Chapter 2
Diversity and Importance of the Relationship Between Arbuscular Mycorrhizal Fungi and Nitrogen-Fixing Bacteria in Tropical Agroforestry Systems in Mexico

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Abstract In Mexico, extensive production systems have caused a drastic reduction in tropical forests and in biological diversity. Most of the agroforestry systems (AFS) in Mexico use leguminous species that naturally associate with arbuscular mycorrhiza fungi (AMF) and bacterial nitrogen fixing that aid the uptake of N and P in poor soils of the tropics. The AMF and bacteria are predominant in tropical agroecosystems with wide ranges of hosts with potential to increase growth in forest species and in crop yield. Mexico is considered one of the countries with high diversity of plants within the countries of America with potentially high number of AMF species and bacteria in different SAF. Although we have considerable knowledge of the plants used in different AFS, the richness of soil microorganisms has received little attention in Mexico's tropics. Understanding of the structure and functional diversity of AMF and bacteria have allowed us to generate the bases for a sustainable AFS, increasing productivity and, at the same time, AFS work as reservoirs and biological corridors that could reduce degradation of forests.

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2.1 Introduction

On a global level, only 23% of the ecosystems can be considered intact while the remainder has been modified by human beings (Watson et al. 2016) due to the ever-increasing demand for food. Tilman et al. (2001) and Hansen et al. (2013) point that in little more than a decade, 2.3 million km^2 of forests would have been lost as a result of the increase in extensive agricultural production. These extensive systems of food production give rise to negative impacts on the environment, low levels of efficiency and rentability caused by the excessive use of fertilizers and pesticides, resulting in a significant impact on the biodiversity, alteration of the geochemical and hydrological cycles and the introduction of exotic species or plagues (Velásquez et al. 2002).

One strategy that can contribute to the implementation of sustainable models of food production is the diversification of crops through the establishment of agroforestry systems (Astier et al. 2017). The functionality of these AFS can be enhanced by means of a better understanding of the ecological interactions, taking into consideration that plant species establish a symbiotic association with soil microorganisms, such as arbuscular mycorrhizal fungi (AMF) and nitrogen-fixing bacteria which form highly functional structures in plant nutrition (Smith and Read 2008). These symbiotic organisms play an important role in soil structure, nutrient recycling, biological fixation of nitrogen and the transport of nutrients of difficult access for the plants (P, Zn, Cu, B, S), protection of the plant from pathogens and stress conditions (Smith and Read 2008; Goltapeh et al. 2008).

In numerous countries, there has been a significant advance in the understanding of the biodiversity and function of the microorganisms and plant species associated with AFS, employing fungi, bacteria and ecological principles to increase productivity. However, in the tropics of Mexico, information regarding the microorganisms and plants in AFS is limited if we consider the significantly larger biological, geographical, climatic, cultural and agricultural diversities in the area. With the intention of recovering degraded sites, while avoiding deforestation, in order to increase agricultural activity with sustainable practices, it is fundamental to have an understanding of the diversity of AMF and nitrogen-fixing bacteria and their potential effect on the development of leguminous plants and other tree species or shrubs with agroforestry potential.

2.2 Agroforestry Systems in the Mexican Tropics

On a global level, Mexico has an extraordinary biological richness, at a genetic level and in the variety of species and agroecosystems. It has been estimated that in any given group of 10 species existing in the world, one can be found in Mexico. For this reason, Mexico belongs to the group of the 12 most mega-diverse countries on the planet (CONABIO 2008; Sarukhán et al. 2009; Villanueva-López et al. 2019).

