
	<i>E. citriodora</i>	61(B;3) 62(B;2) 63(B;2) 64(B;2,3)
	<i>E. cloeziana</i>	61(B;3)
	<i>E. dunnii</i>	62(B;2) 65(B;2) 66(B;3) 67(B;3) 68(B;3) 69(B;3) 71(B;3) 72(B;3)
	<i>E. globulus</i>	25(C;2)
	<i>E. grandis</i>	60(B;4) 61(B;3) 63(B;2) 64(B;2,3) 73(B;2) 74(B;2) 75(B;3) 76(B;3)

<i>E. microcorys</i>	63(B;2) 73(B;2)
<i>E. robusta</i>	62(B;2) 64(B;2,3) 73(B;2)
<i>E. rostrata</i>	77(A;3)
<i>E. tereticomis</i>	63(B;2)
<i>E. saligna</i>	63(B;2)
<i>E. urophylla</i>	61(B;3) 75(B;3) 76(B;3)
<i>E. viminalis</i>	63(B;2) 77(A;3) 78(A;1,2)
<i>Eucaliptus</i> spp.	25(C;2) 79(Co;2) 80(B;2)
<i>Cedrus atlántica</i>	58(A;1)
<i>C. deodara</i>	81(A;1,2)
<i>Cedrus</i> sp.	59(A;2)
<i>Larix decidua</i>	25(C;2) 59(A;2)
<i>Picea abies</i>	25(C;2)
<i>Pinus caribaea</i> var. <i>hondurensis</i>	82(B;3)
<i>P. contorta</i>	25(C;2)
<i>P. elliotii</i>	58(A;1) 59(A;2) 62(B;2) 83(A;1,3)
<i>P. halepensis</i>	59(A;2) 84(A;3)
<i>P. patula</i>	25(C;2) 59(A;2) 79(Co;2)
<i>P. pinaster</i>	25(C;2) 85(A;3) 84(A;3)
<i>P. pinea</i>	25(A;3) 84(A;3)
<i>P. ponderosa</i>	85(A;2,3,4) 86(A;2) 87(A;2) 88(A;1,2) 89(A;3)
<i>P. radiata</i>	25(C;2) 59(A;2) 79(Co;2) 90(C;2) 91(C;2)
<i>P. sylvestris</i>	25(C;2)
<i>P. taeda</i>	59(A;2) 62(B;2) 65(B;2) 68(B;3) 84(A;3) 92(B;3) 93(B;3) 94(A;3)
<i>P. thunbergii</i>	84(A;3)
<i>Pinus</i> sp.	25(C;2)
<i>Pinus</i> spp.	1(A;2) 95(U-A;2) 96(B;2)
<i>Pseudotsuga menziesii</i>	25(C;2) 86(A;2) 88(A;1,2) 97(A;2,3,4) 98(A;2)
<i>Tsuga heterophylla</i>	25(C;2)
<i>Quercus humboldtii</i>	99(Co;2) 100(Co;2) 101(Co;2) 102(Co;2) 103(Co;2)
<i>Q. robur</i>	25(C;2)
<i>Quercus</i> sp.	59(A;2)
<i>Quercus</i> spp.	79(Co;2)

(continued)

Table 2.1 (continued)

Family	Species	Publication with country ^a and ECM characteristics ^b , indication
Salicaceae	<i>Populus nigra</i>	25(C;2)
	<i>Populus</i> spp.	25(C;2)
	<i>Salix viminalis</i>	25(C;2)
	<i>Salix</i> spp.	25(C;2)

Each line within the table represents a studied species, with the indication of the Family to which it belongs and all publications (numbered – all respective citations are found below under References) in which it has been described. Following the paper number is an indication of the characteristics of the study carried (country and ECM characteristics)

^aCountry: A Argentina; B Brazil; C Chile; Co Colombia; E Ecuador; FG French Guyana; P Perú; U Uruguay; V Venezuela

^bECM characteristics studied: 1: anatomical characteristics, 2: list of ECM fungi, 3: ECM inoculations, 4: mycorrhizal status or colonization

