

Mycorrhizae: Diversity and roles in plant ecosystems

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Abstract

Mycorrhizae are fungi that live in association with the roots of plants, thus constituting an essential symbiosis in terrestrial ecosystems. Arbuscular endomycorrhizae, phylum Glomeromycota, are the most widely distributed in all ecosystems. They colonize the roots of the majority of terrestrial plants and provide several ecosystem services. They are involved in plant growth, absorption of water and specific mineral elements (phosphorus, nitrogen, copper, zinc, and some vitamins), structural stability of soils, and participate in the resistance to biotic and abiotic stresses. The interaction between phosphate-solubilizing bacteria (PSB) and arbuscular mycorrhizal fungi (AMF) positively influences soil fertility and plant productivity. This review provides information on previous research carried out in Morocco on mycorrhizal fungi, particularly the endomycorrhizae. Moreover, this review analyzes the positive role that mycorrhizal fungi can play as growth biostimulators and bioprotectors of plant species.

Keywords: Morocco, mycorrhizae, diversity, systematic, importance

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INTRODUCTION

Mycorrhizal symbiosis is a mutualistic symbiotic association between a mycorrhizal fungus (“myco” fungus in Greek) and a host plant root (“rhiza” in Greek) (Sieverding, 1991; Strullu, 1991). It is estimated that 90% of plant families can form mycorrhizal associations (Newman and Reddell, 1987; Brundrett, 2002).

Mycorrhization, a universal phenomenon (Malloch, 1980; Smith and Read, 2008), is present in all types of soil and in all climates (Plenchette, 2005). There are three types of mycorrhizae ectendomycorrhizae, ectomycorrhizae and endomycorrhizae (Peyronel, 1969; Brundrett, 2002, 2004; Smith et Read, 2008). Some are very specific and only develop with a few plant species such as the Ericaceae, while others are more general and are widely distributed in the various ecosystems of the globe (Fortin, 2008).

Arbuscular mycorrhizal fungi (AMF) are part of the endomycorrhizae, the oldest and most widespread type of mycorrhizae (Redecker, 2000). AMFs involve more than 200 species of microscopic fungi that belong to the Glomeromycota phylum (Schüßler., 2001). These AMFs form associations with the roots of approximately 80% of vascular plants on the planet (Garbaye, 2013; Fortin, 2008; Smith, 2003). Ferns, lycophytes, several conifers, monocotyledons, dicots and the majority of flowering plants are all provided with AMF (Fortin, 2008).

Arbuscular mycorrhizal fungi (AMF) bring several benefits to the plants (Read, 1991). They allow better mineral nutrition in plants whose phosphorus (Harrison, 2002; Helgason and Fitter, 2005; Feddermann, 2010), nitrogen (Subramanian and Charest, 1999; Hawkins, 2000; Hamel, 2004; Toussaint, 2004; Tanaka and Yano,

2005) and other essential cations such as zinc, copper, manganese and iron (Liu *et al.*, 2000).

The objective of this review is to identify the different types of mycorrhizal fungi. Particular attention will be given to arbuscular mycorrhizal fungi. Thus, several components concerning these fungi have been elucidated: taxonomy, life cycle, diversity in Morocco, benefits for the host plant, mainly the mobilization of phosphorus, and their interactions with bacteria.

Mycorrhizae: a symbiotic plant-fungus association

Mycorrhizae are symbiotic associations between soil fungi and the roots of most plants (Plenchette, 1991; Smith and Read, 1997). Mycorrhization is a general phenomenon in plants with the exception of a few families such as Brassicaceae, Caryophyllaceae, Cyperaceae, Juncaceae, Chenopodiaceae and Amaranthaceae which show very few mycorrhizal associations (Malloch, 1980; Strullu, 1991; Norman, 1995; Smith and Read, 2008). It is present in all ecosystems, all soil types and in all climates (Wubet, 2003; Plenchette, 2005; Tao and Zhiwei, 2005; Cho, 2006; Khade and Adoleya, 2009; Alguacil *et al.*, 2009; Brundrett, 2009; Smith, 2010).

The main physiological basis of this symbiosis is a sharing of nutrients between the two partners (Dalpé, 2001). The plant receives from the fungal partner carbon compounds produced by photosynthesis, and the fungus supplies the plant with mineral elements, nitrogen, phosphorus (Mosse, 1973), and water from substrates (Hopkins, 2003; Smith and Read, 2008; Hodge, 2010). These fungi, obligatory symbionts of vascularized plants (Bago, 1998; Pfeiffer, 1998; Requena, 2007), belong to the phyla of Ascomycota, Basidiomycota and Glomeromycota of the kingdom of Mycota (Schüßler, 2001; Taylor and Alexander, 2005).

Types of mycorrhizae

Several types of mycorrhizae are distinguished according to morphological characters (Smith and Read, 1997), ecological (Peyronel, 1969) and molecular. There are three main types of mycorrhizal associations: ectomycorrhizae, endomycorrhizae and ectendomycorrhizae (Peyronel, 1969; Brundrett, 2002, 2004; Smith and Read, 2008).

Ectomycorrhizae

Ectomycorrhizal fungi which contract a symbiotic association with plant species remain outside the cells and develop around the fine roots a mycelial sleeve (the mantle), then a network of hyphae develop between the cortical cells of the root via the intracellular spaces (Harley and Smith, 1983; Franck, 1885; Kendrick, 1992; Brundrett, 2004). The formed network is thus called the Hartig network via which the nutrient exchanges (sugars, amino acids, minerals) between the fungus and the plant (Burgess, 1994; Dell, 1994; Smith and Read, 1997), are carried out. This type of association is formed almost exclusively in forest species, mainly trees and shrubs in boreal, temperate and mountainous regions and in certain tropical regions (Harley, 1984; Smith and Read, 2008), which represent about 5% of plant species (Duhoux and Nicole, 2004).

Ectomycorrhizal plants are Gymnosperms and especially Angiosperms represented by different families of plant species belonging to Myrtaceae, Pinaceae, Fagaceae, Diterocarpaceae, Betulaceae, Salicaceae, Myrtiliaceae, Abietaceae, Tiliaceae and Ulmaceae (Smith and Read, 2008; Van der Heijden, 2008; Matsuda, 2009; Brundrett, 2009).

There are species of plants which are both endomycorrhizal and ectomycorrhizal, such as the genera *Eucalyptus*, *Populus* and *Quercus* (Read, 1977; Dos Santos, 2002; Egerton-Warburton and Allen, 2001; Nounsi, 2014).

Representatives of ectomycorrhiza play an important role in the growth of trees developing at various habitats across the globe (Le Tacon, 1985; Dexheimer, 1997; Kernaghan, 2005; Fortin, 2008; Brundrett, 2009).

Ectomycorrhizal fungi belong to the Basidiomycetes (Bolets, Russules, Lactaires, etc), Ascomycota (*Tuber*, *Elaphomyces*, Pezizaceae (Terfezia) (Figure 1) and rarely to Zygomycetes (Endogone) (Strullu, 1991; Bruns et Shefferson, 2004; Hibbett, 2000 et 2007; Matheny, 2007; Tedersoo, 2010). Some ectomycorrhizae can be cultivated in pure culture on culture media, which facilitates their study compared to endomycorrhizae, considered as obligate fungi linked to their host plants.

In Morocco, for example, the most common ectomycorrhizal plant species are oak groves, cedar groves, pine and eucalyptus plantations (Nounsi, 2014). Among the ectomycorrhizal species found under *Eucalyptus* in the Mamora forest, mention is made of *Cenococcum geophilum* Fr (Abourouh, 2000), *Amanita pantherina* (DC) (Outkoumit, 2011), *Amanita spissa* (Outkoumit, 2011), *Paxillus involutus* (Abourouh, 2000), *Pisolithus tinctorius* (Mont.) (Abourouh, 1999; Aouadj, 1997, 2000; Belkouri, 2009, 2011; Abourouh, 1983, 1992 and 2000; Bakkali Yakhlef, 2009 a and b; Zegayeetal., 2012), *Scleroderma verrucosum* (Abourouh, 2000; Ait Aguil, 2002), *Russula virescens* (Abourouh, 2000; Ait Aguil, 2005; El Assfour, 2006).



