Chapter 3
Climate Change, Biotechnology, and Mexican Neotropical Edible Ectomycorrhizal Mushrooms

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> *As for the future, it is not a question of predicting it,* but of making it possible
>
> Antoine de Saint-Exupéry, Citadelle (1948)

3.1 Rationale

Currently, we are living in a geological era called Anthropocene. This term was proposed in 2000 in a meeting in Mexico, by the Dutch chemist Paul Crutzen, winner of the Nobel Prize in Chemistry in 1995, and later on published along with the American biologist Eugene F. Stoermer (Crutzen and Stoermer 2000). The main reasons argued by these authors to propose this geological era were: the enormous increase of human population since the industrial revolution; the excessive use of fossil fuels whose production took hundreds of millions of years; the release of nitrous oxides associated with the combustion of this non-renewable energy sources; the excessive release of SO_2 to the atmosphere by coal and oil burning; the transformation of the land surface by human activities estimated by Lovelock (1992) to be of the order of 70%; the increase of the extinction rates of the species, e.g., from 1000 to 10,000 times in tropical rain forests estimated since more than two decades and a half ago to grow excessively (Wilson 1992); the increase of greenhouse gases into the atmosphere including mainly CO_2 by more than 30% (Vitousek et al. 1997) and CH_4 by even more than 100%; and the release of toxic substances such as chlorofluorocarbons capable of destroying atmospheric ozone. All these changes originated by human activity and the huge population explosion that has taken place from 790 million in 1750 to 7.7 billion people today (Population Matters 2019).

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After his proposal, the concept of Anthropocene has been analyzed on stratigraphic grounds, showing that the earth has suffered strong changes that have leaved a global stratigraphic signature distinct from that of Holocene or of previous Pleistocene interglacial phases, encompassing novel biotic, sedimentary, and geochemical changes (Zalasiewicz et al. 2008). Since its re-evaluation by Crutzen (2002), the concept has gained acceptance in the recent scientific literature (Chakraborty 2019; Svensen et al. 2019) and currently there is for example a scientific journal entitled *Anthropocene* that started in 2013, only devoted to research related with this topic (Anthropocene 2019).

The concept of Anthropocene is strongly linked with the biggest environmental problem that humankind faces currently: global change. Land use change, deforestation, destruction of natural ecosystems, and other human activities have contributed to a thousandfold increase in global extinctions in the Anthropocene compared to the presumed prehuman background rate, with negative profound effects on ecosystem functioning and service (Hooper et al. 2012; Rosenberg et al. 2019). Two iconic examples are the following: in a study over 27 years in Germany a midsummer decline of 82% of flying insect biomass was recorded (Hallmann et al. 2017), and it has been estimated that in the United States, the population of monarch butterflies fell by 80% in the last 20 years (Vidal and Rendón-Salinas 2014). These evidences have been the inception that the sixth Earth's mass extinction has already started (Barnosky et al. 2011). Despite the fact that it has been estimated that around 30% of the world's land area is covered by forests; they are being destroyed at an alarming rate. According to the World Bank, in 1990, the forested global area was 4128 million hectares and by 2015 this area had decreased to 3999 million hectares, i.e., between 1990 and 2015, the earth lost 1.3 million square kilometres of forest, which accounted for over 3% of the total forest area (FAO 2015; World Bank 2016). Deforestation is the major cause of loss of biodiversity, and therefore natural forest conservation is vital for stemming this loss (IPCC 2019). The distribution of the forests on earth is not homogeneous, ten countries hold around 90% of the primary forest of the world (FAO 2005). The decisions, actions, and success related with reforestation, afforestation, or establishment of forest plantations in these ten countries will be of paramount importance in the worldwide maintenance of the forest masses in the future. An iconic recent example of the interconnections of global change and deforestation occurs some months ago. One of the most important forested areas, and wildlife reservoirs worldwide is the Amazon, with an estimated 31 of primary forests of the planet (FAO 2005). According to satellite images, Brazil's National Institute for Space Research counted more than 41,000 "fire spots" between 1 January and 24 August last year (Escobar 2019) which might account for the largest deforestation in the last decades in Brazil, with an estimated loss of 6159 km^2, which is four times greater than those registered in 2010 (Mongabay 2019). Additionally, habitat loss are increasing the risks from zoonoses, including Ebola, Zika and COVID19 (Zohdy et al. 2019; Gropp 2020), which have had direct costs of more than US$100 billion, with that figure jumping to several trillion dollars if the outbreaks become human pandemics (UNEP 2016), like is happening now with COVID19.

Globally, Mexico ranks 8th in the ranking of native forests (FAO 2005). However, historically, the deforestation rates of the country have been one of the highest in the planet. For example, in the period from 1990 to 2005, Mexico lost an average of 318,000 hectares of forest annually. This loss represented one of the highest deforestation rates in the world, being exceeded from 1990 to 2010 only by Brazil, Indonesia, Sudan, Myanmar, Nigeria, and Tanzania (GFR 2010). As a consequence, Mexico currently presents serious environmental problems in terms of soil erosion and greenhouse gas emissions, the country occupying the 13th place in the latter category internationally according to Myers-Madeira (2008) and one of the first 12 Carbon dioxide emitting countries according to UNEP (2012) and Olivier et al. (2013). Mainly during the last decades, about 2 billion hectares of land have been degraded due to human activities. This constitutes about 15% of the total surface of the planet, which has affected more than 1200 million people. In the particular case of Mexico, it has been estimated that 71% of the country's soils are degraded, that is, 142 million of the country's 200 million hectares have physical, chemical, or biological degradation problems and 1.42 million hectares of soil are lost every year (Moncada de la Fuente et al. 2013). Reforestation, which emerge a solution to alleviate this problem, represents a complex challenge, which includes among other technical limitations, a low survival rate when trees are transplanted from greenhouse or nurseries to field. This survival is particularly dramatic for some species of enormous forest importance such as pines whose transplant survival rate varies from 0% to 20% in Mexico. This is particularly alarming because the country is one of the main centres of biodiversity of ectomycorrhizal trees with forest importance, including, for example, 176 species of *Quercus* (Valencia and Flores-Franco 2006) and 72 taxa of *Pinus* (Perry 1991). Additionally, the country has a large cultural diversity which includes 68 ethnic groups, each one with its own cosmovision, natural resources management, and traditional knowledge developed during millennia. As a consequence, the country holds one of the largest diversities of edible wild mushrooms worldwide, with more around 450 species consumed by the different ethnic groups and more than 5000 names used to designate them. This genetic diversity and ethnological traditional knowledge constitute one of the most important in the world (Pérez-Moreno et al. 2014) (Fig. 3.1). However, Mexico faces enormous challenges which include the change of land use, a quick acculturation process with the associated loss of traditional knowledge generated during millennia, and migration of young people from small communities to big cities. One of the reasons that explains the low rate of survival in the case of pine trees is the lack of ectomycorrhizal symbionts in the roots of most forest species produced in the greenhouse, whose presence is required when they grow in natural conditions. However, inoculation with ectomycorrhizal fungi has not been traditionally included in the production of pine trees in the country. Therefore, the biotechnological development of inoculation with trees of forest importance with ectomycorrhizal fungi is an urgent necessity in Mexico, in order to have successful reforestation. In this context, a criterion that has gained enormous importance in the selection of ectomycorrhizal symbionts is currently its edibility, due to the enormous social, economic, and environmental importance of ectomycorrhizal edible fungi in Mexico.

Fig. 3.1 Mexico is one the largest genetic and cultural reservoirs of edible ectomycorrhizal mushrooms. (**a**) *Pinus hartwegii* forest at 3800 masl; (**b**) *Turbinellus floccosus* a popular edible Fig. 3.1 (continued) mushroom in *Abies religiosa* forest; (**c**) "Hongueras" or mushrooms gatherers ready to start the recollection of wild edible mushrooms; (**d**) *Boletus edulis* s.l. one of the most appreciated mushrooms worldwide; (**e**) *Amanita basii*, one of the species belonging to the Caesar's mushroom complex in central Mexico