References: (1) Singer (1953), (2) Singer and Morello (1960), (3) Becerra (2002), (4) Becerra et al. (2002), (5) Becerra et al. (2005a), (6) Becerra et al. (2005b), (7) Becerra et al. (2005c), (8) Becerra et al. (2009a), (9) Noughra et al. (2003), (10) Noughra et al. (2005), (11) Henkel et al. (2002), (12) Henkel (1999), (13) McGuire et al. (2008), (14) Fulgenzi et al. (2007), (15) Henkel et al. (2000), (16) Matheny et al. (2003), (17) Moyersoen (2006), (18) Moyersoen (2008), (19) Friom et al. (1999), (20) Singer et al. (1983), (21) Moyersoen (1993), (22) Palfner (1997), (23) Palfner (2001), (24) Godoy and Palfner (1997), (25) Garrido (1986), (26) Valenzuela et al. (1999), (27) Palfner et al. (2008), (28) Castillo et al. (2006), (29) Flores et al. (1997), (30) Carrillo et al. (1992), (31) Godoy et al. (1994), (32) Diehl et al. (2008), (33) Palfner (2002a), (34) Beenken (2001), (35) Palfner (2002c), (36) Singer (1971), (37) Castillo et al. (2006), (38) Pérez et al. (2007), (39) Palfner (2002b), (40) Palfner and Godoy (1996a), (41) Palfner and Godoy (1996b), (42) Palfner (1996), (43) Palfner (2002d), (44) Villegas et al. (2007), (45) Wright (1988), (46) St John (1980), (47) Singer and Araujo (1979), (48) Haug et al. (2004), (49) Kottke and Haug (2004), (50) Lunt and Hedger (1996), (51) Haug et al. (2005), (52) Janos (1980), (53) Béreau et al. (1997), (54) Alexander and Högberg (1986), (55) Landim de Souza (2003), (56) Becerra et al. (2009b), (57) Fracchia et al. (2009), (58) Noughra (1997), (59) Noughra (1999), (60) Pagano and Scotti (2008), (61) Dos Santos et al. (2001), (62) Giachini et al. (2000), (63) Yokomizo (1981), (64) Schwan (1984), (65) Giachini et al. (2004), (66) Oliveira et al. (1997), (67) Lupatini et al. (2008), (68) Rocci (2006), (69) Voigt et al. (2000), (70) Borges de Souza et al. (2004), (71) Borges de Souza et al. (2008), (72) Pinto Bomassiss (2007), (73) Marx (1977), (74) Hentz de Mello et al. (2006), (75) Arruda Bacchi and Krugner (1988), (76) Liparini Pereira et al. (2005), (77) Halbinger et al. (1986), (78) Brandán de Weth (2006), (79) Guzmán and Varela (1978), (80) Barros et al. (1978), (81) Daniele et al. (2005), (82) Gross et al. (2004), (83) Noughra and Becerra (2001), (84) Tackacs (1961), (85) Barroetaña and Rajchenberg (2003a), (86) Barroetaña et al. (2007), (87) Barroetaña et al. (2005), (88) Barroetaña (2004), (89) Martínez et al. (2007), (90) Garrido (1983), (91) Garrido (1986), (92) Paloschi de Oliveira et al. (2006), (93) Rocci (2006), (94) Tackacs (1964), (95) Singer (1968), (96) Putzke and Pereira (1994), (97) Barroetaña and Rajchenberg (2003b), (98) Barroetaña et al. (2006), (99) Singer (1963), (100) Halling (1989), (101) Franco Molano and Uribe Calle (2000), (102) López-Quintero et al. (2007), (103) Vasco-Palacio et al. (2005)

In South America, most studies on mycorrhizal status and ECM colonization deal with the Fagaceae, Fabaceae, Nyctaginaceae, and Polygonaceae families (Table 2.1). For the *Nothofagus* spp. forests of Chile, a colonization of 1.8–4.8% and 19.6% has been reported by Carrillo et al. (1992) and Palfner et al. (2008), respectively, while for the *Nothofagus* spp. forests of Argentina, it is of 79% (Diehl et al. 2008). Meanwhile, for some genus of the Fabaceae family, Frioni et al. (1999) reported a colonization that ranges between 17 and 36%, while Moyersoen (1993) reported a 65% colonization for *Aldinia kunhardtiana*.