Figure 1: Sporophores of some ectomycorrhizal fungal species found under *Quercus suber* and *Pinus* in the Mamora forest
 A: *Boletus mamorensis*; B: *Xerocomus subtomentosus*; C: *Lactarius rugatus*; D and E: *Lactarius deliciosus*; F: *Lactarius chrysorrheus*
 (Pictures taken by Botany, Biotechnology and Plant Protection Laboratory (BBPPL), Nounsi et al., 2014)

The species encountered in the Mamora forest, North West Morocco, under *Quercus suber* are *Cenococcum graniforme* (Abourouh, 1987), *Amanita boudieri* Barla (Nounsi, 2017), *Helvella lacunosa* (El Assfour, 2006; Haimed, 2007; Larouz, 2005), *Amanita boudieri* Barla (Malençon et Bertaut, 1970; Neville, 2009), *Amanita caesarea* (Malençon and Bertaut, 1970; Ait Aguil, 2005; Neville, 2009), *Amanita muscaria* (L.) Lam (Malençon and Bertaut, 1970; Neville, 2009; Outkoumit, 2011) (Figure 2), *Amanita pantherina* (DC) (Malençon and Bertaut, 1970; Neville, 2009; El Assfour, 2006) (Figure 2), *Amanita spissa* (Outkoumit, 2011), *Cortinarius caesiostramineus* Rob (Malençon and Bertaut, 1975; Consiglio, 2009), *Hygrophorus chrysodon* (Blatch) (Malençon and Bertaut, 1975; Ait Aguil, 2005; Haimed, 2007), *Inocybe asterospora* (Malençon et Bertaut, 1970), *Inocybe pyriodora* (Abourouh, 2000), *Boletus mamorensis* (El-Assfour, 2006a; Outkoumit, 2006) (Figure 1). *Gyroporus subalbellus* (Outkoumit, 2011), *Scleroderma bovista* (Abourouh, 2000; Outkoumit, 2011), *Scleroderma citrinum* (Outkoumit, 2011), *Xerocomus subtomentosus* (Malençon et Bertaut, 1975; El Assfour, 2006) (Figure 1), *Lactarius bertillonii* (El Assfour, 2005), *Lactarius chrysorrheus* (Bertaut, 1978; Abourouh, 2000; El Assfour, 2006; Outkoumit, 2011) (Figure 1), *Lactarius decipiens* (Outkoumit, 2011) (Figure 1), *Lactarius kuehnerianus* (Bertaut, 1978, El Assfour, 2005), *Lactarius rugatus* (Outkoumit, 2011) (Figure 1), *Russula alutacea* (El-Assfour, 2006b), *Russula delica* (El-Assfour, 2006b), *Russula farinipes* Romell (El-Assfour, 2006b), *Russula fragilis* (Bertaut, 1978; Ait Aguil, 2005), *Russula violeipes* (El-Assfour, 2006b), *Russula virescens* (Abourouh, 2000; Ait Aguil, 2005; El Assfour, 2006), *Lactarius rugatus* (Outkoumit, 2011). *Lactarius kuehnerianus* (Bertaut, 1978, El Assfour, 2005), *Lactarius chrysorrheus* (Bertaut, 1978; Abourouh, 2000; El Assfour, 2006; Outkoumit, 2011) (Figure 1).

The ectomycorrhizal species cited in the Mamora forest under *Pinus* are *Inocybe asterospora* (Malençon and Bertaut, 1970), *Inocybe cookie* Bres (Malençon and Bertaut, 1970), *Rhizopogon luteolus* (Outkoumit, 2011), *Scleroderma meridionale* (Bakkali Yakhlef, 2009; Outkoumit, 2011), *Cantharellus lutescens* (Pers.) (Malençon et Bertaut, 1975; El Assfour, 2006), *Lactarius deliciosus* (L.) (Outkoumit, 2011), *Lactarius fulvissimus* Romagn, (Malençon and Bertaut, 2009; Outkoumit, 2011), *Russula fragilis* (Bertaut, 1978; Ait Aguil, 2005), *Russula virescens* (Abourouh, 2000; Ait Aguil, 2005; El Assfour, 2006).

In Morocco, the most studied representatives of ectomycorrhizae, belonging to the class Ascomycetes, are generally Truffles of the genus *Terfezia* represented by several species: *Terfezia olbiensis*, *Terfezia leptoderma*, *Terfezia boudieri*, *Terfezia claveryi* (Khabar, 1992; Tahiri, 1997; Khabar and Najim, 2001; Khabar, 2002; El Assfour, 2006a; Bouziani, 2009b; Abourouh, 2011; El Akil, 2016) (Figure 3).

Ectomycorrhizae play an important role in the growth and development of plants. Indeed, *Acacia holosericea* plants inoculated with ectomycorrhizae showed high growth compared to control plants (Founoune, 2001). Inoculation of *Cedrus atlantica* plants with three ectomycorrhizal fungi, *Cortinarius cedretorum*, *Amanita vaginata* and *Inocybe geophylla*, showed an apparent improvement, compared to that of the control, in growth (height, length of the main root, total dry mass), and foliar phosphorus and nitrogen concentrations of the plants (Gaba-chahboub, 2016).

In this sense, other works have highlighted the beneficial effect on the growth of the controlled inoculation of *Pinus halepensis* plants with *Suillus collinitus* (Rincón, 2007) and of *Eucalyptus* with *Scleroderma* sp. (Chen, 2006b). Mousain (1988) also reported a stimulation of growth in length, of the order of 45%, in cedar plants inoculated in the nursery with *Tuber albidum*.

Ectoendomycorrhizae

Ectoendomycorrhizae are mycorrhizae with both ectomycorrhizae structures and endomycorrhizae structures. These fungi have been cited in Ericaceae, Pinaceae and Monotropaceae (Brundrett, 1996; Barea, 2005). They form a mantle, an intercellular Hartig network reminiscent of the structures developed by ectomycorrhizal fungi, and, in addition, fungal hyphae that penetrate inside the cells in the form of intracellular balls (mycorrhizae arbutoides) (Laiho, 1965; Mikola, 1965; Boullard, 1982; Yu, 2001; Fortin, 2008). Arbutoid ectendomycorrhizae are found particularly in the genera *Arbutus* and *Arctostaphylos* of the family Ericaceae and the monotropoids in the genera *Monotropa* and *Pyrola* of the family Pyrolaceae (Nakas and Hagedorn, 1990; Müntenberger, 1992; Laurent, 1995; Smith and Read, 2008). Sometimes, the ectoendomycorrhizae show much more unusual organizations, this is the case of monotropoid mycorrhizae (*Monotropa hypopitys*)



Figure 2: Sporophores of *Amanita muscaria*, encountered in Mamora Forest under *Quercus suber* (BBPPL, Nounsi et al., 2014)

(Dexheimer and Gérard, 1993). The fungus forms a mantle, a Hartig network. From the hyphae of the base of the mantle or the hyphae of the network of Hartig, a very acute wedge-shaped branching perforates the cell wall and represents the endomycorrhizal formation (Dexheimer, 1993). Most of these symbioses are carried out by Ascomycetes of the *Wilcoxina* genus (Garbaye, 2013), and by representatives of two orders Pezizales and Leotiales (Yu, 2001). Some species of Basidiomycetes can form this type of mycorrhiza (Brundett, 2002).

Endomycorrhizae

Endomycorrhizae are characterized by the absence of a fungal coat and the mycelium penetrates inside the cortical cells of the roots, and the morphology of the mycorrhizal root is not modified (Tisdall and Oades, 1979).

The fungus forms two types of characteristic structures, arbuscules and vesicles. Arbuscules are formed in root cortical cells and vesicles are seen in or between these cells (Abbott, 1982). There are two groups: the vesicular and arbuscular endomycorrhizae (VAM) which represent the most ancestral and most widespread mycorrhizal type in the current flora (Smith and Read, 1997;

Redecker and Schüßler, 2010) and endomycorrhizae with septate hyphae of the ericoid type, associated with orchids (Strullu, 1991).

Vesicular and arbuscular mycorrhizae

Vesicular and arbuscular mycorrhizae form a symbiotic association with 200,000 (80%) plant species (Smith and Read, 2008; Khade et Adholeya, 2009; Bonfante, 2009): Bryophytes, Pteridophytes, Gymnosperms and Angiosperms (Barea and Honrubia, 1993; Smith and Read, 1997; Wubet, 2003; Dickson, 2007; Appelhans, 2008; Muthukumar and Prakash, 2009). They form fungal structures from intracellular hyphae which ramify intensely inside the cells of the root cortex giving off branches called arbuscules (Smith and Read, 1997; Chifflot, 2008; Guether, 2009). Same or other intercellular hyphae can form vesicles (Bonfante-Fasola, 1984).