The mycorrhiza is a symbiosis that has played a key role in the structure and functioning of the land ecosystems. Actually, the colonization of the land was only possible with the combination of plants and its associated mycorrhizal fungi, according to fossil evidence from the Ordovicic and Devonic periods, around 460 million years ago (Remy et al. 1994; Redecker et al. 2000). Currently, one type of mycorrhiza called ectomycorrhiza plays a key role in the maintenance of the forest masses mainly in the low latitudes, high altitudes, and areas with low mineralization rates according to the recently coined "Read's rule" (Steidinger et al. 2019). These authors estimated that around 60% of tree stems on earth have their roots colonized by ectomycorrhizal fungi. The ectomycorrhiza is a widely distributed symbiosis around the planet mainly in boreal and temperate forests in the northern Hemisphere and also in some subtropical and tropical areas in South America, Africa, and Eastern Asia (Read and Perez-Moreno 2003). This symbiosis is established between around 8500 plants (Brundrett and Tedersoo 2018) and more than 20,000 fungal species (Comandini et al. 2012). Through this symbiosis, the forest trees are able to have access to mineral and organic nutrients, and water; and in exchange, they provide carbon compounds to their associated mutualistic mycorrhizal fungi (Smith and Read 2008). Recently, Chen et al. (2019) demonstrated for the first time that ectomycorrhizal symbiosis also play a key role in the control of root pathogens under field conditions, and therefore strongly influence the forest structure of subtropical forests in China, by suppressing the attack of pathogens, increasing the seedling survival rates, and therefore driving the species composition of forests ecosystems. Additionally, ectomycorrhizal symbionts increase the tolerance of host trees to drought, through the involvement of leaf membrane lipid metabolism and increased ability to maintain a stable chloroplast membrane functional integrity under water stress (Sebastiana et al. 2019). It has been demonstrated that ectomycorrhizal fungi also provide protection to their host to potentially toxic elements through a number of mechanisms including extracellular chelation by excreting di- and tricarboxylic acids or oxalic acids, cell wall binding mainly in the Hartig net and external mycelium, reduced uptake, and increased efflux of heavy metals and production of intracellular thiol-rich chelators, such as methallothioneins, glutathionines, phytochelatins, and compartmentation within vacuoles (Khullar and Reddy 2016, 2019; Kalsotra et al. 2018). Due to all of these advantages, countries with a forest tradition have usually incorporated mycorrhizal technologies into their production programs of forest trees. The main sources for ectomycorrhization have been either the use of mycelium or spores. In the case of spores, usually Gasteromycetes have been used, mainly included in the genera *Pisolithus*, *Rhizopogon*, and *Scleroderma* due to the huge amounts of spores that they produce (Charya and Garg 2019). However, the use of pilea of Agaricales and hymenium (which constitute the fertile part of the sporomes, containing the spores) of Boletales has received little attention worldwide. In this scenario, two decades ago, we decided to start a research line in order to produce controlled ectomycorrhized plants inoculated with native edible ectomycorrhizal fungi. The challenge was to generate a biotechnological innovation simple, efficient, and cheap. In this work, we present a synthesis of the advances of this biotechnology that has been developed during the last 20 years, describing the beneficial effects assessed in more than 100 combinations of ectomycorrhizal phytobionts and mycobionts and the future challenges in order to scale this biotechnology and produce controlled mycorrhized plants with reforestation, afforestation, forest plantations, and restauration of degraded areas in the country.

3.2 Summarized Analysis

More than two decades ago, we started in Colegio de Postgraduados some researches related to the controlled mycorrhization of trees native to Mexico by using mycelium of ectomycorrhizal fungi as a source of inoculum (Pérez-Moreno 1992). However, this biotechnology of inoculum production has the disadvantages of being expensive, requiring complex infrastructure, having a short shelf life and reduced genetic diversity, given that from the more than 20,000 species of known ectomycorrhizal fungi, only a small number has possibilities to be isolated in culture media. For these reasons, the possibility of generating a different alternative began to be a goal. Knowing that there was a whole body of knowledge related to the use of fungal spores of ectomycorrhizal Gasteromycetes mainly from species belonging to the genera *Pisolithus*, *Scleroderma*, and *Rhizopogon* as a source of inoculum (Lakshangy and Sandeep 2019; Repác 2011; Martin et al. 2003; Turjaman et al. 2005; García-Rodríguez et al. 2006; Castellano et al. 1985; Bruns et al. 2009), an alternative source of spores was searched. Studies were then started during the following years, first obtaining spore prints of Agaricales and Boletales, on sterilized paper, and then preparing solutions by adding sterile distilled water to inoculate trees with 10^6 to 10^8 spores per plant. Species of the genera *Amanita*, *Boletus*, *Cantharellus*, *Hebeloma*, *Helvella*, *Laccaria*, *Ramaria*, *Russula*, *Suillus*, and *Turbinellus* were mainly tested. In all cases, low or no ectomycorrhizal colonization were observed, independently of the evaluated host trees. From the beginning, the idea of generating a biotechnology fulfilling three criteria was raised: methodological simplicity, low cost, and high mycorrhization efficiency. This with the purpose of generating a useful technology for the mosaic of social, financial, and cultural conditions of nurseries in Mexico, where around 80% have only very basic infrastructure. Then we began to evaluate as a source of inoculum pilea of Agaricales and hymenia of Boletales, included in more than 20 genera. One of the criteria for selecting mycobionts was their edibility, due to the fact that Mexico constitutes one of the most important reservoirs of wild edible fungi worldwide, with more than 450 wild species of edible fungi (Fig. 3.1). Additionally, we used as selection criteria: pioneer species of ectomycorrhizal mushrooms, which grew in conditions of low fertility and which were abundant in inoculum banks in Mexican natural ecosystems (Obase et al. 2009; Ishida et al. 2008; Nara 2006; Garibay-Orijel et al. 2013). Since then, we have studied mainly 18 species of edible ectomycorrhizal mushrooms included in the genera *Hebeloma*, *Helvella*, *Laccaria*, and *Suillus* (Table 3.1). In the case of tree species, the investigations have been mainly focused in pine species native to

Table 3.1 Studied combinations of Mexican Neotropical trees inoculated with edible ectomycorrhizal mushrooms and their growth effect in terms of shoot, root, and total biomass under greenhouse conditions

Cn	Host plant	Mycobiont species	Growth effects				Reference
			Shoot	Root	Total	Stem diameter	
1	*Abies religiosa* (Kunth) Schltdl. et. Cham.	*Inocybe splendens* R. Heim*	+++	+	++	++	Sandoval (2010)
2	***A. religiosa***	***Laccaria proxima* (Boud.) Pat.**	+++	++	+++	++	Ramírez (2018)
3	*A. religiosa*	*Suillus brevipes* (Peck) Kuntze	++	+	+	++	Sandoval (2010)
4	***Pinus arizonica* Engelm.**	***L. proxima***	+++	+++	+++	++	Cortés (2019)
5	***P. arizonica***	***L. proxima***	++	++	+	++	Cruz-Ibáñez et al. (2019)
6	***P. ayacahuite* Ehrenb. ex Schltdl.**	***Hebeloma mesophaeum* (Pers.) Quél.**	++	++	++	–	Arteaga-León (2014); Arteaga-León et al. (2018)
7	***P. ayacahuite***	***Helvella* cf. *lacunosa* Afzel.**	++	++	++	–	Arteaga-León (2014); Arteaga-León et al. (2018)
8	***P. cembroides* Zucc.**	***L. proxima***	+	+	+	–	Zuñiga (2018)
9	***P. cembroides***	***L. proxima* (+ *Cohnella* sp.)**	+++	+++	+++	++	Zuñiga (2018)
10	***P. durangensis* Ehren**	***L. laccata* (Scop.) Cooke**	Nd	Nd	+++	+++	Luciano et al. (2018b)
11	***P. durangensis***	***L. proxima***	++	+++	++	++	Cruz-Ibáñez et al. (2019)
12	***P. durangensis***	***L. proxima***	Nd	Nd	++	++	Rosales-Sánchez et al. (2017)
13	***P. greggii* Engelm.**	***Amanita rubescens* Pers.**	+++	+++	+++	+++	Cruz-Ibáñez et al. (2018)
14	***P. greggii***	***Boletus clavipes [= B. edulis* Bull.*]***	++	+	++	+++	Carrera (2004)

(continued)

Table 3.1 (continued)

Cn	Host plant	Mycobiont species	Growth effects				Reference
			Shoot	Root	Total	Stem diameter	
15	***P. greggii***	***H. leucosarx* P.D. Orton**	+++	+++	+++	+++	Rentería-Chávez et al. (2017)
16	***P. greggii***	***H. mesophaeum***	Nd	Nd	+++	+++	Carrasco (2014)
17	***P. greggii***	***H. mesophaeum***	+++	+++	+++	+++	Martínez-Reyes et al. (2012)
18	***P. greggii***	***H. mesophaeum***	++	++	++	Nd	Pérez-Moreno et al. (2009)
19	***P. greggii***	***H. mesophaeum* + *L. bicolor* + *S. pseudobrevipes***	++	++	++	Nd	Pérez-Moreno et al. (2009)
20	***P. greggii***	***H. mesophaeum* s.l.**	+++	++	+	+	Méndez-Neri et al. (2011)
21	***P. greggii***	***H. mesophaeum* s.l. + *L. laccata* s.l. + *S.* cf. *pseudobrevipes***	+++	++	+	+	Méndez-Neri et al. (2011)
22	***P. greggii***	***L. bicolor* (Maire) P.D. Orton**	++	+	++	Nd	Pérez-Moreno et al. (2009)
23	***P. greggii***	***L. bicolor***	+++	++	+++	++	Rentería-Chávez et al. (2017)
24	***P. greggii***	***L. laccata***	++	+	++	+++	Carrera (2004)
25	***P. greggii***	***L. laccata***	+++	++	+++	++	Rentería-Chávez et al. (2017)
26	***P. greggii***	***L. laccata* s.l.**	+++	+	+	+	Méndez-Neri et al. (2011)
27	***P. greggii***	***L. proxima***	Nd	Nd	+++	+++	Carrasco (2014)
28	***P. greggii***	***L. proxima***[a]	+++	+++	+++	++	Cortés (2019)
29	***P. greggii***	***L. proxima***[b]	+++	+++	+++	++	Cortés (2019)