Most studies carried out for the Nyctaginaceae and Polygonaceae families refer to the status of their species in terms of presence/absence of ECM (Singer and Araujo 1979, St John 1980, Janos 1980, Béreau et al. 1997). In the particular case of *Neea obovata*, *N. robusta*, and *Guapira sancarlosiana* (Nyctaginaceae), colonization was 100%, 7%, and 96%, respectively, while it was of 56% in *Coccoloba excelsa* (Polygonaceae) (Moyersoen 1993).

Inoculation technologies appear as an alternative to the use of fertilizers since they reduce both the costs of production and environmental contamination (Garbaye 1990). ECM inoculations in South America have been carried almost exclusively in introduced plants (*Eucalyptus* spp., *Pinus* spp., and *Pseudotsuga menziesii*), with the exception of *Nothofagus* spp. and *Alnus acuminata*. For this, various techniques have been applied: spores from sporocarps mainly belonging to the Basidiomycota phylum (*Alpova diplophloeus*, *Laccaria laccata*, *Rhizopogon roseolus*, *Suillus granulatus*, among others); ECM culture micelia (micelia, airlift bioreactors) in *Eucalyptus* spp. and *Pinus* spp.; and natural soil (potential inoculum) for *Pinus* spp., *Pseudotsuga menziesii*, *Eucalyptus dunii*, *E. citriodora*, *Nothofagus alpina*, *N. dombeyi*, and *Alnus acuminata*. All three techniques have been used for introduced trees, while only spores and natural soil have been used for native species.

2.3 Morphological and Anatomical Features of the ECM in South America

The morphological and anatomical description of mycorrhizae and the identification of their fungal partners are prerequisites for recognizing mycorrhizal biodiversity in ecosystems (Agerer 1991; Miller et al. 1991). Meanwhile, the occurrence of natural ECM associations in the indigenous vegetation types from South America has been virtually unexplored.

Table 2.2 summarizes the volume of ECM anatomotypes described in South America for both native and introduced plants. Four anatomical complexes for recognition of fungal relationships were used: (a) structure of outer mantle layers in plan view, (b) structure of rhizomorphs, (c) shape of cystidia, and (d) features of emanating hyphae (Agerer 1999, 2006). Besides, the cross section of mantle area (e) was also considered, which showed useful for comparing the relative

Table 2.2 Anatomical characterization of ECM in native and introduced plants in South American forests

Ecotomorrhiza/host tree ^a /country ^b /publication ^c	Mantle layers (Plect.: plectenchymatous; Pseud.: pseudoparenchymatous)	Rhizomorphs	Cystidia	Emanating hyphae (color, branching, clamps, septa, anastomoses)	Cross section (µm)
<i>Naucoria escharoides</i> /Aa/A/1	Plect. with parallel arranged hyphae (Mantle type B)	Uniform-loose hyphal bundles	Lacking ^d	Hyaline abundant, branched, with clamps; simple anastomoses	39–56
<i>Cortinarius helodes</i> /Aa/A/2	Plect. loosely interwoven (type B)	Uniform-loose	Lacking	Hyaline abundant, branched, clamped, anastomoses open	130–220
<i>Gyrodon monticola</i> /Aa/A/2	Plect. with globular cells (type F)	Boletoid	Spherical to clavate	Hyaline and brown abundant, branched, with clamps	24–57
<i>Russula alnijorullensis</i> /Aa/A/3	Pseud. with angular cells (type L)	Lacking	Lacking	Colorless, few, clamps lacking	40–60
<i>Cortinarius tucumanensis</i> /Aa/A/3	Plect. with irregularly arranged hyphae (type B)	Uniform-loose	Lacking	Colorless abundant, clamps present, anastomoses open	62–120
<i>Lactarius aff. omphaliformis</i> /Aa/A/3	Pseud. with angular cells (type P-Q)	Lacking	Lacking	Colorless to membranaceously yellowish, clamps lacking	11–30
<i>Tometella</i> cf. <i>subtilacina</i> /Aa/A/4	Plect. with hyphal net arrangement (type A)	Undifferentiated	Lacking	Yellowish to brownish, branched, with clamps	23–36
<i>Tometella</i> cf. <i>stuposa</i> /Aa/A/4	Pseud., with angular and roundish cells (type L)	Not found ^d	Bottle-shaped with a straight to bent neck	Membranaceously brownish, branched with clamps	45–65
<i>Tometella</i> cf. <i>ellisii</i> /Aa/A/4	Plect. with irregularly arranged hyphae (type B)	Not found	Lacking	Colorless, branched with clamps	70–105
		Not found	Lacking		44–58