Mycorrhizae with clusters of septate ericoid hyphae

The mycorrhizal association with clusters of septate ericoid hyphae is found in the Ericaceae families (Dexheimer, 1997) and Epacridaceae. It is predominant in acidic soils rich in organic matter but poor in phos-

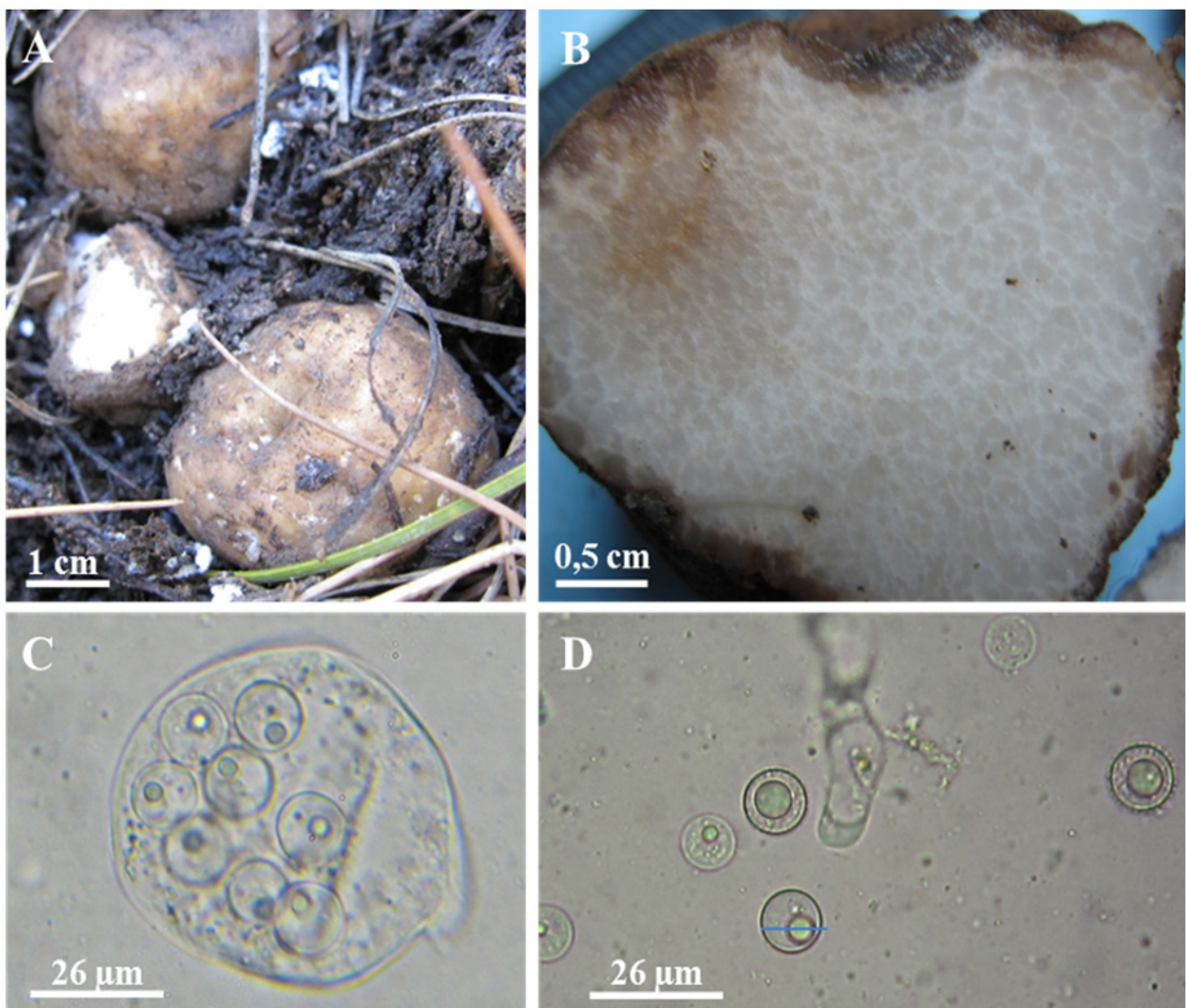


Figure 3: *Terfezia olbiensis*: Ascocarps in situ A; cross section of ascocarp showing color of gleba B; asci containing 8 ascospores C; Ascospores D; microscopic observations are made in water at x 400 magnification (Photos BBPPL (El Akil et al., 2016))

phorus and nitrogen (Cairney and Burke, 1998), and in cold wet soils (Issac, 1992). The fungal partner (Martin, 2007) is an Ascomycete of the genus of *Pezizella* (Smith and Read, 1997): *Scytalidium vaccinii* (order Helotiales) (Egger and Sigler, 1993) and *Oidiodendron* spp. (Order of Onygenales) (Sharples, 2000; Johansson, 2001) and *Hymenoscyphus ericae*. These fungi, characterized by penetration at the end of the root, are called “balloon” mycorrhizae (Smith and Read, 1997).

Mycorrhizae with clusters of orchidoid septate hyphae

Orchidoid mycorrhizae are characterized by the formation of clusters of hyphae in the cortical cells of the root tissue. These endomycorrhizae are formed between Orchidaceae and Basidiomycetes fungi (Issac, 1992) and are of great importance throughout the part of the life cycle of Orchidaceae during which these species depend on mycorrhization to obtain carbonaceous substrates (Smith and Read, 1997; Fortin, 2008). All orchids form a symbiotic association with fungi in the early stages of their development (Issac, 1992).

The roles of mycorrhizae

Mycorrhizal fungi play an important role in the stability of terrestrial ecosystems (Gianinazzi ., 2010), and also on the diversity of the microflora of the vegetation and consequently in the conservation and the structural stability of the soils (Rayn and Graham, 2002; Rillig, 2004; Cardoso and Kuyper, 2006). They play an essential role in increasing the uptake of very low mobility nutrients in the soil, such as Phosphorus (P) (Rhodes and Gerdemann, 1975; Bolan, 1991; Gianinazzi & Schüepp, 1994; Smith and Read, 1997; Duponnois, 2005a; Lambers, 2008) and metals (Abbott et Robson, 1982). But the role of these microorganisms is not limited to mineral nutrition alone; they also participate in resistance to biotic and

abiotic stresses, and soil aggregation (Harley and Smith, 1983; Smith and Read, 1997; Rillig, 2001; Selosse, 2001). Research has shown that inoculation with endomycorrhizal fungi stimulates the growth of seedlings of *Olea europaea*, *Eucalyptus*, *Quercus suber*, *Citrus aurantium L*, *Argania spinosa* and others (Chliyeh et al., 2014; Nounsi, 2015; Semane, 2017; Hamidi, 2017; Artib, 2017; Sellal, 2019) (Figures 4; 5; 6; 7).



Figure 4: *Eucalyptus*: control plants (A and B), mycorrhizal plants (C and D) (BBPPL, Nounsi, 2015)



Figure 5: Effects of a consortium of endomycorrhizal fungi on the development of aerial (A) and root (B) parts of cork oak plants, observation after 5 months of culture (Myc): mycorrhizal plants; (T): control plants (BBPPL, Hamidi .,2017)

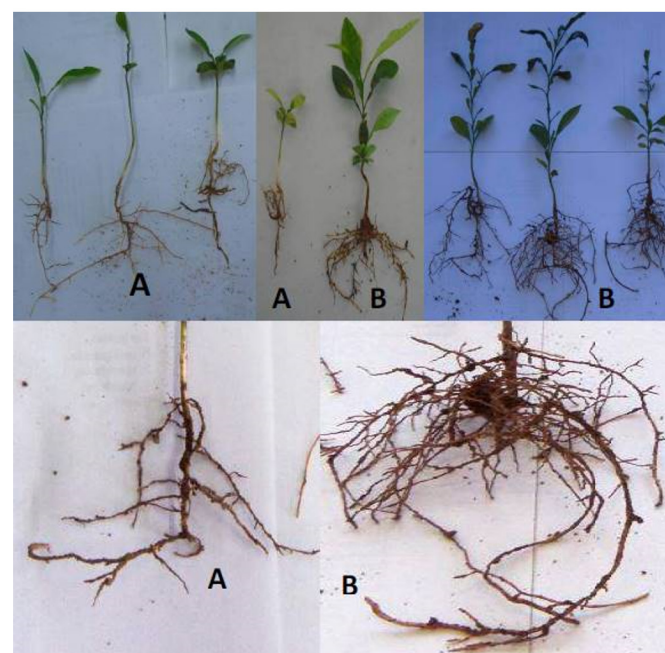


Figure 6: Effects of a consortium of endomycorrhizal fungi on the growth of the aerial and root parts of *Citrus aurantium L.*: control plants (A), mycorrhizal plants (B) (BBPPL, Artib, 2017)



Figure 7: Effect of seed treatment with a consortium of endomycorrhizal fungi on the development of argan plants: (A) control plants; (B) Plants grown from seeds treated with endomycorrhizae (BBPPL, Sellal, 2019)

Phosphate nutrition

The mobilization and uptake of inorganic phosphate (PO_4^{3-}) from the soil by AMFs are the key processes that improve plant growth (Cardoso, 2006; Babana and Antoun, 2006; Bucher, 2007).