30	***P. greggii***	***L. proxima***[c]	+++	+++	+++	++	Cortés (2019)
31	***P. greggii***	***L. proxima***[a]	–	+	–	+	Morales-Rivera (2017)
32	***P. greggii***	***L. proxima***[b]	–	++	++	+	Morales-Rivera (2017)
33	***P. greggii***	***L. proxima***[c]	–	–	–	–	Morales-Rivera (2017)
34	***P. greggii***	***Morchella* sp.**	+++	+++	+++	+++	Cruz-Ibáñez et al. (2018)
35	***P. greggii***	***S. brevipes***	Nd	Nd	+++	+++	Carrasco (2014)
36	***P. greggii***	***S. brevipes* + *L. proxima* + *H. mesophaeum***	Nd	Nd	+++	+++	Carrasco (2014)
37	***P. greggii***	***S. pseudobrevipes* A.H. Sm. and Thiers**	++	++	++	+++	Carrera (2004)
38	***P. greggii***	***S. pseudobrevipes***	+	-	+	++	Flores-Armas (2017)
39	***P. greggii***	***S.* cf. *pseudobrevipes***	+++	++	+	+	Méndez-Neri et al. (2011)
40	***P. greggii***	***S. pseudobrevipes***	++	+	++	Nd	Pérez-Moreno et al. (2009)
41	***P. greggii***	***S. pungens* Thiers and A.H. Sm.**	Nd	Nd	+++	+++	Luciano et al. (2018b)
42	***P. greggii***	***S. pungens***[d]	+++	+++	+++	+++	Ortiz-Lopez (2019)
43	***P. greggii***	***S. pungens***[e]	+++	+++	+++	+++	Ortiz-Lopez (2019)
44	***P. greggii***	***S. pungens***	Nd	Nd	+++	+++	Ortiz-Lopez et al. (2018)
45	***P. hartwegii* Lindl.**	***Clavulina* cf. *cinerea* (Bull.) J. Schröt.**	++	++	++	++	Perea-Estrada et al. (2009)
46	***P. hartwegii***	***Hebeloma* sp.**	++	++	++	+	Perea-Estrada et al. (2009)
47	*P. hartwegii*	*I. splendens∗*	–	+	-	+	Nuñez (2013)
48	*P. hartwegii*	*I. splendens∗*	++	+	+	++	Sandoval (2010)
49	***P. hartwegii***	***L. bicolor***	Nd	Nd	+++	+++	Lazo-Montaño et al. (2018)
50	***P. hartwegii***	***L. laccata***	Nd	Nd	+++	+++	Lazo-Montaño et al. (2018)

(continued)

Table 3.1 (continued)

Cn	Host plant	Mycobiont species	Growth effects				Reference
			Shoot	Root	Total	Stem diameter	
51	***P. hartwegii***	***Laccaria* sp.**	++	+++	+++	++	Perea-Estrada et al. (2009)
52	*P. hartwegii*	*S. brevipes*	–	+	–	+	Nuñez (2013)
53	*P. hartwegii*	*S. brevipes*	++	++	++	++	Sandoval (2010)
54	***P. hartwegii***	***S. pungens***	Nd	Nd	+++	++	Lazo-Montaño et al. (2019)
55	***P. maximartinezii* Rzedowski**	***Helvella lacunosa* Afzel.**	+	++	+	+	Almaraz (2019)
56	***P. maximartinezii***	***H. lacunosa* (+ *Azospirillum brasilense*)**	+	+	+	+	Almaraz (2019)
57	***P. maximartinezii***	***L. proxima***	++	++	++	+	Almaraz (2019)
58	***P. maximartinezii***	***L. proxima***	+	+	+	+	Fuentes and Garzón (2017)
59	***P. maximartinezii***	***L. proxima* (+ *A. brasilense*)**	+	++	+	+	Almaraz (2019)
60	***P. maximartinezii***	***S. tomentosus* Singer**	+	+	+	+	Fuentes and Garzón (2017)
61	***P. montezumae* Lamb.**	***H. mesophaeum***	+++	+++	+++	+++	Barragán-Soriano et al. (2018)
62	***P. oaxacana* Mirov.**	***L. trichodermophora* G.M. Muell.**	+++	+++	+++	+++	Hernández (2016)
63	***P. patula* Schl. et Cham**	***Amanita caesarea* (Scop.) Pers.**	+	+	+	+	Carrera (2004)
64	***P. patula***	***A. fulva* Fr.**	+	+	+	++	Carrera (2004)
65	***P. patula***	***B. clavipes* [= *B. edulis*]**	++	+	++	++	Carrera (2004)
66	***P. patula***	***B. clavipes* [= *B. edulis*]**	+++	+++	+++	+++	Carrera (2004)
67	***P. patula***	***C.* cf. *cinerea***	–	+	–	+	Perea-Estrada et al. (2009)
68	***P. patula***	***Hebeloma alpinum* (J. Favre) Bruchet**	+++	+++	+++	++	Carrasco-Hernández et al. (2011)

69	***P. patula***	***H. leucosarx***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
70	***P. patula***	***H. mesophaeum***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
71	***P. patula***	***H. mesophaeum + H. alpinum + H. leucosarx***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
72	***P. patula***	**_Hebeloma_ sp.**	++	++	++	+	Perea-Estrada et al. (2009)
73	***P. patula***	***L. bicolor***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
74	***P. patula***	***L. laccata***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
75	***P. patula***	***L. laccata + L. bicolor + L. proxima***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
76	***P. patula***	***L. laccata + L. bicolor + L. proxima. + H. mesophaeum + H. alpinum + H. leucosarx***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
77	***P. patula***	***L. proxima***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
78	***P. patula***	**_Laccaria_ sp.**	+++	++	++	+	Perea-Estrada et al. (2009)
79	***P. patula***	**_S. granulatus_ (L.) Roussel**	+	+	+	+	Carrera (2004)
80	***P. patula***	***S. pseudobrevipes***	+++	++	+++	++	Carrera (2004)
81	**_P. pringlei_ Shaw**	***H. alpinum***	+++	+++	+++	++	López-Gutiérrez et al. (2018)
82	***P. pringlei***	***L. trichodermophora***	+++	+++	+++	++	López-Gutiérrez et al. (2018)
83	**_P. pseudostrobus_ Lindl.**	***H. alpinum***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
84	***P. pseudostrobus***	***H. leucosarx***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)

(continued)

Table 3.1 (continued)

Cn	Host plant	Mycobiont species	Growth effects				Reference
			Shoot	Root	Total	Stem diameter	
85	***P. pseudostrobus***	***H. mesophaeum***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
86	***P. pseudostrobus***	***H. mesophaeum***	++	++	++	Nd	Pérez-Moreno et al. (2009)
87	***P. pseudostrobus***	***H. mesophaeum* + *H. alpinum* + *H. leucosarx***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
88	***P. pseudostrobus***	***H. mesophaeum* + *L. bicolor* + *S. pseudobrevipes***	++	++	++	Nd	Pérez-Moreno et al. (2009)
89	***P. pseudostrobus***	***H. mesophaeum* s.l.**	+++	+++	++	++	Méndez (2007)
90	***P. pseudostrobus***	***H. mesophaeum* s.l. + *L. laccata* s.l. + *S.* cf. *pseudobrevipes***	++	+	–	–	Méndez (2007)
91	***P. pseudostrobus***	***L. bicolor***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
92	***P. pseudostrobus***	***L. bicolor***	+	+	+	Nd	Pérez-Moreno et al. (2009)
93	***P. pseudostrobus***	***L. laccata***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
94	***P. pseudostrobus***	***L. laccata* + *L. bicolor* + *L. proxima***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
95	***P. pseudostrobus***	***L. laccata* + *L. bicolor* + *L. proxima* + *H. mesophaeum* + *H. alpinum* + *H. leucosarx***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
96	***P. pseudostrobus***	***L. laccata* s.l.**	+	–	+	+	Méndez (2007)
97	***P. pseudostrobus***	***L. proxima***	+++	+++	+++	++	Carrasco-Hernández et al. (2011)
98	***P. pseudostrobus***	***L. proxima***	+++	+++	+++	+++	Jiménez (2011)

99	***P. pseudostrobus***	***S.* cf. *pseudobrevipes***	++	++	+	+	Méndez (2007)
100	***P. pseudostrobus***	***S. pseudobrevipes***	++	+	+	+	Flores-Armas (2017)
101	***P. pseudostrobus***	***S. pseudobrevipes***	+	++	++	Nd	Pérez-Moreno et al. (2009)
102	***P. teocote* Schiede ex Schltdl.**	***L. laccata***	Nd	Nd	+++	+++	Luciano et al. (2018b)
103	***P. teocote***	***L. proxima***	Nd	Nd	+++	+++	Luciano et al. (2018b)
104	***Quercus castanea* Née**	***L. trichodermophora***	+++	+++	+++	+++	Hernández (2016)

Cn = combination number; ∗Recorded as edible in India (Sharma and Gautam 2015); − = no increase; + = increase from 0% to 30%; ++ = increase from 31% to 60%; +++ = increase >60%; all of the increases compared with non-inoculated plants. Nd = No data; Inoculation dose of ^{a}1, ^{b}2, and ^{c}3 g. Inoculation with hymenia of mature^{d} and young^{e} basidiomata. The nomenclature of scientific names for fungi is based on Index Fungorum (2019) and for forest species in USDA database (2019). Scientific names in bold type correspond to experiments carried out in Colegio de Postgraduados under the supervision of the authors of this chapter. Some of these contributions have been published and others are currently in the form of Thesis, and their formal publications are in the process of being completed.