<i>Lactarius</i> <i>omphaliiformis</i> /Aa/ A/4	Pseud. with epidermoid cells bearing a hyphal net (type Q)				Colorless to membranaceously yellowish, without clamps
<i>Russula</i> sp. /Aa/A/4	Plect. irregularly arranged hyphae (type B)	Not found	Lacking		25–75
<i>Unidentified</i> A/No/V/5	Plect.	NR ^d	NR		75–86
<i>Unidentified</i> B/No/V/5	Compactly mantle	NR	NR		31–49
<i>Unidentified</i> /Nr/V/5	Compactly mantle	NR	NR		33–46
<i>Russula puiggarii</i> / Nsp.1/E/6	Plect., loosely with gelatinous matrix	NR	Not observed		Whitish to light yellowish
<i>Lactarius</i> sp./Nsp.1/ E/6	Plect. hyphae of larger and irregular diameter	Undifferentiated	Not observed		30 thick
<i>Tomentella</i> <i>Thelephora</i> sp.1/ Nsp.1/E/6	Plect. loosely, hyphae net-like arranged	NR	NR		40 thick
<i>Tomentella</i> <i>Thelephora</i> sp.2/ Nsp.1/E/6	Plect., hyphae with clamp	NR	NR		40 thick
Ascomycete/Nsp.1/E/6	Plect., hyphae arranged star-like	NR	NR		30 thick
<i>Thelephoral</i> <i>Tomentella</i> /Nsp.2/E/6	Plect. loosely	NR	NR		NR
<i>Unidentified</i> /Gs/V/5	Compactly mantle	NR	NR		21–36
<i>Thelephoral</i> <i>Tomentella</i> /Gsp./E/6	Plect. loosely arrangement	NR	NR		NR
<i>Unidentified</i> /Ce/V/5	Compactly mantle	NR	NR		40–48
<i>Unidentified</i> /Cr/B/7	Plect.	NR	NR		40–65
<i>Unidentified</i> /Ah/V/5	Plect.	NR	NR		33–60
<i>Clavulinaceae</i> 1/Pd/ V/8	NR	NR	NR		NR

(continued)

Table 2.2. (continued)

Ectomycorrhiza/host tree ^a /country ^{b/} publication ^c	Mantle layers (Plect.: plectenchymatous; Pseud.: pseudoparenchymatous)	Rhizomorphs	Cystidia	Emanating hyphae (color; branching, clamps, septa, anastomoses)	Cross section (µm)
<i>Clavulinaceae</i> 2Pd/V/8	Plect. on top of a Pseud.	Not found	Lacking	White, non ramified, thick and rough wall	NR
<i>Sebacina</i> sp./Pd/V/8	Plect. (net on top of a plectenchyma)	Present (not described)	NR	Yellowish	NR
<i>Cortinarius</i> sp./Pd/V/8	Plect.	Frequent, hairy, ramified	Lacking	Whitish, with clamps	NR
<i>Inocybe</i> 1Pd/V/8	NR	NR	NR	NR	NR
<i>Inocybe</i> 2Pd/V/8	Plect. covered by a loose net	With smooth margin; clamp connections	Lacking	Whitish	NR
<i>Amanita</i> sp./Pd/V/8	NR	NR	NR	NR	NR
<i>Unidentified</i> /Pd/V/8	Plect. (net on top a plect.)	Lacking	Elongated	White, simple septa	NR
<i>Unidentified</i> 2Pd/V/8	Plect. or pseud.	Telephoroid rhizomorphs	Lacking	Brown often ornamented, simple septa	NR
<i>Nothofagiarhiza vinicolor</i> /Np/C/9	Plect., loosely, interwoven hyphae (type B, E)	Lacking	Lacking	Pinkish to dark red, very abundant, with clamps	10–20
<i>Russula fuegiana</i> /Np/C/10	Plect. loose net of thin hyphae (type C, D)	Not frequent, agglutinated hyphae	Cylindrical to gradually tapering with apical knobs	Not found	13–30
<i>Thaxterogaster albocanus</i> /Np/C/11	Plect., loosely, interwoven hyphae (type B)	Numerous undifferentiated	Lacking	Frequent, branched	13–27
<i>Austropaxillus boletinoides</i> /Np/C/12	Plect. (type A, B)	Rather frequent, highly differentiated	Cistidia-like hyphal ends of variable shape	Rather frequent	15–25
<i>Gautieria inapire</i> /Np/C/15	Plect., loosely interwoven (type B)	Unconspicuous, simple or slightly differentiated	Rarely with acanthocystidia	Gelatinous, cell walls with short protuberances	1–25
<i>Nothofagiarhiza reticulosa</i> /Np/C/16	Plect. (type B), mantle surface often parallelly blunted by anastomoses and short ramifications	Rhizomorphs-like strands or simple	Lacking	Light brown, verrucose, septa mostly with clamps, anastomoses also closed by a clamp	20–30