Plants colonized by mycorrhiza benefit from a better phosphorus uptake (Lange and Vlek, 2000; Hopkins, 2003; Finlay, 2004; Helgason and Fitter, 2005; Plenchette, 2005; Feddermann, 2010). The mycorrhizal fungus is able to more efficiently absorb certain forms of phosphorus and transport them to the plant (Xinshu and Runjin, 1990; Plenchette, 2005). The hyphae of the fungus also produce various extracellular enzymes (phosphatase, phytase) which catalyze the hydrolysis of organic bonds by releasing orthophosphate and promoting the release of immobile phosphorus in the soil and the mineralization of organic sources of soil phosphates (Gobat, 2003). The phosphorus thus mobilized is easily absorbed and transported through the hyphae to the arbuscules and then to the host plant.

Phosphorus inputs to the plant can fluctuate from 20 to 100%, depending on the plant and fungal species and this independently of the effect of the fungus on the plant biomass (Smith, 2004; Faceli, 2010). Besides phosphorus, mycorrhizal symbiosis can facilitate the absorption of various other mineral elements such as N, K, Mg, Na, S, B, Br, Cl, Cu, Cr, Cs, Co, Fe, Mo, Mn, Ni, Si, Zn (Smith and Read, 1997; Caris, 1998; Duponnois and Bâ, 1999; Trépanier, 1998; Liu, 2002; Nogueira, 2004; Sorensen, 2005; Cardoso, 2006; He, 2007; Guether, 2009) are some of the minor elements often present in higher concentrations in mycorrhizal plants. The absorption of these elements, often difficult to assimilate by the plant, is improved by the mycorrhizal association (Srivastava, 1996).

Nitrogen nutrition

Like Phosphorus, Nitrogen is a vital component for the AMF and the plant (Smith, 2010). It enters into the formation of phospholipids, coenzymes and amino acids. Nitrogen is present in two forms in the soil: organic and mineral (nitrites, nitrates and ammonium ions). The AMF mycelium is able to take up N in the form of ammonium ions (NH_4^+) (Johansen, 1996), in the form of nitrates (NO_3^-) (Bago, 1996; Johansen, 1996) and in the form of amino acids (Hawkins, 2000), with a clear preference for ions NH_4^+ (López-Pedrosa, 2006). It can also accelerate the breakdown of organic matter to increase its bioavailability to plants (Hodge, 2001).

For legumes, AMF symbiosis plays an indirect role in nitrogen fixation, especially in phosphorus-poor soils (Dianda, 1991; Houngnandan, 2000). The presence of mycorrhizae allows optimal growth of the host plant; it is more regular and sometimes better than that produced by high fertilizer inputs (Abbott, 1983).

Hormonal activities

The concentration of phytohormones such as cytokinin, gibberellin, ethylene, abscisic acid, auxin and jasmonic acid can vary in the plant depending on whether or not

the mycorrhizal fungus is present (Hausse, 2005; Danneberg, 1992). Johansson (2004) showed the influence of AMFs on increasing and stimulating the level of growth hormones. The overall action of the hormones produced by the fungus affects the general habit of the plant, the growth of the aerial parts of which is often favored over that of the roots (Fortin, 2008).

Aggregation of soils

Arbuscular mycorrhizal symbiosis appears as a factor that positively influences soil aggregation through various mechanisms that improve their structure and stability (Bethlenfalvay, 1999). The AMF hyphae being present in large quantities in the soil, between 81 and 111 m^3 per cm^3 of soil (Miller, 1995), they have the property of acting on the macroaggregation of soil constituents and therefore on its stability (Tisdall, 1991). Indeed, these hyphae produce extracellular polysaccharides to which microaggregates (with a diameter of less than 250 μm) are attached to form stable macroaggregates (greater than 250 μm) (Tisdall, 1994). These polysaccharides would in fact be a glycoprotein, glomalin which acts as a glue (Rillig and Mummey, 2006) and which assembles the finest particles of the soil to make aggregates whose fundamental role for soil fertility is known, by retaining water and mineral elements and by promoting gas exchange and aeration (Fortin, 2008). The concentration of glomalin in soils depends on the host plant and the associated fungus (Rillig, 2002). This stability of the soil thus produced makes it possible to fight against erosion, the loss of nutrients and organic matter by leaching, which lead to a drop in productivity in agriculture (Schreiner and Bethlenfalvay, 1995).

Resistance to biotic stresses

In the different biotopes, the plants are continuously subjected to attacks from bacteria, fungi, nematodes, insects and fungal diseases. Indeed, AMFs appear to reduce the incidence and/or severity of deleterious effects caused by root-borne phytopathogenic fungi such as *Rhizoctonia*, *Fusarium*, *Verticillium*, *Phytophthora*, *Pythium* and *Aphanomyces* (St-Arnaud, 1995; Azcón-Aguilar and Barea, 1996; Whipps, 2004; Dalpé, 2006) and bacteria such as *Xanthomonas campestris* (Liu, 2007).

Plants inoculated with arbuscular mycorrhizal fungi have been experimentally proven to be more resistant to attack by pathogenic fungi and exposure to soil toxins (Moser and Haselwandter, 1983; Schtiepp, 1987; Fitter, 1991). Mycorrhizal fungi protect the host plant against pathogens by competing directly with them for energy resources and infection sites (Helgason and Fitter, 2005; Dalpé, 2006).

Studies have shown the effect of mycorrhization on plant protection against pathogens, case of tomato plants inoculated with *Glomus mosseae* against *Phytophthora parasitica* and *Gaeumannomyces graminis*, and barley plants inoculated with *Glomus versiforme* against *Ralstonia solanacearum* (Cordier, 1998; Pozo, 2002; Zhu et Yao, 2004; Khaosaad, 2007). Tomato plants inoculated with *Glomus mosseae* also showed protection against the nematodes *Meloidogyne neincognita* and *Pratylenchus penetrans* (Vos, 2012).

Unlike root diseases, little work has been done on the protection conferred by AMFs on leaf diseases and the results are less conclusive and contradictory (Whipps, 2004). Better tolerance against the fungi responsible for powdery mildew (*Blumeria* sp. and *Bremia lactucae*), rust (*Uromyces*) and gray rot (*Botrytis cinerea*) has been described in mycorrhizal plants (Whipps, 2004; Jung, 2009; Moller, 2009). A delay in disease progression caused by *Phytophthora infestans* was also observed in potato plants inoculated with a commercial mycorrhizal inoculum (O'Herlihy, 2003). Plant resistance was also increased in mycorrhizal plants against necrotrophic pathogens, case of *Alternaria solani* (Fritz, 2006, De La Noval, 2007). This effect is, however, controversial in hemi-biotrophic fungi such as *Colletotrichum orbiculare*. Lee (2005) observed a decrease in anthracnose on the leaves of cucumber plants colonized by *Glomus intraradices*, whereas no effect was observed on cucumber plants mycorrhizal by *Glomus mosseae* (Chandanie, 2006).

However, if the induction of defense reactions in the root system of mycorrhizal plants has been clearly demonstrated for a long time, these mechanisms were only reported around 2009 in the leaves of mycorrhizal plants (Liu, 2007; Pozo, 2009).

Resistance to abiotic stresses

Besides the protection of plants by arbuscular mycorrhizal fungi against biotic stresses, several studies show a protective effect of AMFs against abiotic stresses such as drought, salinity and pollution.