Together with Brazil, Colombia and Indonesia, Mexico is among the countries with the greatest richness of species, which includes between 60 and 70% of the diversity as well as a large number of endemic species (Rzedowski 1991; CONABIO 2008). In addition, Mexico also maintains high levels of diversity in the hyper-diverse taxonomic groups of microorganisms and arthropods (Llorente-Bousquets and Ocegueda 2008). This richness, among other elements, is due to several factors such as the geographical position occupied by Mexico, between two bio-geographical regions, (Nearctic and Neotropical), the diversity of environments, its rugged topography resulting from its geological history and the climatic variability manifested in the different regions (CONABIO 2008; Sarukhán et al. 2009; Rodríguez-Estrella et al. 2016). Mexico is also an important center of domestication and diversification of cultivated species, some of which are of global importance. More than 15% of the species consumed as food in the world originate in Mexico. By maintaining wild parents or ancestors, these crops can potentiate genetic diversity and thus improve food security (Sarukhán et al. 2009). This sophisticated and prolonged process of domestication and diversification has been possible thanks to the simultaneous development of the crops with their extensive biodiversity.

One worldwide strategy for the conservation of natural resources, biodiversity, genetic resources and ecological and evaluative processes has been through the determination of natural wild areas. In Mexico, these areas are identified as protected areas. However, given the size of their areas and interconnection (barely 13% of the national territory), they are still too small and isolated to safeguard stable, wild populations, ecosystems and the necessary processes for life and productivity on the planet (Torres-Orozco et al. 2015; Ferreira et al. 2018). In this sense, the AFS can serve as a bridge that connects, both functionally and structurally, areas destined for conservation, keeping in mind the integrity of the microorganism-soil-plant system and the sustainable agricultural productivity of large regions and rural sectors. Thus, there is a growing need to understand how to achieve greater yields in the agricultural production with fewer impacts, which requires quantitative evaluations of how the different production practices and the environmental variables affect yields (Tilman et al. 2001).

The trees used in the AFS belong to a wide diversity of native, functional groups, pioneer species and species of the original woodland flora (González-Valdivia et al. 2016), which can potentially host a good representativeness of the richness of species in the natural woodlands. In Mesoamerica, Mexico occupies the first place in richness of trees used in the AFS with dominance of the families: Fabaceae, Bignoniaceae, Malvaceae, Moraceae, Rubiaceae and Rutaceae (González-Valdivia et al. 2016). In the tropics of Mexico, multiple conformations of AFS have been identified with different degrees of complexity. One of the most studied AFS is probably that of coffee production, which is also one of the more complex systems, with respect to plant structure (Arias et al. 2012; Bertolini et al. 2018). For example, in the Peninsula of Yucatan a large diversity of tree species has been identified, among which the family Fabaceae is particularly noteworthy, given that it has approximately 225 species (Carnevali et al. 2010), which have been registered as alternatives for the transformation and improvement of agricultural systems. Among these species can be found *Leucaena leucocephala* (Lam.) de Wit, which has been studied under different agroforestry arrangements such as cultivation in alleys, fodder banks and improved fallow land. In fact, recently in Mexico, approximately 10,000 hectares of AFS, in the modality of silvopastoral systems, have been established in the states of Michoacan, Campeche, San Luis Potosi, Veracruz, Tamaulipas, Chiapas, Nayarit, Quintana Roo and Yucatan, among others, corresponding to the tropical belt of Mexico (Broom et al. 2013). These systems function under a rotational grazing system with the use of electric fencing in pastures cultivated with legumes associated with diverse tropical pasture such as *Panicum maximum* cv. Tanzania, *Cynodon plectostachyus* (K. Schum.) Pilg, and others grasses (López-Santiago et al. 2018).

In the humid and subhumid tropics of Mexico, the main tree species or bushy plant types preferred by the producers, due to their multiple uses as fodder, timber, fruit trees, honeybees, fuel or firewood, are the following: *Cedrela odorata* L., *Swietenia macrophylla* King, *Moringa oleifera* Lam. *Guazuma ulmifolia* Lam., *Piscidia piscipula* (L.) Sarg., *Gliricidia sepium* (Jacq.) Kunth ex Walp., *Lysiloma latisiliquum* (L.) Benth., *L. leucocephala* Wet. *Cocos nucifera* L., *Theobroma cacao* L., *Cordia alliodora* (Ruiz & Pav.) and *Tithonia diversifolia* (Hemsl.) A. Gray. (Fig. 2.1) (Villanueva-Partida et al. 2016, 2019).