<i>Cenococcum geophilum</i> /Np/ C/16	Plect. (type G) formed by very densely arranged, star-like pattern	Lacking	Lacking	Numerous black, bristle-like	NR
<i>Russula nothofaginea</i> / Nd/A/19	Pseud., covered by hyphal net embedded in a distinct gelatinous matrix (type Q)	Not found	Lacking	Colorless infrequent	15–20
<i>Cortinarius magellanicus</i> /Nd/ C/14	Plect. (type B)	Abundant, with attached spherical sclerotia	Lacking	Colorless-hyaline hyphae, with clamps	30–60
<i>Stephanopus stropharoides</i> /Nd/ C/16	Plect. (type B)	Abundant, blue-bruising when squeezed	Lacking	Abundant, with clamps	30–50
<i>Nothofagiriza vesiculosa</i> /Nd/ C/16	Pseud. (type K), without clamps, thick-walled	Without	Lacking	Very few short	20–45
<i>Cortinarius austrosalor</i> /Nn/ C/13	Plect. (type B)	Differentiated	Lacking	With clamps, open anastomoses	20–30
<i>Austropaxillus boletinoides</i> f. <i>olivascens</i> /Nb/ C/16	Plect. (type B)	Dark brown, pigmented hyphae	Scattered Clavate	Clamped	15–25
<i>Boletus loyo</i> /Nob/C/16	Plect. (type B)	Scattered, highly differentiated	Occasionally clavate, slightly thickened hyphal ends	Scarse, without clamps	36–45
<i>Boletus putidus</i> /Nob/ C/16	Plect. (type A/B)	Highly differentiated, thicker, margin with inflated hyphal elements	Poorly differentiated or weakly clavate cystidia or cystidia-like hyphal ends	Hyphae without clamps	15–25

(continued)

Table 2.2 (continued)

Ecotomicorrhiza/host tree ^a /country ^b / publication ^c	Mantle layers (Plect.: plectenchymatus; Pseud: pseudoparenchymatus)	Rhizomorphs	Cystidia	Emanating hyphae (color; branching, clamps, septa, anastomoses)	Gross section (µm)
<i>Nothofagiarhiza tricytidis</i> /Nob/C/16	Plect. (type D)	Not found	Three types: slightly tapering with an enlarged barrel-shaped; awl-shaped or worm-shaped with enlarged basal cell; ampullate with an apical knob	Rare, clamps lacking	15–22
<i>Descolea antarctica</i> /Na/C/17	Plect. with awl-shaped cystidia (type D)	Not found	Lateral, tapering, knob-bearing outgrowth	Infrequent, with clamps	15–20
Hymenoscyphoid (probably <i>Rhizoscyphus ericae</i>)/Na/C/18	Compact plect.	Lacking	Lacking	Black hyphae, without clamps	NR
Inocyboid/Na/C/18	Loose plect.	Lacking	Lacking	Abundant, with clamps, inocyboid	NR
Russuloid/Na/C/18	Plect.	Lacking	Russuloid gloecystidia	Lacking	NR
Thelephoroid/Na/C/18	Compact plect.	Whitish or lacking	Thelephoroid	Abundant, with clamps	NR
Tomentelloid/Na/C/18	Pseud. or plect.	Dark brown or lacking	Present or lacking	Scarce or lacking, present or lacking clamp connections	NR
<i>Rhizoscyphus ericae</i> /Gm/E/20	No hyphal mantle; a superficial Hartig net (fingerlike branched hyphae)	Lacking	Lacking	Lacking	NR
<i>Lactarius panuoides</i> /Da/G/21	Mantle densely tomentose to substrigose mass	NR	Occasionally similar hyphae forming capitate cystidia	Abundant, with septa	NR
<i>Russula campinensis</i> /Da/G/21	Well developed mantle; coarse net of irregularly shaped	NR	NR	No evident	NR