Water stress

Mycorrhization has an influence on the water status of plants. The extra-radicular hyphae of endomycorrhizal fungi can explore a much larger volume of soil than the roots and have access to a larger water reservoir, so it can help maintain the water and mineral balance of the plant. In addition, endomycorrhizal fungi lead to an increase in the resistance of the plant to lack of water (Sylvia, 1993; Meddich, 2000).

Mycorrhizal plants are less affected during periods of drought (Fortin, 2008; Smith and Read, 2008 ; Roy-Bolduc and Hijri, 2010). AMFs are important in sustainable agriculture because they improve the water relations of host plants and thus increase their resistance to drought (Allen, 1986; Nelsen, 1987). The extensive network of extra-radicular hyphae of endomycorrhizal fungi gives plants access to a larger water reservoir. AMFs can prevent irreversible wilting in plants and ensure, under water stress, faster stomata closure (Davies, 1992; Subramanian and Charest, 1997). Mycorrhizal colonization also induces an increase in water conductivity in the host plant under conditions of osmotic stress and a better regulation of abscisic acid levels and consequently a better transpiration rate (Sánchez-Blanco, 2004; Aroca, 2007, 2008). These improvements seem to be related to the alleviation of oxidative stress, resulting in the production of antioxidant enzymes (superoxide dismutase, catalase and guaiacol-peroxidase) and non-enzymatic antioxidants (ascorbate and glutathione) (Wu and Zou, 2008; Ruiz-Sánchez, 2010).

Salt stress

High salinity (NaCl , NaCO_3^- , NaSO_4^{2-} or magnesium salts) in soils can affect plant establishment, growth, development, and cause huge losses in productivity (Ramoliya, 2004; Evelin, 2009). Mycorrhizal fungi play a role in plant protection against salt stress. This protection is the result of better nutrition of mycorrhizal plants illustrated by an increase and/or a better selection in the uptake of nutrients, an accumulation of osmoregulatory compounds, an important stomatal conductance, a better transpiration, an increase in the photosynthetic activity or a limitation of leaf dehydration (Cantrell et Linderman, 2001; Feng, 2002; Aroca, 2006; Porcel, 2006; Sheng, 2008, Evelin, 2009).

Moreover, under salt stress conditions, it seems that the accumulation of K^+ by mycorrhizal plants (Hanway and Heidel, 1952; Ojala, 1983; Mohammad, 2003; Giri, 2007) helps maintain a high K/Na ratio, thus preventing disruption of many enzymatic processes and inhibition of protein synthesis (Porcel, 2012).

In addition, under high salinity, mycorrhizal plants have been shown to accumulate more proline (osmotic adjustment molecule), betaine and soluble sugars than non-mycorrhizal plants (Jindal, 1993; Porcel et Ruiz-Lozano, 2004; Al-Garni, 2006; Sharifi, 2007). These molecules are known to protect subcellular structures, to maintain enzymatic activities and to limit oxidative damage induced by free radicals in the event of salt stress (Yokoi, 2002). It has also been reported that arbuscular mycorrhizal symbiosis may decrease salt stress in plants by increasing the activity of antioxidant enzymes such as peroxide dismutase, ascorbate-peroxidase and peroxidase activities. These enzymes will allow the degradation of ROS and therefore limit the induction of membrane damage (Alguacil, 2003; He, 2007; Zhong, 2007).

Pollutants

AMFs play an important role in the phyto-stabilization of soils polluted by trace and potentially toxic elements (Garg and Chandel, 2010), and they also protect trees from the toxic effects of pollutants and heavy metals (lead, cadmium, nickel, mercury, etc.) (Shetty, 1994). In mycorrhizal plants, certain heavy metals, such as aluminum which binds to the mycelium, retained by the fungal coat only reach the root in a reduced quantity (Brunner and Frey, 2000; Brunner and Brodbeck, 2001). Other work on radioactive cesium has shown that this substance contained in the soil accumulates in the 'fruiting bodies' of the hyphae of certain mycorrhizae (Brunner and Brodbeck, 2001; Dupré de Doulois, 2007). On the other hand, several research works have demonstrated the impact of mycorrhizal infection on the process of phyto-restoration of soils contaminated by heavy metals (Salido, 2003; Giasson, 2005).

Arbuscular mycorrhizal fungi (AMF)

The AMF symbiosis is the most widespread and oldest terrestrial symbiosis in the terrestrial ecosystem (Smith and Read, 1997; Harisson, 1997; Stürmer, 1998; Wubet, 2003; Fitter, 2005; Smith and Read, 2008; Guether, 2009 ; Khade and Adholeya, 2009). Indeed, the mycorrhizal symbiosis with vesicles and arbuscules is formed by more

than 80% of terrestrial vascular plants (Strullu, 1985; Smith et Gianinazzi-Pearson, 1988; Newsham et al., 1995; Bonfante and Perotto, 1995; Smith et Read, 1997; Fortin, 2008; Smith and Read, 2008; Brundrett, 2009; Garbaye, 2013). Ferns, lycopods, several conifers, monocotyledons, dicots and the majority of flowering plants are all provided with AMF (Fortin, 2008). The arbuscular mycorrhizal association is an obligatory symbiotic association (Ferrol, 2002; Vestberg and cassells, 2009). AMFs belong to the monophyletic phylum (Redecker, 2000; Schwarzott, 2001), Glomeromycota (Schubler, 2001), the order Glomales of the class Zygomycetes (Gerdemann and Trappe, 1974). The most common genera are *Glomus*, *Gigaspora* and *Acaulospora* (Torrey, 1992).

AMFs have co-evolved with plants for at least 460 million years (Simon, 1993), probably allowing the colonization of land masses by vascular plants (Remy, 1994; Redecker, 2000; Selosse, 2000; Wang, 2006) through improved plant nutrition.

AMFs are special organizations for several reasons

AMFs are obligate symbionts (Harrier and Watson, 2004). Their cultivation requires a symbiotic association with a host plant (Smith and Read, 2008). The same endomycorrhizal fungus can colonize several plants and the same plant can be infected by several AMF species (Mosse, 1981).

The genetics of these fungi, degree of ploidy, number of chromosomes, segregation of nuclei, existence or not of meiosis, remains little studied (Sanders, 2010). Sexual reproduction has never been observed in these fungi, although the necessary genes appear to be present (Tisserant, 2012; Corradi and Bonfante, 2012).

An important aspect of fungal development is that some species can fuse hyphae between genetically close individuals, a phenomenon called anastomosis. This process allows the exchange of nutrients (Mikkelsen, 2008) but also nuclei (Giovannetti, 1999; Croll, 2009) further complicating the genetic structure/plasticity of these organisms.

Structure of arbuscular mycorrhizal fungi

AMFs develop different specific structures in the rhizospheric soils of plants, these are spores and/or sporocarps containing several spores, vesicles, arbuscules, and extracellular and intracellular mycelium (Ouahmane, 2007).

Spores

The spores are asexual, unicellular structures, usually globoid in shape, thick-walled formed by several layers of different textures, connected to the filamentous networks by a suspensory hypha of various morphology (Gerdemann and Trappe, 1974; Morton, 1988; Giovannetti and Gianinazzi, 1994; Stürmer, 1998; Dalpé, 2004). They contain a very large number of nuclei (polynucleates), for example, in the species *Scutellospora castanea*, up to 700 have been counted (Hosny, 1998) and in *Gigaspora margarita* up to 2000 (Bécard et Pfeffer, 1993). Spores can range in size from 30 μm to 130 μm (Koffi, 2009). The relatively large, multinucleate spores are rich in lipid and protein globules. They are found separated or in sporocarps (Redecker and Schüßler, 2013), with a diameter between 22 and 1050 μm (Souza, 2015). AMF

spores are grouped in clusters and sporocarps surrounded or not by a peridium (Redecker, 2007), case of the species *Redeckera fulva*.

Spores are storage and dissemination organs of AMF (Bouchet, 2005). They germinate and give rise to mycelial filaments which come into contact with a young root, form an appressorium, penetrate, settle and spread rapidly at the level of the root cortex by differentiating inside these cells from arbuscules and in certain case of vesicles (Souza, 2005) (Figure 15).