Mexico useful for reforestation, plantation establishment, and restoration of degraded areas. To date, 19 tree species have been evaluated: 16 from *Pinus*, 1 from *Abies*, and 2 from *Quercus* distributed along the north, centre, and southeast of the country. Research has also been conducted on species that are threatened according to the International Union for Conservation of Nature (IUCN) such as *Pinus maximartinenzii* and *P. chiapensis*. Special attention has been focused on *Pinus greggii* which is a fast-growing tree species, adapted to drought, and one of the Mexican pine species with the greatest potential in reforestation programs (e.g., Martínez-Reyes et al. 2012; Méndez-Neri et al. 2011; Ramírez-Herrera et al. 2005). Interestingly, this species is also found in the red list of the IUCN which is considered as vulnerable (Farjon 2013).

After more than two decades of research, a technological package has been generated that meets the requirements set out from the beginning. Ground pilea have been used, as a source of inoculum, or hymenia of mushrooms with short shelf life as *Suillus* species (e.g., Flores-Armas 2017). Subsequently, these pilea are dried and ground before being used. Despite the fact that storage at 4 °C maintain a certain viability for up to 1 or 2 years, the optimal condition is their use as soon as possible, not more than 6–9 months after their preparation. Additionally, slurries have been used successfully, in which case, it is required to have the plants ready to inoculate. For the elaboration of this latter type of inoculum, fresh pilea are cut from their stipes or hymenia are separated from their contexts in the case of fungi with short shelf lives, and subsequently they are ground along with distilled sterile water (Figs. 3.2 and 3.3). The shelf life of these solutions is variable, but in general terms, it is very short, varying from 1 week to 2 months depending on the species involved. The advantages of these techniques in relation to the use of mycelial inoculation are the following: (1) inoculum preparation is cheap and efficient; (2) the genetic diversity involved is large; (3) inoculums prepared with these techniques include microbiomes that are naturally associated with sporomes; and (4) the methodological simplicity for the elaboration of these inoculums allows a wide use in a range of rustic nursery conditions.

In general terms, there has been a beneficial effect both in terms of growth of the shoots, roots, total biomass, and stem diameter in the inoculated plants (Fig. 3.4). Table 3.1 summarizes the results obtained in terms of growth as a result of ectomycorrhizal inoculation using inoculum sources prepared with the described methodologies. In most cases, there have been beneficial effects on inoculated plants, over 60% in growth variables compared to non-inoculated plants, mainly in *Pinus arizonica*, *P. cembroides*, *P. greggii*, *P. montezumae*, *P. oaxacana*, *P. patula*, *P. pringlei*, and *P. pseudostrobus*. In other cases, there have been modest increases in growth, from 30% to 60%, and in very few cases, there has been low or no beneficial effect, e.g. in *Pinus hartwegii*, *P. leiophylla*, *P. montezumae*, *P. pseudostrobus*, *P. rudis*, and *P. teocote* inoculated with some mycobionts. However, even these tree species have shown beneficial effects when they are inoculated with the proper mycobionts, which demonstrate variations in terms of genetic compatibility depending on the different phytobiont–mycobiont combinations. Our research has also included the study of increases in nutritional terms to the shoot, root, and total plants as a result of inoculation (Table 3.2). Differential increases have been demonstrated depending

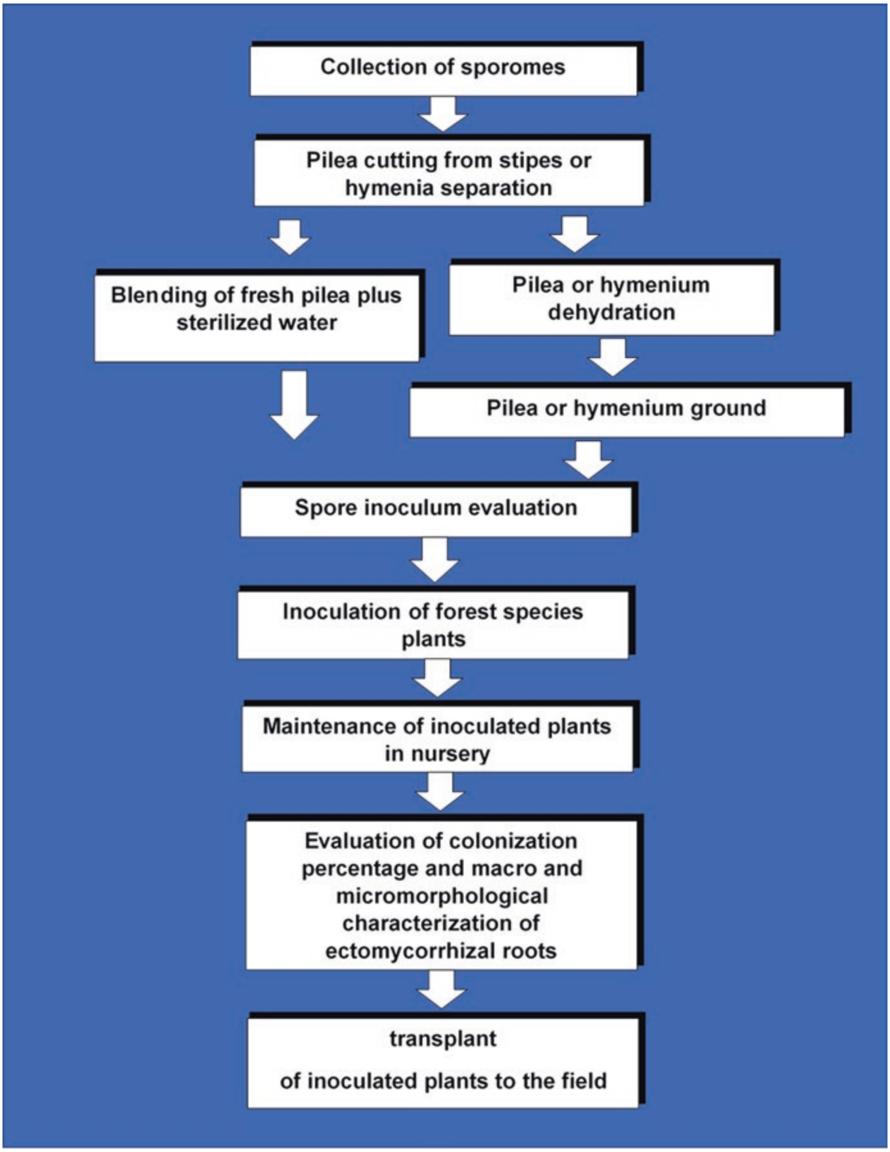

Fig. 3.2 General protocol used to produce ectomycorrhizal inoculum by using fresh or dried pilea or hymenium of edible Agaricales and Boletales

on the combinations for both macronutrients (N, P, K, Ca, and Mg) and micronutrients (Mn, Fe, Zn, Cu, B, and Na). In some cases, these increases have reached values greater than 60% compared to non-inoculated plants, for example, in the case of *Pinus pringlei* with *Hebeloma alpinum*, these increases were recorded in 9 of 10 nutrients evaluated, demonstrating enormous efficiency in terms of nutritional

Fig. 3.3 Production of ectomycorrhizal inoculum. (**a**) Pilea of *Laccaria* spp.; (**b**) Dried and ground pilea of *Laccaria* spp. ready to be used as inoculum; (**c**) Slurries of *Laccaria proxima* (left) and *Suillus pseudobrevipes* (right) ready to be used as inoculum; (**d**) General view of experiments in greenhouse using different combinations of pine and ectomycorrhizal mushroom species

Fig. 3.4 Beneficial effect of inoculation with ectomycorrhizal inoculum. (**a**) *Pinus greggii* inoculated with *Hebeloma mesophaeum* and *Laccaria laccata* compared with non-inoculated plants. (**b**) *Quercus castanea* with (left) or without (right) *Hebeloma mesophaeum*; (**c**) *Pinus greggii* with (left) or without (right) *Amanita rubescens*; (**d**) *Pinus hartwegii* with (left) or without (right) *Suillus pungens*; (**e**) Bioassays with 15 pine species inoculated with different Agaricales and Boletales

transfer in this specific combination (López-Gutiérrez et al. 2018). In general terms worldwide, there is a shortage of studies related to micronutrient transfer as a result of ectomycorrhizal inoculation and this should be a research area that deserved more attention, due to the enormous importance of micronutrients in the physiology and metabolism of trees of forest importance.