<i>Inocybe</i> sp./Sh/A/22	Plect. irregularly arranged hyphae (type A)	Lacking	Lacking	Hyaline clamped	19–35
<i>Tometella</i> sp./Sh/A/22	Plect. irregularly arranged hyphae (type A)	Lacking	Lacking	Hyaline clamped, not branched	25–31
Anatomotype III/Sh/A/22	Plect., hyphae without clamps	Lacking	Lacking	Lacking	7–16
Anatomotype IV/Sh/A/22	Plect.	Lacking	Lacking	Scarce, with clamps	12–16
Anatomotype V/Sh/A/22	Plect.	Lacking	Lacking	Scarce, without clamps	12–20
Anatomotype VI/Sh/A/22	Plect.	Lacking	Lacking	Few light to brown, with clamps	12–15
Anatomotype VII/Sh/A/22	Plect.	Lacking	Lacking	Few hyaline, without clamps	12–30
<i>Leccinum scabrum</i> /Bp/A/23	Plect. (type A)	Boletoid, abundant	Lacking	Rough abundant, clamps lacking	NR
<i>Suillus granulatus</i> /Pe/A/23	Plect. with brownish drops of pigments	Boletoid, abundant	Lacking	Abundant, clamps lacking	NR
<i>Amphinema byssoides</i> /Pp/A/24	Plect.	Lacking	NR	Abundant yellowish, clamped, with spines	NR
<i>Rhizopogon roseolus</i> /Pp/A/24	Plect. with a ring-like hyphal pattern	Branched white, abundant hyaline crystals	Lacking	Lacking	NR
<i>Rhizopogon</i> aff. <i>ellenae</i> /Pp/A/24	Plect. with yellow-brown crystals	Abundant, branched, white to pink, with hyaline or yellow crystals	Lacking	Lacking	NR
<i>Rhizopogon</i> immature type/Pp/A/24	Plect. with squarrosely hyphae with crystals	Thin branched, with crystals	Lacking	Abundant	NR
<i>Rhizopogon</i> coralloid type/Pp/A/24	Plect. with hyaline crystals	Abundant, branched, with crystals	Lacking	NR	NR
<i>Rhizopogon</i> brownish type 42/Pp/A/24	Plect. with abundant crystals	Lacking	NR	Lacking	NR
<i>Tuber</i> type/Pp/A/24	Pseud. with irregular cells	Lacking	Awl-shaped, bristle like	NR	NR

(continued)

Table 2.2 (continued)