2.3 Functionality of Soil Microorganisms in AFS

Soil microorganisms are one of the elements that contribute to the maintenance of plant biodiversity and to the functioning of ecosystems. Most of the trees and shrubs in the AFS present mixed association with nitrogen fixing bacteria and AMF, which facilitates the uptake of phosphorous and nitrogen, respectively. The family Fabaceae is predominant due to the large contribution of organic material and enrichment of the soils from the presence of nitrogen fixing bacteria (Barea et al. 2005). In order to increase the potential of these microorganisms, an adequate selection of the symbionts (fungi and plants) must be carried out. In addition, the tree species must be selected according to their functional compatibility, given that the species of AMF and bacteria respond in a differential manner within their host, and many plants are more susceptible than others to the mycorrhization and/or nodulation (van der Heijden et al. 1998; Smith and Read 2008; Sridhar and Bagyaraj 2017). The presence of bacteria and AMF in only one plant provides multifunctional benefits for the AFS, as it can result in a synergism that benefits nitrogen fixing. This is due to the fact that the nodulation requires high levels of P, which the mycorrhiza could translocate on arrival beyond the depletion zone of this element (Atangana et al. 2014).

In general, plant species present a category according to the dependence to associate with fungi in mycorrhizae: highly dependent, medium dependency or facultative and not mycorrhizal (Brundrett 2009; Atangana et al. 2014). The hyphae of the AMF function as an extension of the roots, which facilitates the translocation

Fig. 2.1 Schematic representation of some agroforestry systems characteristic to the Mexican tropics. (**a**) Grazing in *Cedrela odorata* plantations. (**b**) Grazing in *Cocos nucifera* plantations. (**c**) Living fence of *Gliricidia sepium*. (**d**) Plantations of *Theobroma cacao* in the shade. (**e**) Plantations of *Cordia alliodora* associated with banana. (**f**) Pastures in alleys of *Leucaena leucocephala*. (**g**) Fodder banks of *Tithonia diversifolia*. (**h**) Cultivation of corn in alleys of *L. leucocephala*. Photographs: G. Villanueva-López and F. Casanova-Lugo

of elements with poor mobility, such as phosphorous (P) and, in exchange, the fungus receives carbohydrates and lipids from the plant. In addition to these benefits, the mycorrhiza increases tolerance to saline and water stress, protects the root from pathogens, phytotoxic elements and heavy metals and also improves the structure while increasing the carbon input (C) to the soil (Smith and Read 2008). The mycorrhiza helps in the establishment and survival of plants in the field and has the potential to increase production. They are also essential for restoration and sustainable agricultural production. The majority of the trees and shrubs in the AFS are considered facultative and can include the presence of ectomycorrhiza (Brundrett 2009; Atangana et al. 2014). It has been considered that with a greater stratification of the AFS, the competition for light and nutrients is accentuated, which could reduce crop yield. However, the low selectivity of the AFS permits a food wide web of common hyphae that form a continuum in the roots with different plant species (Giovannetti et al. 2006). These networks of common hyphae would potentially allow interplant mobilization of carbon, water and nutrients as well as the suppression of non-mycorrhizal weeds (Cameron 2010). Although it has been demonstrated that the presence of trees or shrub species and the planting distance in the AFS considerably increases the harvest yields (Balakrishna et al. 2017), it is necessary to determine the influence and synergies of the AMF or nitrogen-fixing bacteria in the transfer of nutrients and carbon in the crops.