Table 3.2 Effect on nutrient contents of ectomycorrhizal combinations of Mexican Neotropical trees, including as a source of inoculum edible wild mushrooms

			Macronutrients					Micronutrients						Reference
No	Host plant	Mycobiont	N	P	K	Ca	Mg	Mn	Fe	Zn	Cu	B	Na	
1	***Abies religiosa* (Kunth) Schltdl. et. Cham.**	***Laccaria proxima* (Boud.) Pat.**	+++	+++	+++	+++	+++	++	++	+++	+++	Nd	+++	Ramírez (2018)
2	***Pinus arizonica* Engelm.**	***L. proxima***	+++	+++	+++	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Cortés (2019)
3	***P. ayacahuite* Ehrenb. ex Schltdl.**	***Hebeloma mesophaeum* (Pers.) Quél.**	++	++	+	++	++	+	–	Nd	Nd	Nd	Nd	Arteaga-León et al. (2018)
4	***P. ayacahuite***	***Helvella* cf. *lacunosa* Afzel.**	++	++	+	+	+	+	++	Nd	Nd	Nd	Nd	Arteaga-León et al. (2018)
5	***P. cembroides* Zucc**	***L. proxima***	++	++	+		+	+	++	++	+	Nd	Nd	Zuñiga (2018)
6	***P. greggii* Engelm.**	***H. leucosarx* P.D. Orton**	+++	+++	+++	+++	+++	-	+++	+++	+++	+++	+++	Rentería-Chávez et al. (2017)
7	***P. greggii***	***H. mesophaeum***	+++	+++	+++	+++	+++	Nd	Nd	Nd	Nd	Nd	Nd	Martínez-Reyes et al. (2012)
8	***P. greggii***	***H. mesophaeum***	+++	+++	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Pérez-Moreno et al. (2009)
9	***P. greggii***	***H. mesophaeum* + *L. bicolor* + *S. pseudobrevipes* A. H. Sm. and Thiers**	+++	++	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Pérez-Moreno et al. (2009)
10	***P. greggii***	***L. bicolor* (Maire) P.D. Orton**	++	++	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Pérez-Moreno et al. (2009)
11	***P. greggii***	***L. bicolor***	+++	+++	+++	+++	+++	–	+++	+++	+++	+++	++	Rentería-Chávez et al. (2017)
12	***P. greggii***	***L. laccata* (Scop.) Cooke**	+++	+++	+++	+++	+++	–	+++	+++	+++	+++	+++	Rentería-Chávez et al. (2017)
13	***P. greggii***	***L. proxima***^{a}	+++	+++	+++	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Cortés (2019)
14	***P. greggii***	***L. proxima***^{b}	+++	+++	+++	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Cortés (2019)
15	***P. greggii***	***L. proxima***^{c}	+++	+++	+++	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Cortés (2019)
16	***P. greggii***	***Suillus pseudobrevipes***	+++	+	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Pérez-Moreno et al. (2009)

17	***P. greggii***	***S. pungens* Thiers and A.H. Sm.**[d]	+++	+++	+++	Nd	Nd	+++	+++	Nd	+++	Nd	Nd	Ortiz-Lopez (2019)
18	***P. greggii***	***S. pungens***[e]	+++	+++	+++	Nd	Nd	+++	+++	Nd	+++	Nd	Nd	Ortiz-Lopez (2019)
19	***P. maximartinezii* Rzedowski**	***Helvella lacunosa***	++	++	+	Nd	Nd	Nd	+	++	Nd	Nd	++	Almaraz (2019)
20	***P. maximartinezii***	***H. lacunosa* (+ *Azospirillum brasilense*)**	+	++	++	Nd	Nd	Nd	+	++	Nd	Nd	+++	Almaraz (2019)
21	***P. maximartinezii***	***L. proxima***	++	++	++	Nd	Nd	Nd	–	++	Nd	Nd	+	Almaraz (2019)
22	***P. maximartinezii***	***L. proxima* (+ *A. brasilense*)**	+	++	++	Nd	Nd	Nd	–	+	Nd	Nd	++	Almaraz (2019)
23	***P. montezumae* Lamb.**	***H. mesophaeum***	+++	+++	+++	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Barragán-Soriano et al. (2018)
24	***P. oaxacana* Mirov.**	***L. trichodermophora* G.M. Muell.**	+++	+++	+++	+++	+++	+++	+++	++	++	+++	Nd	Hernández (2016)
25	***P. pringlei* Shaw**	***L. trichodermophora***	+++	+++	+++	+++	+++	+++	+++	+++	–	+++	Nd	López-Gutiérrez et al. (2018)
26	***P. pringlei***	***H. alpinum* (J. Favre) Bruchet**	+++	+++	+++	+++	+++	+++	+++	+++	–	+++	Nd	López-Gutiérrez et al. (2018)
27	***P. pseudostrobus* Lindl.**	***H. mesophaeum***	++	++	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Pérez-Moreno et al. (2009)
28	***P. pseudostrobus***	***H. mesophaeum* + *L. bicolor* + *S. pseudobrevipes***	++	+++	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Pérez-Moreno et al. (2009)
29	***P. pseudostrobus***	***L. bicolor***	++	++	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Pérez-Moreno et al. (2009)
30	***P. pseudostrobus***	***S. pseudobrevipes***	++	++	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Nd	Pérez-Moreno et al. (2009)
31	***Quercus castanea* Née**	***L. trichodermophora***	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	Nd	Hernández (2016)

No = Combination number; – = no increase; + = increase from 0% to 30%; ++ = increase from 31% to 60%; +++ = increases >60%; all of the increases compared with non-inoculated plants. Nd = No data. Inoculation dose of [a]1, [b]2, and [c]3 g. Inoculation with hymenia of mature[d] and young [e] basidiomata. The nomenclature of scientific names for fungi was based on Index Fungorum (2019) and for forest species in USDA database (2019). Experiments of all combinations were carried out in Colegio de Postgraduados under the supervision of the authors of this chapter. Some of these contributions have been published and others are currently in the form of thesis, and their formal publications are in the process of being completed.

In recent years, we have been carrying out studies related to the influence of ectomycorrhizal inoculation on physiological variables including photosynthetic rate, chlorophyll a, b, and total contents, as well as carotenes (Table 3.3). The evaluation of these variables is essential for the understanding of a complex phenomenon that can explain the reasons why there have been increases in growth in the associated hosts. Another area of enormous importance is the coinoculation of ectomycorrhizal fungi with plant growth promoting bacteria. It has been shown that the co-inoculation of these groups of microorganisms has caused synergism in plant growth, nutritional transfer, and physiological quality of host plants, for example, in combinations of *Pinus cembroides* with *Laccaria proxima* plus the N-fixing bacteria *Cohnella* (Zuñiga 2018) and *Pinus montezumae* with *Hebeloma mesophaeum* plus the phosphate-solubilizing bacteria *Azospirillum brasilense* (Barragán-Soriano et al. 2018). In order to verify that the beneficial effects recorded in terms of plant growth, nutritional increases, and improvement in the physiological quality of inoculated plants, detailed studies of colonization percentages have been carried out in all bioassays (Table 3.4). Although there have been variations in these colonizations, in most cases, they have been greater than 60%, reaching up to 100%, which has demonstrated the effectiveness of the biotechnology (Fig. 3.5). In recent years, field studies have begun, transplanting ectomycorrhizal and non-ectomycorrhizal trees (Table 3.5). In most cases, non-ectomycorrhizal trees have had very low survival rates ranging from 0% to 20%, similar to those recorded historically in Mexico. In contrast, in the case of bioassays using controlled ectomycorrhizal trees, higher survival rates have been recorded depending on the combinations evaluated. In some cases, the survival rates of ectomycorrhizal plants have been around 85%, for example, in the cases of *Pinus greggii* inoculated with *Suillus brevipes* (Luciano 2018), with *S. pseudobrevipes* (Luciano et al. 2018c), with *S. pungens* (Cardoso 2017), and *P. hartwegii* with *S. brevipes* (Nuñez 2013). Interestingly, when co-inoculations have been performed, synergistic results have been observed, for example in the case of *P. greggii* co-inoculated with *H. mesophaeum* + *L. bicolor* + *S. pseudobrevipes* (Pérez-Moreno et al. 2009).

The presence of abundant ectomycorrhizal external mycelium, which is the structure responsible for nutritional translocation, has often been observed in the experiments associated with high mycorrhization. Additionally, sporome formation of ectomycorrhizal fungi, mainly species of the *Laccaria* and *Hebeloma* genera, has been frequently recorded (Fig. 3.6). And in the case of field experiments, the first Neotropical ectomycorrhizal fungus *Suillus pseudobrevipes* and *S. pungens* has begun, with the initial production of sporomes, which has started as early as after 2 years of transplantation (Fig. 3.7).