Ectomycorrhiza/host tree ^a /country ^b /publication ^c	Mantle layers (Plect.: plectenchymatous; Pseud.: pseudoparenchymatous)	Rhizomorphs	Cystidia	Emanating hyphae (color, branching, clamps, septa, anastomoses)	Cross section (µm)
Brownish coralloid anamototype/Pp/A/24	Plect., hyphae with septa	Lacking	Lacking	Lacking	NR
Whitish anamototype/Pp/A/24	Plect. with a ring-like arrangement	Lacking	Lacking	With septa	NR
Dichotomous yellowish anamototype/Pp/A/24	Plect.	Lacking	Lacking	Clamped	NR
Brownish anamototype/Pp/A/25	Plect., hyphae with septa	Lacking	NR	Lacking	NR
<i>Xerocomus chrysenteron</i> /Ca/A/23	Plect. (type A)	Boletoid, abundant	Lacking	Smooth abundant, clamps lacking	40
<i>Amanita muscaria</i> /Cd/A/25	Plect. (type A)	Undifferentiated, abundant	Lacking	Smooth, with clamps	32–57
<i>Tuber</i> type 1/Pm/A/24	Pseud.	Lacking	Awl-shaped, bristle like	Abundant	NR
<i>Rhizopogon</i> type 1/Pm/A/24	Plect.	White branched	NR	Hyaline, with septa	NR
White coralloid anamototype/Pm/A/24	NR	White branched	NR	NR	NR
Brownish anamototype/Pm/A/24	Plect.	Lacking	NR	Abundant	NR

Each line within the table represents a studied ectomycorrhiza, with an indication of its host trees, country for which it has been described and citation (numbered — all respective citations are found below under References), followed by a detailed description of the anatomical characteristics of the referred ECM (structure of outer mantle layers and of rhizomorphs, shape of cystidia, features of emanating hyphae and cross section)

^aHost Tree: Aa *Alnus acuminata*; No *Neea obovata*; Nr *Neea robusta*; N sp. 1 *Neea* sp. 2; Gs *Guapira sancarlosiana*; G sp. *Guapira* sp.; Ce *Coccoloba excelsa*; Cr *Coccoloba rosea*; Ah *Aldinia kunhartiana*; Pd *Pakaraimaea dipterocarpacea*; Np *Nothofagus pumilio*; Nd *Nothofagus dombeyi*; Nn *Nothofagus nitida*; Nb *Nothofagus betuloides*; Nob *Nothofagus obliqua*; Na *Nothofagus alpina*; Ge *Graffenrieda emarginata*; Da *Dicymbe altsonii*; Sh *Salix humboldtiana*; Bp *Betula pendula*; Pe *Pinus elliotii*; Pp *Pinus ponderosa*; Ca *Cedrus atlantica*; Cd *Cedrus deodara*; Pm *Pseudotsuga menziesii*

^bCountry: A: Argentina; B: Brazil; C: Chile; E: Ecuador; G: French Guyana; V: Venezuela

^cReferences: (1) Becerra et al. (2002), (2) Becerra et al. (2005a), (3) Becerra et al. (2005b), (4) Pritsch et al. (2010), (5) Moyersoen (1993), (6) Haug et al. (2005), (7) Landim de Souza (2003), (8) Moyersoen (2006), (9) Palfner and Godoy (1996a), (10) Palfner and Godoy (1996b), (11) Palfner (1996), (12) Palfner (2002a), (13) Palfner (2002b), (14) Palfner (2002c), (15) Palfner (2002d), (16) Palfner (2001), (17) Palfner (1997), (18) Palfner et al. (2008), (19) Beenken (2001), (20) Haug et al. (2004), (21) Henkel et al. (2000), (22) Becerra et al. (2009b), (23) Noulhra (1997), (24) Barroetaña (2004), (25) Daniele et al. (2005)

^dLacking: the author makes its inexistence explicit, NR (not recorded): the author makes no mention to either its presence or absence, Not found: the author describes it as not found

importance of the fungal partner in different plants for different ecosystems, climates, and soils (Landim de Souza 2003). Table 2.2 does not consider morphological descriptions of seedlings grown under greenhouse conditions since, as Agerer (2006) states, descriptions of ECM that are exclusively based on synthesized material often do not provide features occurring in nature.

Out of the 85 ECM anatomotypes described in the different studies (every ECM not identified to the species level was considered to be a different ECM), 35 were identified up to their species, 20 to their genus, 5 to supraspecific groups, 1 to its phylum, 4 were unidentified ECM morphotypes published under a binomial name (Agerer 1986, 1987–2002, 1994, 1999), and 20 were unidentified ECM anatomotypes lacking a name.

The associated fungi recorded in the 85 ECM descriptions were mostly Basidiomycota (55) and Ascomycota (6), although in 29 descriptions, the fungal division could not be determined.