Arbuscules

Arbuscules are units at which nutrient exchanges occur between two host plant/fungus partners (Scannerini and Bonfante-Fasolo, 1982; Gianinazzi, 1983; Smith and Read, 1997; Chiffot, 2008; Guether, 2009). They result from a series of dichotomous divisions of an intra-root hypha resembling the antlers of a tree, an arbuscule of 2-6 μm (Dexheimer, 1997). It is a lateral branching of fungal hyphae in the cells of the root cortex where the fungus enters and grows inside (Manchanda and Garg, 2007). The terminal branches are short and very tenuous, with a diameter varying from 0.5 μm to 1 μm . The host cell membrane invaginates and envelops the fungus, this new compartment provides direct contact between the fungus and the plant. Their lifespan is very short 2 to 15 days (Harley, 1986), 7 to 11 days (Ferrol, 2002), sometimes one to three weeks (Smith et Read 1997; Harrison, 1999). Once the arbuscule is degraded, the cytoplasm of the cortical cell returns to its original position without influencing cell function. The exact shape of the arbuscules varies according to the genus of the AMF (Smith et Read, 2008) (Figures 8; 9; 10; 11; 112; 13; 14).

Vesicles

Vesicles are thin-walled storage structures, present within or between cortical cells (Harley and Smith, 1983; Smith and Read, 1997; Dodd, 2000). They have thick walls of various shapes, and are formed from the intra-root mycelium (Pawlowska, 1999). They play a role in the storage of reserves, mainly present in the form of lipids and trehalose (Harley and Smith, 1983; Bonfante-Fasolo, 1984; Fontaine, 2001; Duhoux and Nicole, 2004), and ensure the survival of the fungus. Their size varies between 30 and 250 μm (Declerck, 1998) (Figures 8; 9; 10; 11; 12; 13; 14).

The intra and extra-root mycelial network

Intra- and extra-root mycelial networks are propagation organs that can colonize a plant other than the plant from which they originate. The mycelial network absorbs nutrients from the soil (nitrogen, phosphorus in particular) acting as an extension of the root system of plants in the soil (Newman and Reddell, 1987). The external mycelial hyphae are protected by a very thick and stratified wall (Scannerini and Bonfante-Fasolo, 1982), with cytochemical characteristics different from those of the walls of the internal hyphae (Bonfante-Fasolo et Grippioli, 1982). Along these hyphae are differentiated branched structures resembling arbuscules considered as privileged sites of nutrient uptake for the plant (Bago, 1998). These extra-root hyphae promote the aggrega-

tion of soil particles thanks to glomalin while improving its aeration (Murulanda, 2003; Porcel, 2003; Rillig and Mummy, 2006; Dodd, 2000) (Figures 8; 11; 13; 14).

Taxonomy of endomycorrhizae

AMFs are coenocytic (hyphae lacking a septa) and multinucleated organisms. They would be heterokaryotic, with haploid nuclei, or homokaryotic, with polyploid nuclei (Kuhn, 2010; Pawlowska and Taylor, 2004; Hijri and Sanders, 2005).

The taxonomy of endomycorrhizae remains always complex, it is based mainly on the morphological characters of the spores which are of great importance. The identification keys that allowed the determination of endomycorrhizae are based on different criteria (Gerdemann and Nicolson, 1963; Morton and Benny, 1990; Giovannetti and Gianinazzi-Pearson, 1994):

- Form of the hypha carrying the terminal spores,
- Presence or absence of the septum, membrane that separates the contents of the spore from the hypha),
- Internal aspect of the spores;
- Color of spores, usually variable, yellow or brown, black or colorless;
- Structure of the spore wall.

However, in the absence of spores, it is difficult to identify the species from its mycelium. To overcome these difficulties, molecular approaches using specific probes have made it possible to support microscopic observations (Moutoglis, 1997; Corradi, 2004; Hijri, 2001; Hijri and Sanders, 2005).

In recent years, many changes have been noted regarding the classification of Glomeromycota (Morton and Msiska, 2009; Schüßler and Walker, 2010; Oehl, 2011a and b). Recent morphological and phylogenetic studies have made it possible to group all arbuscular mycorrhizal species into the Zygomycota phylum and placed in their own Glomeromycota phylum. Recent morphological and phylogenetic studies have made it possible to group all arbuscular mycorrhizal species into the Zygomycota phylum and placed in their own Glomeromycota phylum (Gerdemann and Trappe, 1974). The Glomeromycota phylum mentions about 240 species described to date, divided into 4 orders, 11 families and 25 genera (Redecker, 2013).

Molecular taxonomy, based on analyzes of the small subunit of 18S ribosomal RNA, has made it possible to construct the phylogenetic tree of the Glomeromycetes (Krüger, 2012). This technique consists in amplifying by polymerase chain reaction (PCR) regions of nuclear ribosomal DNA (rDNA) which encode the different ribosomal RNAs (rRNA), 5S, 18S, 28S and 5.8S, using universal and fungi-specific nucleotide primers (White, 1990). DNA must be extracted first from a spore (Schwarzott and Schüßler, 2001) or a root sample (Edwards, 1997). As the majority of the DNA extracted from the colonized roots comes from the plant, the primers used must be very specific for Glomeromycota and the PCR must be carried out under very astringent conditions.

Molecular biology tools have made it possible to characterize new ancestral lines of Glomeromycota, such as Archaeosporaceae and Paraglomaceae (Morton and Redecker 2001;

Redecker, 2000a, b). Molecular biology has also shown that the diversity of Glomales sensu Morton and Benny (1990) is much higher than previously found (Sanders, 2002).

Life cycle of AM fungi

The life cycle of AMF is complete only in the presence of a plant partner (Azcón-Aguilar, 1998; Giovannetti, 2000). The establishment of the symbiosis between the plant and the AMF takes place via an exchange of molecular signals (Vierheilig and Piché, 2002; Requena, 2007). Recognition between the fungus and the host plant involves

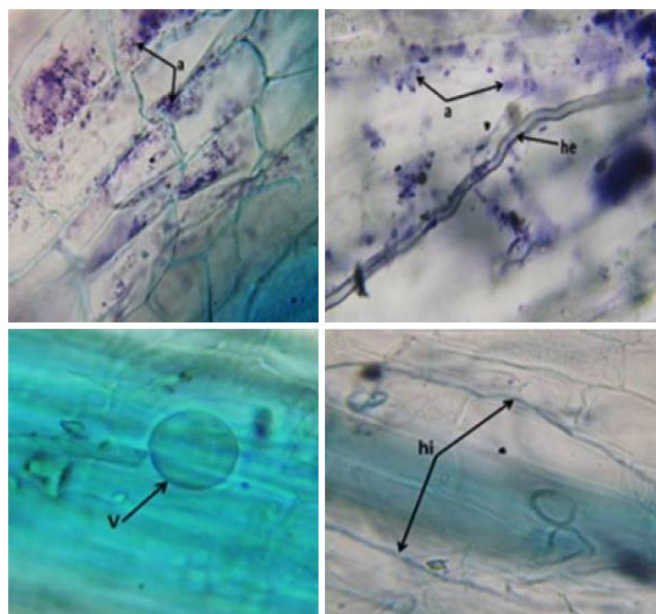


Figure 8: Different AMF structures observed in the roots of mycorrhizal *Ceratonia siliqua* plants. a: arbuscules; hi: internal hyphae; he: external hyphae; v: vesicles (G. × 400) (BBPPL, Talbi, 2016)

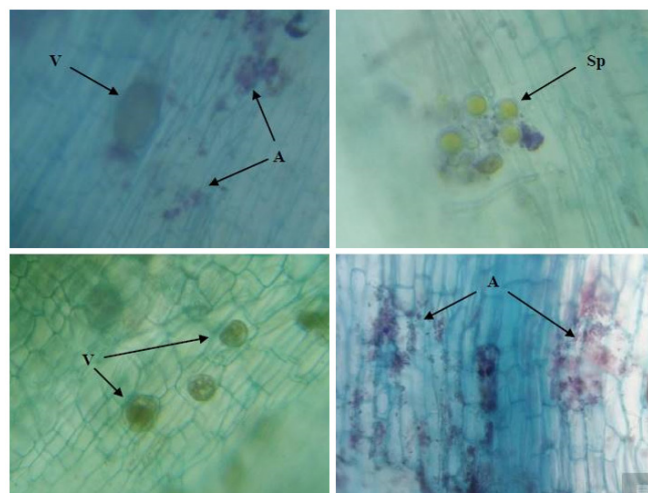


Figure 9: Different structures of endomycorrhizal fungi observed in the roots of argan plants. SP: spores, V: vesicles, A: arbuscules, h: hyphae (BBPPL, Sellal, 2019)