3.3 Conclusions

An innovating biotechnology using the pilea or the hymenium of Agaricales or Boletales as a source of inoculum developed in Mexico, during the last two decades is presented. The pilea and the hymenia of sporomes are a suitable source for the

Table 3.3 Effect on physiological variables of Mexican neotropical trees ectomycorrhizal combinations, under greenhouse conditions

No	Host plant	Mycobiont	Photosynthetic rate	Cholorophyll contents			Carotens	Reference
				a	b	Total		
1	***Pinus arizonica* Engelm.**	***Laccaria proxima* (Boud.) Pat.**	++	+++	+++	+++	+++	Cortés (2019)
2	***P. cembroides* Zucc.**	***L. proxima***	++	++	++	++	+++	Zuñiga (2018)
3	***P. cembroides***	***L. proxima* (+ *Cohnella* sp.)**	+++	++	++	++	+++	Zuñiga (2018)
4	***P. greggii* Engelm.**	***L. proxima***[a]	+++	+++	+++	+++	+++	Cortés (2019)
5	***P. greggii***	***L. proxima***[b]	+++	+++	+++	+++	+++	Cortés (2019)
6	***P. greggii***	***L. proxima***[c]	+++	+++	+++	+++	+++	Cortés (2019)
7	***P. greggii***	***Suillus pungens* Thiers and A.H. Sm**[d]	+++	++	+	++	+++	Ortiz-Lopez (2019)
8	***P. greggii***	***S. pungens***[e]	+++	++	++	++	++	Ortiz-Lopez (2019)
9	***P. montezumae* Lamb.**	***Hebeloma mesophaeum* (Pers.) Quél.**	+++	+	+	+	+	Barragán-Soriano et al. (2018)
10	***P. montezumae***	***H. mesophaeum* (+ *Azospirillum brasilense*)**	+++	+	+	+	+	Barragán-Soriano et al. (2018)

No = Combination number; + = increase from 0% to 30%; ++ = increase from 31% to 60%; +++ = increases >60%; all of the increases compared with non-inoculated plants. Inoculation dose of [a]1, [b]2, and [c]3 g. Inoculation with hymenia of young[d] and mature basidiomata[e]. The nomenclature of scientific names for fungi was based on the Index Fungorum (2019) and for the forest species in USDA database (2019). Experiments of all combinations were carried out in Colegio de Postgraduados under the supervision of the authors of this chapter. Some of these contributions have been published and others are currently in the form of thesis, and their formal publications are in the process of being completed

Table 3.4 Effect on colonization rates in evaluated Mexican neotropical ectomycorrhizal combinations, under greenhouse conditions, using a source of inoculum either edible ectomycorrhizal mushrooms

No	Host plant	Mycobiont	Colonization rate	Reference
1	*Abies religiosa* (Kunth) Schltdl. et. Cham.	*Inocybe splendens* R. Heim*	+	Sandoval (2010)
2	***A. religiosa***	***Laccaria proxima* (Boud.) Pat.**	+++	Ramírez (2018)
3	***Pinus arizonica* Engelm**	***L. proxima***	++	Cruz-Ibáñez et al. (2019)
4	***P. arizonica***	***L. proxima***	+++	Cortés (2019)
5	***P. ayacahuite* Ehrenb. ex Schltdl.**	***Hebeloma alpinum* (J. Favre)**	+	Carrera-Martínez et al. (2017)
6	***P. ayacahuite***	***Suillus luteus* (L. Fries) Gray**	+	Carrera-Martínez et al. (2017)
7	***P. ayacahuite***	***S. granulatus***	+	Santiago-Hernández et al. (2017)
8	***P. cembroides Zucc.***	***L. proxima***	++	Pérez-Téllez et al. (2017)
9	***P. cembroides***	***Hebeloma leucosarx* P.D. Orton**	++	Pérez-Téllez et al. (2017)
10	***P. cembroides***	***L. proxima***	++	Zuñiga (2018)
11	***P. cembroides***	***L. proxima* (+ *Cohnella* sp.)**	+++	Zuñiga (2018)
12	***P. chiapensis* (Martínez) Andresen**	***L. proxima***	++	Caballero (2019)
13	***P. chiapensis***	***Ramaria* sp.**	+++	Caballero (2019)
14	***P. chiapensis***	***Suillus pseudobrevipes* A.H. Sm. and Thiers**	+++	Caballero (2019)
15	***P. durangensis* Ehren**	***L. laccata* (Scop.) Cooke**	+++	Luciano et al. (2018b)
16	***P. durangensis***	***L. proxima***	++	Cruz-Ibáñez et al. (2019)
17	***P. engelmannii* Carr.**	***L. proxima***	+++	Ríos-García et al. (2017a)
18	*P. engelmannii*	*Russula delica* Fr.	+++	Martínez-Nevárez et al. (2016)
19	***Pinus greggii* Engelm.**	***Amanita rubescens* Pers.**	+++	Cruz-Ibáñez et al. (2018)
20	***P. greggii***	***Boletus clavipes [= B. edulis* Bull.*]***	+	Carrera (2004)
21	***P. greggii***	***Hebeloma leucosarx* P.D. Orton**	+++	Rentería-Chávez et al. (2017)
22	***P. greggii***	***H. mesophaeum* (Pers.) Quél.**	+++	Martínez-Reyes et al. (2012)
23	***P. greggii***	***H. mesophaeum* s.l.**	+++	Méndez-Neri et al. (2011)

24	***P. greggii***	***H. mesophaeum***	++	Pérez-Moreno et al. (2009)
25	***P. greggii***	***H. mesophaeum***	+++	Villegas (2014)
26	***P. greggii***	***H. mesophaeum* + *L. bicolor* + *S. pseudobrevipes***	++	Pérez-Moreno et al. (2009)
27	***P. greggii***	***H. mesophaeum* s.l. + *L. laccata* s.l. + *S.* cf. *pseudobrevipes***	++	Méndez-Neri et al. (2011)
28	***P. greggii***	***L. bicolor* (Maire) P.D. Orton**	++	Pérez-Moreno et al. (2009)
29	***P. greggii***	***L. bicolor***	+++	Rentería-Chávez et al. (2017)
30	***P. greggii***	***L. laccata***	++	Carrera (2004)
31	***P. greggii***	***L. laccata* s.l.**	+++	Méndez-Neri et al. (2011)
32	***P. greggii***	***L. laccata***	+++	Rentería-Chávez et al. (2017)
33	***P. greggii***	***L. laccata***	+++	Villegas (2014)
34	***P. greggii***	***L. proxima***	+++	Díaz-Balbuena (2017); Franco-Ramírez et al. (2019)
35	***P. greggii***	***L. proxima***[a]	+++	Cortés (2019)
36	***P. greggii***	***L. proxima***[b]	+++	Cortés (2019)
37	***P. greggii***	***L. proxima***[c]	+++	Cortés (2019)
38	***P. greggii***	***L. proxima***[a]	+	Morales-Rivera (2017)
39	***P. greggii***	***L. proxima***[b]	++	Morales-Rivera (2017)
40	***P. greggii***	***L. proxima***[c]	++	Morales-Rivera (2017)
41	***P. greggii***	***Morchella* sp.**	+++	Cruz-Ibáñez et al. (2018)
42	***P. greggii***	***S. brevipes* (Peck) Kuntze**	+++	Luciano (2018)
43	***P. greggii***	***S.* cf. *pseudobrevipes***	+++	Méndez-Neri et al. (2011)
44	***P. greggii***	***S. pseudobrevipes***	++	Carrera (2004)
45	***P. greggii***	***S. pseudobrevipes***	+++	Díaz-Balbuena (2017)
46	***P. greggii***	***S. pseudobrevipes***	++	Flores-Armas (2017)
47	***P. greggii***	***S. pseudobrevipes***	+++	Luciano et al. (2018c)
48	***P. greggii***	***S. pseudobrevipes***	+++	Pérez-Moreno et al. (2009)

(continued)

Table 3.4 (continued)

No	Host plant	Mycobiont	Colonization rate	Reference
49	***P. greggii***	***S. pungens* Thiers and A.H. Sm.**	+++	Luciano et al. (2018b)
50	***P. greggii***	***S. pungens***[d]	+++	Ortiz-Lopez (2019)
51	***P. greggii***	***S. pungens***[e]	+++	Ortiz-Lopez (2019)
52	***P. greggii***	***S. pungens***	+++	Ortiz-Lopez et al. (2018)
53	***P. greggii***	***T. terrestris***	+++	Luciano et al. (2018b)
54	***P. hartwegii* Lindl.**	***Clavulina* cf. *cinerea* (Bull.) J. Schröt.**	+	Perea-Estrada et al. (2009)
55	***P. hartwegii***	***Hebeloma* sp.**	+	Perea-Estrada et al. (2009)
56	*P. hartwegii*	_I. splendens_*	+++	Nuñez (2013)
57	***P. hartwegii***	***Laccaria* sp.**	–	Perea-Estrada et al. (2009)
58	***P. hartwegii***	***L. bicolor***	+++	Lazo-Montaño et al. (2018)
59	***P. hartwegii***	***L. laccata***	+++	Lazo-Montaño et al. (2018)
60	*P. hartwegii*	*S. brevipes*	++	Nuñez (2013)
61	*P. hartwegii*	*S. brevipes*	+	Sandoval (2010)
62	***P. hartwegii***	***S. pungens***	+++	Lazo-Montaño et al. (2019)
63	***P. maximartinezii* Rzedowski**	***Hebeloma alpinum***	+	Carrera-Martínez et al. (2017)
64	***P. maximartinezii***	***L. proxima***	+	Carrera-Martínez et al. (2017)
65	***P. maximartinezii***	***S. pseudobrevipes***	+	Carrera-Martínez et al. (2017)
66	***P. maximartinezii***	***Helvella lacunosa* Afzel.**	+++	Almaraz (2019)
67	***P. maximartinezii***	***H. lacunosa* Afzel. (+ *A. brasilense*)**	+++	Almaraz (2019)
68	***P. maximartinezii***	***L. proxima***	+++	Almaraz (2019)
69	***P. maximartinezii***	***L. proxima***	++	Fuentes and Garzón (2017)
70	***P. maximartinezii***	***L. proxima* (Boud.) Pat. (+ *Azospirillum brasilense*)**	+++	Almaraz (2019)
71	***P. maximartinezii***	***S. tomentosus* Singer**	+++	Fuentes and Garzón (2017)
72	***P. montezumae* Lamb.**	***H. mesophaeum***	+++	Barragán-Soriano et al. (2018)