2.4 Soil Microorganisms in AFS in the Tropics of Mexico

2.4.1 Arbuscular Mycorrhizal Fungi

Within the tropical AFS, the AMF are the most important group due to their wide distribution, diversity and their capacity to improve the fitness of the plants (Cardoso and Kuyper 2006; Marinho et al. 2018; Prasad et al. 2017). The AMF belong to the subphylum of the Glomeromycota, which has approximately 316 species described at a global level (http://www.amf-phylogeny.com/). Fossil and molecular evidences suggest that this group of fungi has co-evolved with the plants for approximately 400 million years (Strullu-Derrien et al. 2014). Today, the AMF are widely distributed in most ecosystems and form mutualistic associations with bryophytes, ferns, lycopodium, gymnosperms and angiosperms (Wang and Qiu 2006; Brundrett 2009; Prasad et al. 2017; Varma et al. 2017). In Mexico, there are approximately 105 species of AMF registered, representing 36.3% of world richness (Alarcón et al. 2012). The main contributions to the taxonomic knowledge of the AMF derive from the herbaceous and fruit-producing plants in extensive agricultural systems; however, very few studies have focused on the agroforestry systems with only 21 species registered (Montaño et al. 2012).

In Mexico, the mycorrhiza were studied in different plant species; however, it has not been examined in the context of the AFS where a greater effort is required due to the richness, heterogeneity and spatiality of the trees in these systems (González-Valdivia et al. 2016; Villanueva-López et al. 2019; Villanueva-Partida et al. 2019). The diversity of AMF in the AFS will depend greatly on the diversity of the species integrated. The richness and abundance of plant species used in the AFS contain a greater richness of microorganisms in comparison with monoculture and a high representativeness of the conserved woodlands (Villanueva-López et al. 2019). Due to this influence, the AFS can be considered as reservoirs of AMF diversity, while allowing the connectivity of the landscape and habitat fragments that function as biological corridors of potential animal vectors of AMF, coming from adjacent, conserved environments (Janos 1996; Mangan and Adler 2000; Jose 2009). Given the traditional AFS can be simple or complex in their plant structures, comparative studies are required in order to determine the richness of organisms above and below the soil in these models of sustainable production. In the case of the tropics of Mexico, the most representative agroforestry system is the agrosilvopastoral, which includes mainly legumes, such as *G. ulmifolia*, *P. piscipula*, *G. sepium* and *L. latisiliquum* as well as forest trees such as *C. odorata* as living fences.

In this sense, we have addressed the study of the diversity of microorganisms associated with the legume and other tree species or tropical shrubs with agroforestry potential (unpublished data). We evaluate in study sites of the subhumid tropics the diversity of AMF spores in *L. leucocephala*, *L. latisiliquum*, *Cocos nucifera* and *Tithonia diversifolia* under natural and in silvopastoral systems (Fig. 2.2) as well as the level of colonization from *L. leucocephala* associated with *Cynodon plectostachyus* and *L. leucocephala* associated with *Panicum maximum*, adults and seedlings of *G. ulmifolia*, seedlings of *Moringa oleifera* at field capacity and at permanent wilting point (PWP), seedlings of *Cedrela odorata* at field capacity and at PWP, adults of *Swietenia macrophylla* and *Cocos nucifera*. (Fig. 2.3). It has been registered that the total colonization in roots by vesicles and arbuscules, at least on individuals of *L. leucocephala*, collected in natural sites, does not show significant differences in comparison with individuals of agroforestry systems. In seedlings of *Leucaena, Mahogany* and *C. odorata* in greenhouse cultivation inoculated with native AMF, we have observed high levels of total colonization, while colonization by AMF and dark septate fungi (DSF) has been found specifically in mahogany roots. The principal species of AMF with potential to integrate in agroforestry systems are *Acaulospora* spp., *Clareidoglomus* spp., *Diversispora* spp., *Glomus* spp., *Gigaspora* spp., *Rhizophagus* spp. and *Scutellospora* spp. (Fig. 2.2).