Morphotypes belonging to the Helotiaceae family (Ascomycota) showed plectenchymatous mantles or, exceptionally, no mantle, as seen in *Graffenrieda emarginata* from Ecuador (Haug et al. 2004). *Cenococcum*, the most cosmopolitan morphotype, showed a black plectenchymatous mantle forming a characteristically star-like pattern and frequently numerous black hyphae. Morphotypes belonging to the Tuberaceae family showed a pseudoparenchymatous mantle with irregular cells and awl-shaped cystidia.

Fungal families in the Basidiomycota were represented in ECM descriptions as follows: Amanitaceae (2), Atheliaceae (1), Bolbitiaceae (1), Boletaceae (4), Clavulinaceae (2), Cortinariaceae (11), Ramariaceae (1), Rhizopogonaceae (6), Russulaceae (10), Paxillaceae (3), Sebacinaceae (1), Suillaceae (1), Thelephoraceae (8), plus four supraspecific groups: Inocyboid (1), Russuloid (1), Thelephoroid (1), and Tomentelloid (1).

Boletoid rhizomorphs were present in most Boletaceae, Paxillaceae, Rhizopogonaceae, and Suillaceae ECM of Boletales families. In general, these morphotypes showed plectenchymatous mantles frequently with ring-like patterns and the presence of crystals.

Among the Russulaceae, and as Agerer (2006) states, russuloid rhizomorphs are combined with plectenchymatous mantles. Meanwhile, Russulaceae species with pseudoparenchymatous mantles do not form rhizomorphs at all.

ECM belonging to the Cortinariaceae family was characterized by an extramatrical organized mycelia and undifferentiated or slightly differentiated rhizomorphs, while ECM of the Thelephoraceae family was characterized by a heterogeneous mantle type assemblage (Agerer 2006). In this ECM, anatomotypes plectenchymatous and pseudoparenchymatous mantles were found. Different from Agerer (2006), the morphotype associated with *Amanita muscaria* (Amanitaceae) showed a plectenchymatous mantle, while the *Sebacina* sp. morphotype (Sebacinaceae) presented rhizomorphs.

The morphotypes of *Amphinema byssoides* (Atheliaceae), *Descolea anarctica* (Bolbitiaceae), and *Gautieria inapire* (Ramariaceae) show similar characteristics than those described by Agerer 2006.

2.4 Conclusion

Although more than 90% of terrestrial plants are associated with mycorrhizal fungi, and two-thirds of them are AM, ECM tree species are also notorious in South American forests. This review summarizes the ectomycorrhizal studies carried out in the neotropical ecozone and provides information about ECM fungi and their anatomical characteristics.

The analyzed studies reveal that most fungal symbionts are Basidiomycota, and that most studies on mycorrhizal status and ECM colonization deal with the Fagaceae, Fabaceae, Nyctaginaceae, and Polygonaceae families. Meanwhile, the three inoculum techniques (spores from sporocarps, culture mycelia, and natural soil) have been used for introduced trees (*Eucalyptus* spp., *Pinus* spp., and *Pseudotsuga menziesii*), whereas only spores and natural soil have been used for native species (*Nothofagus* spp. and *Alnus acuminata*). The associated fungi recorded in the 85 ECM anatomotypes reviewed were mostly Basidiomycota and a few Ascomycota, mostly found on native species (77%).

An important byproduct of this review is the realization of the existence of many gaps in the existing knowledge of ECM in South America. This suggests that mycorrhizologists should focus on little known/studied geographic areas, ecosystems, host trees, and fungal groups to reveal those aspects of the ECM symbiosis in South America, which may have practical applications in, for example, afforestation and environmental management programs. This knowledge may also be an important contribution to the conservation community, in a time when firsthand knowledge for urgent decisions is required.

Acknowledgments This work was supported by Conicet, Agencia de Promoción Científica y Tecnológica (PICT 438-2006), Secyt, and the National University of Córdoba. The authors wish to thank all other researchers whom through their continuous efforts contributed with the studies on which this review was based.

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Diversity and Biotechnology of Ectomycorrhizae

Rai, M.; Varma, A. (Eds.)

2011, XVI, 459 p., Hardcover

ISBN: 978-3-642-15195-8