73	***P. montezumae***	***H. mesophaeum***	+++	Villegas (2014)
74	***P. montezumae***	***H. leucosarx***	+++	Villegas-Olivera et al. (2017)
75	***P. montezumae***	***L. laccata***	+++	Villegas (2014)
76	*P. montezumae*	*L. trichodermophora* G.M. Muell.	+++	Galindo-Flores et al. (2015); Rodríguez-Gutiérrez et al. (2017)
77	*P. montezumae*	*L. bicolor*	+++	Rodríguez-Gutiérrez et al. (2017)
78	*P. montezumae*	*S. tomentosus*	+++	Galindo-Flores et al. (2015)
79	***P. oaxacana*** **Mirov.**	***L. trichodermophora***	+++	Hernández (2016)
80	***P. oocarpa*** **Schiede ex Schltdl**	***A. rubescens***	+	Almazán (2019)
81	***P. oocarpa***	***H. leucosarx***	+++	Almazán (2019)
82	***P. oocarpa***	***H. leucosarx***	+++	Villegas-Olivera et al. (2018)
83	***P. oocarpa***	***H. lacunosa***	++	Almazán (2019)
84	***P. oocarpa***	***L. laccata***	+++	Almazán (2019)
85	***P. oocarpa***	***L. laccata***	+++	Villegas-Olivera et al. (2018)
86	***P. oocarpa***	***L. proxima***	++	Almazán (2019)
87	***P. oocarpa***	***S. brevipes***	+++	Villegas-Olivera et al. (2018)
88	***P. patula*** **Schl. et Cham.**	***A. caesarea*** **(Scop.) Pers.**	+	Carrera (2004)
89	***P. patula***	***A. fulva*** **Fr.**	+	Carrera (2004)
90	***P. patula***	***Boletus clavipes [= B. edulis*** **Bull *]***	++	Carrera (2004)
91	***P. patula***	***C.*** **cf.** ***cinerea***	+	Perea-Estrada et al. (2009)
92	***P. patula***	***H. alpinum*** **(J. Favre) Bruchet**	++	Carrasco-Hernández et al. (2011)
93	***P. patula***	***H. leucosarx***	++	Carrasco-Hernández et al. (2011)
94	***P. patula***	***H. mesophaeum***	+	Carrasco-Hernández et al. (2011)
95	***P. patula***	***H. mesophaeum + H. alpinum + H. leucosarx***	+++	Carrasco-Hernández et al. (2011)
96	***P. patula***	***Hebeloma*** **sp.**	+	Perea-Estrada et al. (2009)
97	***P. patula***	***L. bicolor***	+++	Carrasco-Hernández et al. (2011)
98	***P. patula***	***L. laccata***	+++	Carrasco-Hernández et al. (2011), Portillo-Manzano et al. (2017)

(continued)

Table 3.4 (continued)

No	Host plant	Mycobiont	Colonization rate	Reference
99	***P. patula***	***L. laccata* + *L. bicolor* + *L. proxima***	+++	Carrasco-Hernández et al. (2011)
100	***P. patula***	***L. laccata* + *L. bicolor* + *L. proxima* + *H. mesophaeum* + *H. alpinum* + *H. leucosarx***	+++	Carrasco-Hernández et al. (2011)
101	***P. patula***	***L. proxima***	+++	Carrasco-Hernández et al. (2011)
102	***P. patula***	***Laccaria* sp.**	+++	Perea-Estrada et al. (2009)
103	***P. patula***	***S. granulatus* (L.) Roussel**	++	Carrera (2004)
104	***P. patula***	***S. pseudobrevipes***	+++	Carrera (2004)
105	***P. pringlei* Shaw**	***H. alpinum***	+++	López-Gutiérrez et al. (2018)
106	***P. pringlei***	***L. trichodermophora***	+++	López-Gutiérrez et al. (2018)
107	***P. pseudostrobus* Lindl.**	***H. alpinum***	++	Carrasco-Hernández et al. (2011)
108	***P. pseudostrobus***	***H. leucosarx***	+++	Carrasco-Hernández et al. (2011)
109	***P. pseudostrobus***	***H. mesophaeum***	++	Carrasco-Hernández et al. (2011)
110	***P. pseudostrobus***	***H. mesophaeum***	+++	Heredia (2011)
111	***P. pseudostrobus***	***H. mesophaeum***	+++	Pérez-Moreno et al. (2009)
112	***P. pseudostrobus***	***H. mesophaeum* s.l.**	+++	Méndez (2007)
113	***P. pseudostrobus***	***H. mesophaeum* + *H. alpinum* + *H. leucosarx***	+++	Carrasco-Hernández et al. (2011)
114	***P. pseudostrobus***	***H. mesophaeum* + *L. bicolor* + *S. pseudobrevipes***	+++	Pérez-Moreno et al. (2009)
115	***P. pseudostrobus***	***H. mesophaeum* s.l. + *L. laccata* s.l. + *S.* cf. *pseudobrevipes***	+++	Méndez (2007)
116	***P. pseudostrobus***	***L. bicolor***	+++	Pérez-Moreno et al. (2009)
117	***P. pseudostrobus***	***S. pseudobrevipes***	+++	Pérez-Moreno et al. (2009)
118	***P. pseudostrobus***	***Hellvella* sp. + *Laccaria* sp. + *Russula* sp. + *Ramaria* sp. + *Cantharellus* sp. + *Boletus* sp. + *Morchella* sp. + *Lactarius* sp.**	+++	Ramírez (2017)

119	***P. pseudostrobus***	***L. bicolor***	+++	Carrasco-Hernández et al. (2011)
120	***P. pseudostrobus***	***L. laccata***	+++	Carrasco-Hernández et al. (2011)
121	***P. pseudostrobus***	***L. laccata***	+++	Ramírez (2017)
122	***P. pseudostrobus***	***L. laccata* s.l**	+++	Méndez (2007)
123	***P. pseudostrobus***	***L. laccata* + *L. bicolor* + *L. proxima***	+++	Carrasco-Hernández et al. (2011)
124	***P. pseudostrobus***	***L. laccata* + *L. bicolor* + *L. proxima* + *H. mesophaeum* + *H. alpinum* + *H. leucosarx***	+++	Carrasco-Hernández et al. (2011)
125	***P. pseudostrobus***	***L. proxima***	+++	Carrasco-Hernández et al. (2011)
126	***P. pseudostrobus***	***L. proxima***	+++	Jiménez (2011)
127	***P. pseudostrobus***	***S. pseudobrevipes***	++	Flores-Armas (2017)
128	***P. pseudostrobus***	***S.* cf. *pseudobrevipes***	+++	Méndez (2007)
129	***P. teocote* Schiede ex Schltdl.**	***L. laccata***	+++	Luciano et al. (2018a)
130	***P. teocote***	***L. proxima***	+++	Luciano et al. (2018b)
131	***Quercus castanea* Née**	***L. trichodermophora***	+++	Hernández (2016)
132	***Q. uxoris* McVaugh**	***L. proxima***	+	Ríos-García et al. (2017b)

No = combination number; ∗Recorded as edible in India (Sharma and Gautam 2015); − = no increase; + = increases from 0% to 30%; ++ = increases from 31% to 60%; +++ = increases >60%. Nd = No data; Inoculation dose of ^{a}1, ^{b}2, and ^{c}3 g. Inoculation with hymenia of young^{d} and mature basidiomata^{e}. The nomenclature of scientific names for fungi was based on Index Fungorum (2019) and for forest species in USDA database (2019). Scientific names in bold type correspond to experiments carried out in Colegio de Postgraduados under the supervision of the authors of this chapter. Some of these contributions have been published and others are currently in the form of thesis, and their formal publications are in the process of being completed.