2.4.2 Nitrogen-Fixing Bacteria

The microbiota is one of the most important components in the maintenance of soil fertility (Sridhar and Bagyaraj 2017). In the AFS, the diversity of microorganisms includes the symbiotic nitrogen-fixing bacteria (Cardoso and Kuyper 2006; Atangana et al. 2014; Sridhar and Bagyaraj 2017). The nitrogen-fixing bacteria comprise three groups: (1) alpha and Betaproteobacteria (nodulated plants), (2) Actinobacteria (Frankiaceae) and (3) Cyanobacteria (nodulated plants) (Sridhar and Bagyaraj 2017) and are associated mainly with legume plants (Table 2.1). Each

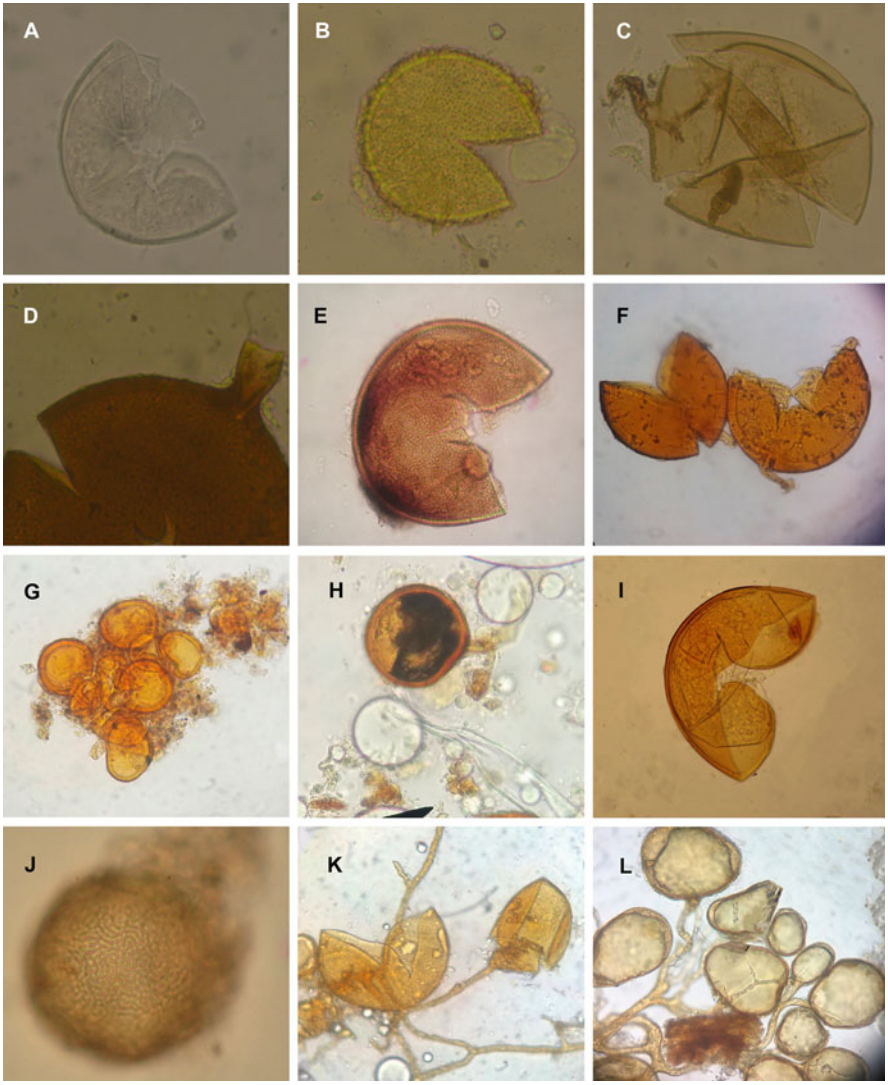

Fig. 2.2 AMF diversity in tree and shrub tropical species with agroforestry potential in the Mexican tropics. (**a–e**) *Leucaena leucocephala* + Grass – estrella + Grass – bombaza. (**f–h**) *Lysiloma latisiliquum*. (**i, j**) *Cocos nucifera*. (**k, l**) *Tithonia diversifolia*. (**a**) *Claroideoglomus*. (**b**) *Acaulospora*. (**e**) *Acaulospora scrobiculata.* (**g**) *Glomus* (**i**) *Gigaspora.* (**j**) *Acaulospora remhii*. (**k**) *Rhizophagus intraradices*. (**l**) *Rhizophagus irregularis.* Photographs: L. Lara Pérez, A. Salbador, L.F. Estrada, E. Mundo and J. L. Moen