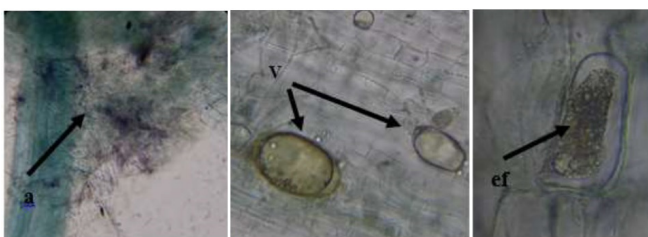


Figure 10: Endomycorrhizal structures noted in mycorrhizal olive plants: v: vesicles; ef: endophytes; a: arbuscules. G × 400 (BBPPL, Semane, 2017)

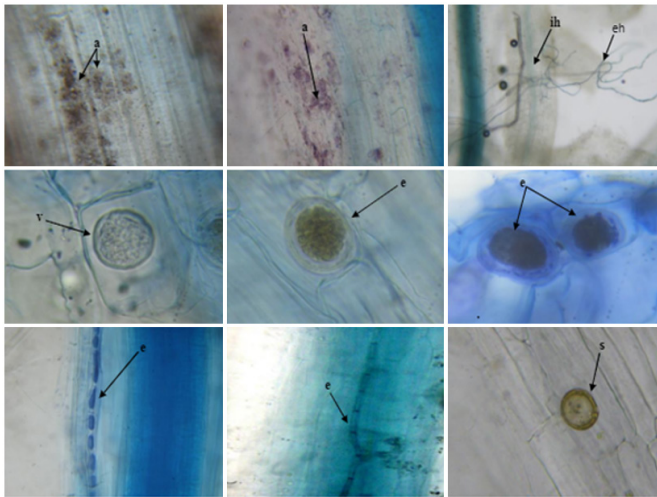


Figure 11: Structures of endomycorrhizal fungi and presence of endophytes in the roots of Eucalyptus plants. a: arbuscule; e: endophytes; ih: internal hyphae; eh: external hyphae; v: vesicles; s: spores (G. × 400) (BBPPL, Nounsi, 2015)

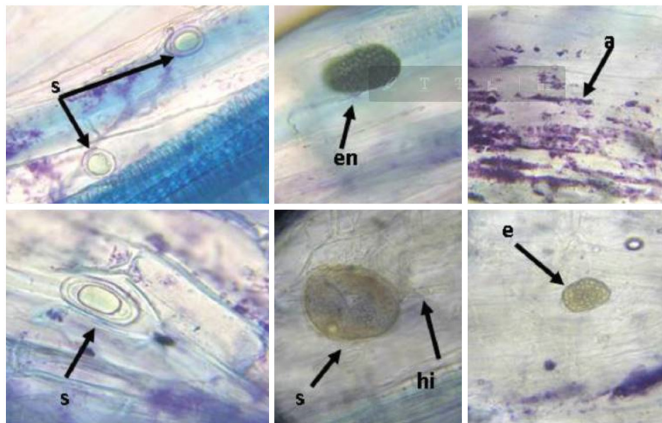


Figure 12 : Roots of Crocus sativus with endomycorrhizal structures: (a); Internal hyphae (hi), spores (s) and endophytes (en). (G. x400) (BBPPL, EL aymani, 2019)

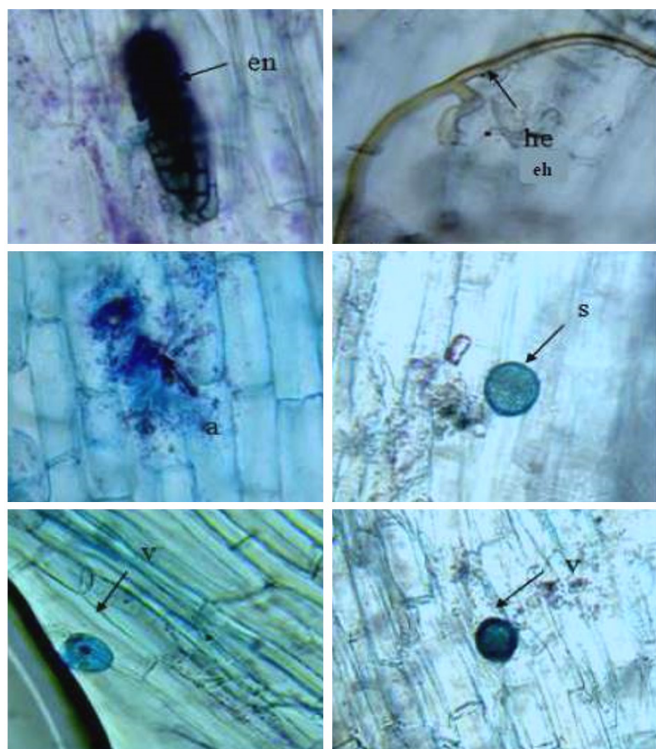


Figure 13: Eryngium maritimum roots showing endomycorrhizal fungi. (a): external hyphae (he) and spores (s); vesicles (v) and endophytes (en) (G. × 400) (Photos LBBPP Hibilik, 2016)

root and fungal exudates: flavonoids and strigolactones, chemical substances secreted by the host plant, will stimulate the metabolic activity of the fungus (Akiyama, 2007; Reinhardt, 2007; Stevenin, 2011; Gavériaux, 2012). The morphology of the hyphae changes and adopts an intense branching growth (Buée, 2000). Thus, there is spontaneous germination of a spore followed by the formation of germinal hyphae. In the absence of host recognition, germination can slow down, or even stop, but retain enough carbon resources to be able to repeat this germination. The AMF then releases “Myc” factors into the soil which will lead, in the plant, to the activation of the symbiosis signaling pathway (Delaux, 2013) and thereby more lateral roots are put in place (Oláh, 2005; Genre, 2013), elongate and form, by branching, a pre-symbiotic mycelial network developing in the direction of the root (Stevenin, 2011).

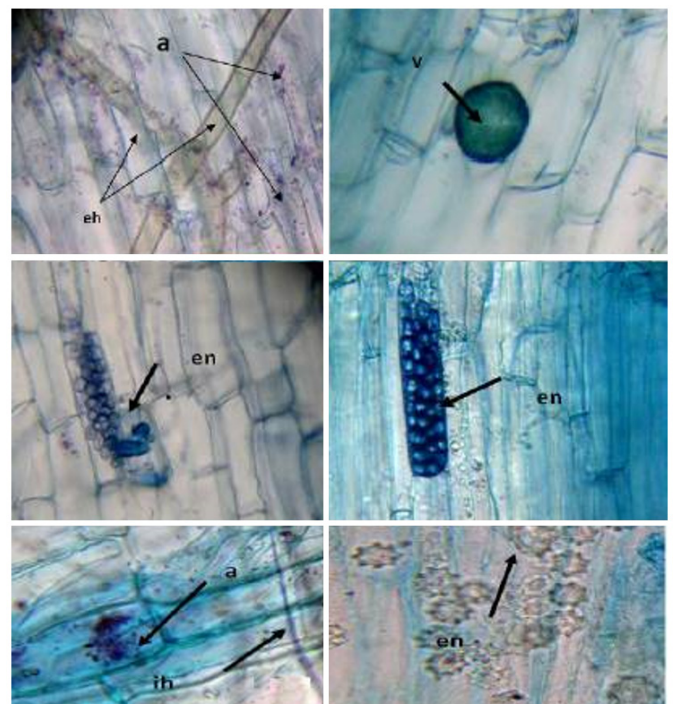


Figure 14: Roots of Citrus aurantium L. showing endomycorrhizal structures: arbuscules (a); extra (he) and intraradicular (ih) hyphae (ih); vesicles (v) and endophytes (en), kinds of intracellular sclerotia. (G. × 400) (BBPPL, Artib, 2016)

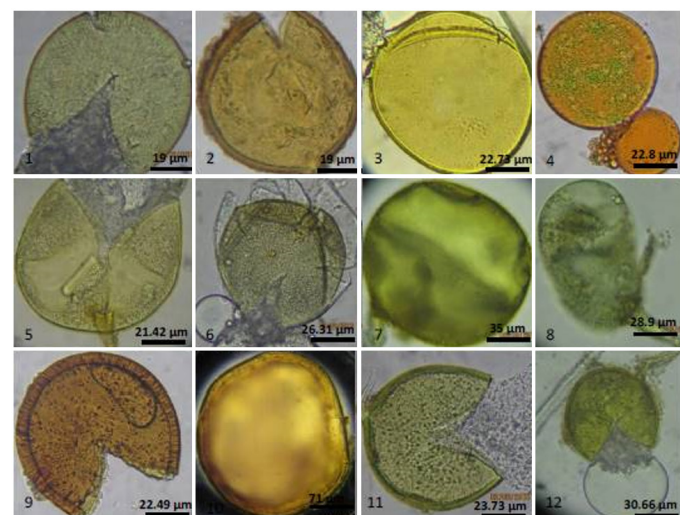


Figure 15: Different types of endomycorrhizal fungal spores isolated from the rhizosphere of mycorrhizal leek plants (BBPPL, Hibilik, 2018)

The fungus forms appressoria which are structures for attaching then penetrating cells of the epidermis (penetration can be achieved in 36 hours) (Kendrick, 1992). At this stage, other fungal signals must intervene; they lead to a cytoplasmic rearrangement of the epidermal cells and the formation of a pre-penetration apparatus (PPA) thanks to which the fungus can cross the plant cell (Bago, 1998; Genre, 2005). The hyphae of the fungus will then progress intercellularly to the cells of the root cortex, where they will form highly branched intracellular structures of exchange (arbuscules) and reserve (vesicles).