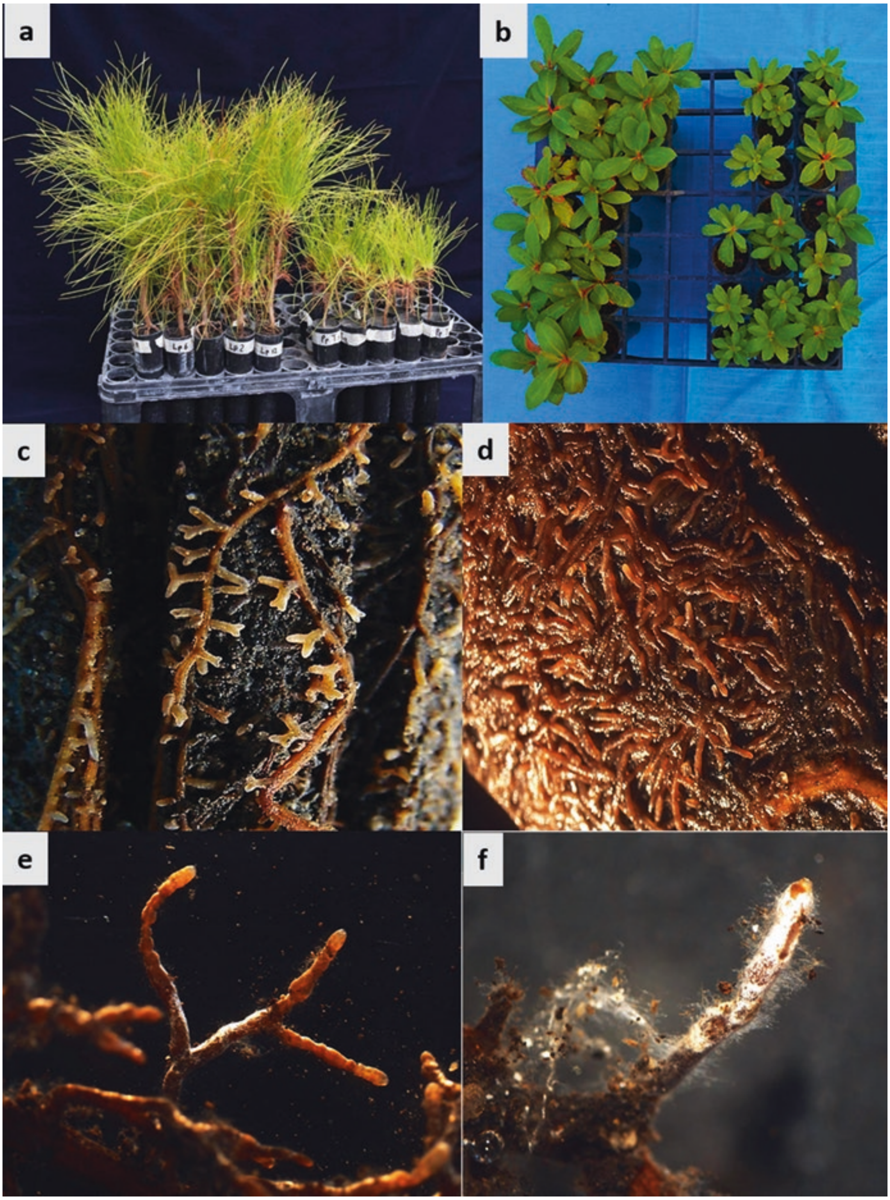

Fig. 3.5 General views of beneficial effect of ectomycorrhizal inoculation and colonization. (**a**) *Pinus pringlei* with (left) and without (right) *L. trichodermophora*; (**b**) Foliar area of *Arbutus xalapensis* with (left) or without (right) *Laccaria trichodermophora*; (**c**–**f**) Ectomycorrhizas of: (**c**) *Pinus oaxacana* with *Laccaria trichodermophora*; (**d**) *Quercus castanea* with *Laccaria trichodermophora*; (**e**) *Pinus greggii* with *Laccaria bicolor*; (**f**) *Pinus pseudostrobus* with *Hebeloma alpinum*

Table 3.5 Effect on increased survival under field conditions in Mexican neotropical trees ectomycorrhizal combinations

No	Host tree	Mycobiont	Increases in survival rates	Reference
1	*Abies religiosa* (Kunth) Schltdl. et. Cham.	*Inocybe splendens* R. Heim*	+	Sandoval (2010)
2	*A. religiosa*	*Suillus brevipes* (Peck) Kuntze	+	Sandoval (2010)
3	***Pinus greggii* Engelm.**	***H. mesophaeum* (Pers.) Quél.**	+	Carrasco (2014)
4	***P. greggii***	***H. mesophaeum***	+	Pérez-Moreno et al. (2009)
5	***P. greggii***	***H. mesophaeum* + *L. bicolor* + *S. pseudobrevipes***	+++	Pérez-Moreno et al. (2009)
6	***P. greggii***	***L. bicolor* (Maire) P.D. Orton**	++	Pérez-Moreno et al. (2009)
7	***P. greggii***	***L. proxima* (Boud.) Pat.**	+	Carrasco (2014)
8	***P. greggii***	***S. brevipes* (Peck) Kuntze**	++	Carrasco (2014)
9	***P. greggii***	***S. brevipes***	+++	Luciano (2018)
10	***P. greggii***	***S. brevipes* + *L. proxima* + *H. mesophaeum***	+	Carrasco (2014)
11	***P. greggii***	***S. pseudobrevipes* A.H. Sm. and Thiers**	++	Pérez-Moreno et al. (2009)
12	***P. greggii***	***S. pseudobrevipes***	+++	Luciano et al. (2018c)
13	***P. greggii***	***S. pungens* Thiers and A.H. Sm.**	+++	Cardoso (2017)
14	***P. greggii***	***S. pungens***	++	Luciano et al. (2018b)
15	*P. hartwegii* Lindl.	*I. splendens**	+++	Nuñez (2013)
16	*P. hartwegii*	*I. splendens**	++	Sandoval (2010)
17	*P. hartwegii*	*S. brevipes*	+++	Nuñez (2013)
18	*P. hartwegii*	*S. brevipes*	++	Sandoval (2010)
19	***P. patula* Schl. et Cham**	***S. pungens***	+	Cardoso (2017)
20	***P. pringlei* Shaw**	***H. alpinum* (J. Favre) Bruchet**	++	López-Gutiérrez et al. (2018)
21	***P. pringlei***	***L. trichodermophora* G.M. Muell.**	+	López-Gutiérrez et al. (2018)
22	***P. pseudostrobus* Lindl.**	***H. alpinum***	+	Jiménez (2011)
23	***P. pseudostrobus***	***H. leucosarx* P.D. Orton**	++	Jiménez (2011)
24	***P. pseudostrobus***	***H. mesophaeum***	++	Jiménez (2011)

(continued)

Table 3.5 (continued)

No	Host tree	Mycobiont	Increases in survival rates	Reference
25	***P. pseudostrobus***	***H. mesophaeum* + *H. alpinum* + *H. leucosarx***	+	Jiménez (2011)
26	***P. pseudostrobus***	***L. bicolor***	+	Jiménez (2011)
27	***P. pseudostrobus***	***L. laccata* (Scop.) Cooke**	++	Jiménez (2011)
28	***P. pseudostrobus***	***L. laccata* + *L. bicolor* + *L. proxima***	+	Jiménez (2011)
29	***P. pseudostrobus***	***L. laccata* + *L. bicolor* + *L. proxima* + *H. mesophaeum* + *H. alpinum* + *H. leucosarx***	++	Jiménez (2011)
30	***P. pseudostrobus***	***L. proxima***	+	Jiménez (2011)

No = combination number; *Recorded as edible in India (Sharma and Gautam 2015); + = increases from 0% to 30%; ++ = increase from 31% to 60%; +++ = increase >60%; all of the increases compared with non-inoculated plants. The nomenclature of scientific names for fungi was based on Index Fungorum (2019) and for forest species in USDA database (2019). Scientific names in bold type correspond to experiments carried out in Colegio de Postgraduados under the supervision of the authors of this chapter. Some of these contributions have been published and others are currently in the form of thesis, and their formal publications are in the proccess of being completed

Fig. 3.6 Formation of sporomes in *Pinus greggii* inoculated with edible ectomycorrhizal mushrooms. (**a**) *Hebeloma mesophaeum*; (**b**) *Laccaria bicolor*; (**c**) close-up to (**d**) *Hebeloma mesophaeum* and *Laccaria trichodermophora* in the same pot; (**d**) General view of a tree of *Pinus greggii* co-inoculated with *Hebeloma mesophaeum* and *Laccaria trichodermophora* producing sporomes of both species

production of bioinoculants useful in the production of controlled ectomycorrhizal plants. The results of more than 100 combinations of phytobionts and mycobionts are analyzed. In general, inoculation with these techniques enhances the growth, nutrient contents, and physiological quality of the associated neotropical hosts. Before this, the use of sporomes of Gasteromycetes, mainly in the genera *Pisolithus*, *Scleroderma*, and *Rhizopogon* were known to be useful in the production of inoculants. The new biotechnology is simple, efficient, and cheap and then it has a great potential to be used in

Fig. 3.7 Studies under field conditions with *Pinus greggii*. (**a**) Abundant external ectomycorrhizal mycelium of *Hebeloma leucosarx*; (**b**) Mexican *campesino* holding a tree inoculated with *Hebeloma alpinum* showing white external ectomycorrhizal mycelium; (**c**) Field bioassays with different Agaricales and Boletales with individual meshes protecting the trees against herbivory; (**d**) adjacent ditch, filled with mulch, an ancient Mexican technique used to enhance water supply to a recently planted tree; (**e**, **f**) view of a site before and 5 years after plantation of *Pinus greggii* trees inoculated with *Suillus pseudobrevipes*; (**g**) Formation of sporome of *Suillus pseudobrevipes* in the base of inoculated trees 2 years after plantation

greenhouses or nurseries with basic infrastructure in developing countries. In this case, the microbiome associated with the pilea or the hymenia of the sporomes rather to be excluded constitute part of the bioinoculants. The validation of this biotechnology is demonstrated by the high ectomycorrhizal colonization rates recorded in most cases. Studies under field conditions proved to dramatically increase the survival rates, compared with non-inoculated trees. Despite the initial success of this innovation, due to the large number of ectomycorrhizal mycobionts and phytobionts to be tested, is possible to state that the development of this biotechnology is in its infancy.

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