year, the legumes of agricultural importance fix approximately 40–60 million metric tons of nitrogen while the legumes in natural ecosystems fix 3–5 million metric tons. Consequently, nitrogen fixing is a highly efficient process which requires only a tiny

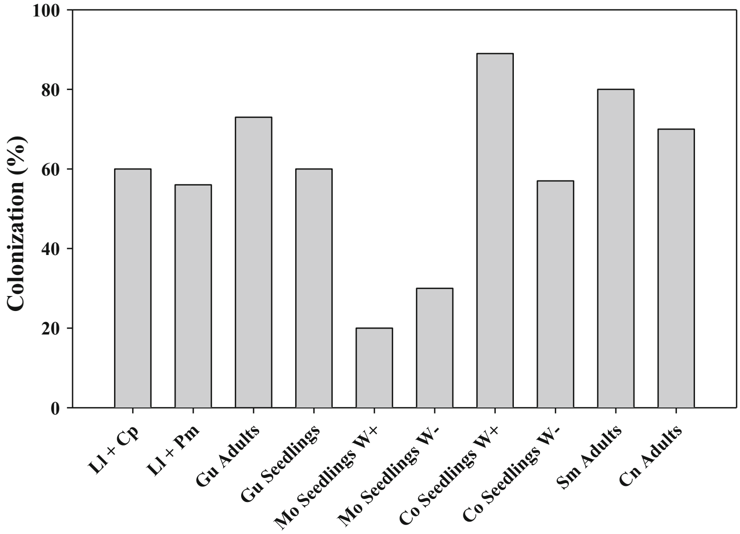

Fig. 2.3 Percentage of mycorrhizal colonization in roots of tropical tree/bush species under different growth conditions. Abbreviations: *Ll* + *Cp Leucaena leucocephala* associated with *Cynodon plectostachyus*, *Ll* + *Pm L. leucocephala* associated with *Panicum maximum*, *Gu Guazuma ulmifolia*, *Mo Moringa oleifera*, *W*+ at field capacity, *W*− near at permanent wilting point, *Co Cedrela odorata*, *Sm Swietenia macrophylla*, *Cn Cocos nucifera*

Table 2.1 Principal characteristics of legume subfamilies (Sprent 2001)

	Caesalpinioideae	Mimosoideae	Papilionoideae
Number of genera (approximate total)	157	78	479
Confirmed as nodulant	8	42	297
Distribution	Mainly in the humid tropics	In tropical/subtropical areas, often in dry areas	From the tropics to the arctic, from dry areas to flood-prone areas
Growth habit	Mainly trees	Mainly trees and bushes	Trees, bushes and herbaceous
Nodulation	Rare, nodule structure is usually primitive	Common but with important exceptions	Very frequent with a few exceptions

amount of nitrogenase (an enzyme used by bacteria for the fixing of nitrogen) in order to carry out the process.

Phenotypes and the genetic diversity of various groups of fast-growing rhizobia have been described as associated with tree species such as *Acacia senegal* and *Prosopis chilensis* in some countries of Africa, where genetic similarity was found between the isolated strains of the two continents and strains belonging to the genera *Sinorhizobium* and *Azorhizobium*. Bryan (2000) mentions the existence of a very close relationship among the legumes and the dispersion of populations of rhizobia of tropical soils in symbiosis and free life (depending on the organic matter and the concentration of nitrogen in soil). This was demonstrated in studies carried out on the island of Maui where native strains of *Rhizobium* and *Bradyrhizobium* were isolated and associated with *L. leucocephala, Sesbania rostrata and Acacia mangium.* Similarly, other species of *Rhizobium* were isolated from shrub legumes (Woomer et al. 1988). Nonetheless, the diversity of the microorganisms present in the soil depends on a number of factors, such as the chemical composition, texture, availability of water, among other characteristics that intervene in the availability of nutrients, including oxygen tension in the different particles forming the soil (Mahmood et al. 2006). The main importance of discovering the microbial diversity in the soils lies in the fact that the microorganisms are intimately related with the productivity of the ecosystem (Zvyagintsev et al. 1991) and it is known that the microorganisms participate in the different biogeochemical cycles in the soil, or interact with the plants, promoting plant growth and increasing the productivity of the ecosystem.

Despite the great diversity of plants integrated in the AFS, studies of the Mexican tropics have focused only on a few species. For example, Roskoski (1986), determined nitrogen fixing in *G. sepium, L. leucocephala* and *Acacia pennatula* in association with *Rhizobium.* Similarly, by means of molecular biology, it was possible to identify the presence of the species *Sinorhizobium terangae*, *R. ettli* and two types of *R. tropici* in *G. sepium.* Another study carried out in Yucatan, on secondary vegetation, reported the species of *R. legominusarum*, *R. tropici*, *Allirhizobium spp.* and *Mesorhizobium* spp. associated with *L. leucocephala*, *G. sepium* and *Calliandra calothyrsus* (Bala et al. 2003). Other species of plants associated with AFS which have been addressed are *A. farnesina* and *A. tamentac*ea where the bacteria of the *Rhizobium* group have been identified (Martínez-Scott et al. 2002).

Nowadays, one of the main challenges is to measure and identify the diversity and composition of the communities of symbiotic bacteria in the AFS of the Mexican tropics, for example, the manner in which this was carried out in Mozambique, where they identified the symbiont bacteria in *Acacia xanthophloea* Benth., *Albizia versicolor* Welw. Ex Oliv. and *Faidherbia albida* (Delile) by sequencing the genes 16S rRNA, *glnII* and *recA* and found mainly in the classes *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium* and species of *Ensifer.* In general, studies relating to symbiotic nitrogen-fixing bacteria are quite scarce and have focused on understanding the diversity and observing the effect of the inoculation on productivity in species of interest.

2.5 Conclusion and Future Prospects

Despite the fact that the AMF and the nitrogen-fixing bacteria are a functional, ecological group of importance for plant diversity, in the processes of establishment, productivity and forestry dynamics in Mexico, very few studies have been conducted on mycorrhizal status, diversity and distribution of these microorganisms. The knowledge of these interactions is of great value for the integration of new native species to the AFS. Unfortunately, there are areas and AFS where a deeper knowledge of the diversity is required as well as a coordination and systematization of the AMF and bacteria. Many of the studies of AMF diversity only identify the species at a genus level, perhaps due to the presence of species which have not yet been described. The integration of trap culture, and molecular studies could help in the correct identification of bacteria and AMF species that colonize the plants used in the AFS. The latest sequencing techniques offer a general panorama of the structure and diversity of functional groups of microorganisms and allow us to compare different scenarios and plant assemblage used in the AFS. With the correct identification of the symbionts and the establishment of pure cultures or in consortium, these are the basis for conducting physiological experiments in controlled environments and follow up in the field with the molecular identification of species. The compilation of this information would not only help us to understand the functional role of the microorganisms in the AFS but would also complement the strategies in agricultural production and the restoration of perturbed ecosystems. The results of this study of the AFS and the importance of their microbiological interactions can be directly incorporated to the strategies and public policies dealing with the interconnection of ecosystems, ecological integrity, food self-sufficiency and productivity. The mitigation of climate change must also be addressed in regions with high biological diversity and latent anthropogenic threats (hot spots), i.e. regions lacking alternatives to resolve the current problems.

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