Extracellular hyphae develop to follow root growth or establish other foci of infection in the root (Bago, 1998). The plasma membrane of the plant cell greatly increases its surface area and invaginates all around. It is at this cellular interface that the exchange of nutrients between partners mainly takes place (Reinhardt, 2007), water and mineral elements, such as phosphorus, which are then exchanged with the plant in return for carbohydrates (Graham, 1997). After differentiation of intra-root structures, the fungus produces spores from its extra-root mycelium (Akiyama, 2007). All these molecular communication mechanisms are still little known, but research is progressing steadily thanks in particular to advances in genomics (Garbaye, 2013).

The diversity of AMFs in Morocco

In Morocco, the study of the diversity of endomycorrhizal fungi was carried out at the level of the rhizosphere of a large number of plant species: olive tree (Chliyah, 2014; Semane, 2018), Poplar (Talbi, 2014) (Figure 16), oleaster (Sghir, 2013), carob tree (Talbi, 2015) (Figure 17), argan tree (Sellal, 2016), date palm (Sghir, 2015),

citrus (Artib, 2016), martorn (Hibilik, 2016), Chickpea (El Hazzat, 2018), saffron (El Aymani, 2019), sugarcane (Selmaoui, 2017) (Figure 18). It also concerned various types of soils, case, for example, of coastal dunes (Touati, 2015) and highway embankments (El Hazzat, 2017). Among the species of endomycorrhizal fungi reported, representatives of the genus *Glomus* are the most dominant (Chliyah, 2014; Kachkouch, 2014; Semane, 2018; Talbi, 2015; Sghir, 2015; Sghir, 2013; Talbi, 2014; Artib, 2016; Selmaoui, 2017; Bahouq et Douira, 2017; Hibilik, 2016; Hibilik, 2018; Touati, 2015; El Hazzat, 2017; Sellal, 2016; El Aymani, 2019; El Hazzat, 2017; Nounsi, 2015).

Transfer of phosphorus (P) from arbuscular mycorrhizal fungi to the plant

Soils contain large amounts of organic or inorganic P (Sanyal and De Datta, 1991), these quantities are estimated between 200 and 3,000 mg/kg of soil (Harrison, 1997). Plants adsorb Phosphorus in the form of inorganic orthophosphate with the other cationic constituents of the soil to form CaPO_4 complexes with calcium at high pH and FePO_4 or AlPO_4 complexes with iron (Fe) or aluminum at low pH. As well as in the form of organic molecules such as lecithin (Sanyal and De Datta, 1991; Javot, 2007b; Richardson, 2009; Smith and Smith, 2012). In addition, P is very poorly mobile in soils (Javot, 2007b). When the proportion of phosphorus in the soil is low, plants always find themselves in difficult situations to meet their needs (Richardson, 2009; Smith, 2011). Indeed, P is an essential element for the life of the plant, it enters into the synthesis of many molecules such as adenosine triphosphate (ATP) and phospho-nucleotides: uridine triphosphate (UTP), cytidine triphosphate (CTP) and gua-

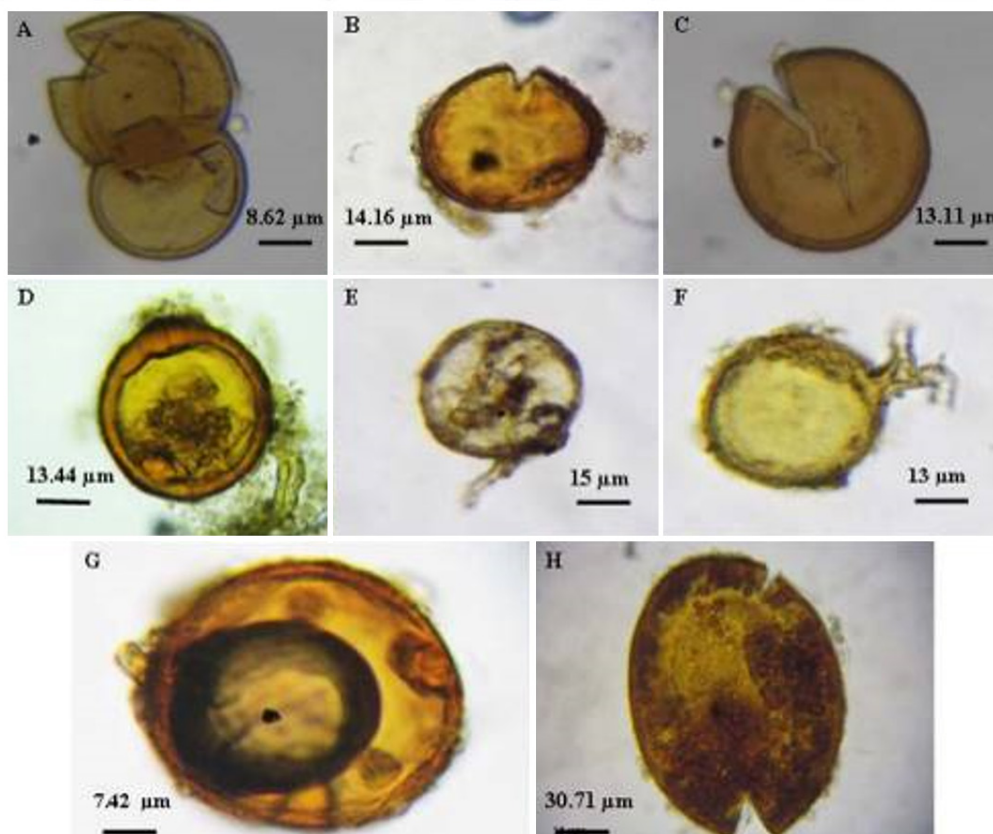


Figure 16: Some species of endomycorrhizal fungi isolated from the rhizosphere of *Populus alba*: *Acaulospora laevis* (A) and (C); *Kuklospora colombiana* (B); *Glomus macrocarpum* (D); *Scutellospora sp1.* (E); *Acaulospora lacunosa* (F); *Glomus rubiformis* (G); *Gigaspora sp1.* (H) (G. ×400) (Photos LBBPP, Talbi, 2014)

nosine triphosphate (GTP), phospholipids, certain enzymes and co-enzymes (Marschner, 1995; Gaude, 2008; Maathuis, 2009). Phosphorus is also stored in the vacuoles in the form of inositol-hexa-phosphate also called phytic acids (phytates) which are excellent chelators of cations such as Ca^{2+} , Mg^{2+} , K^+ , Fe^{2+} and Zn^{2+} (Mitsuhashi, 2005). The formation and hydrolysis of pyrophosphate bonds is a central mechanism in the regulation of cellular energy (Maathuis, 2009).

Mycorrhization is a strategy used by the plant to directly take P from the soil, via the extra-root mycelium of the

AMF (Karandashov et Bucher, 2005; Smith, 2011). Also plant cells containing mycorrhizal structures contain a higher amount of P than other root cells (Schoknecht and Hattin, 1976; Weiersbye, 1999). Other work has reported that the amount of phosphorus transferred by AMFs to plants is greater than that of other nutrients (Smith, 2003, 2004; Harrison, 2010). In addition, the mycorrhizal pathway could be essential for the survival of certain plants that do not have root hairs and whose absorption of nutrients would be difficult.

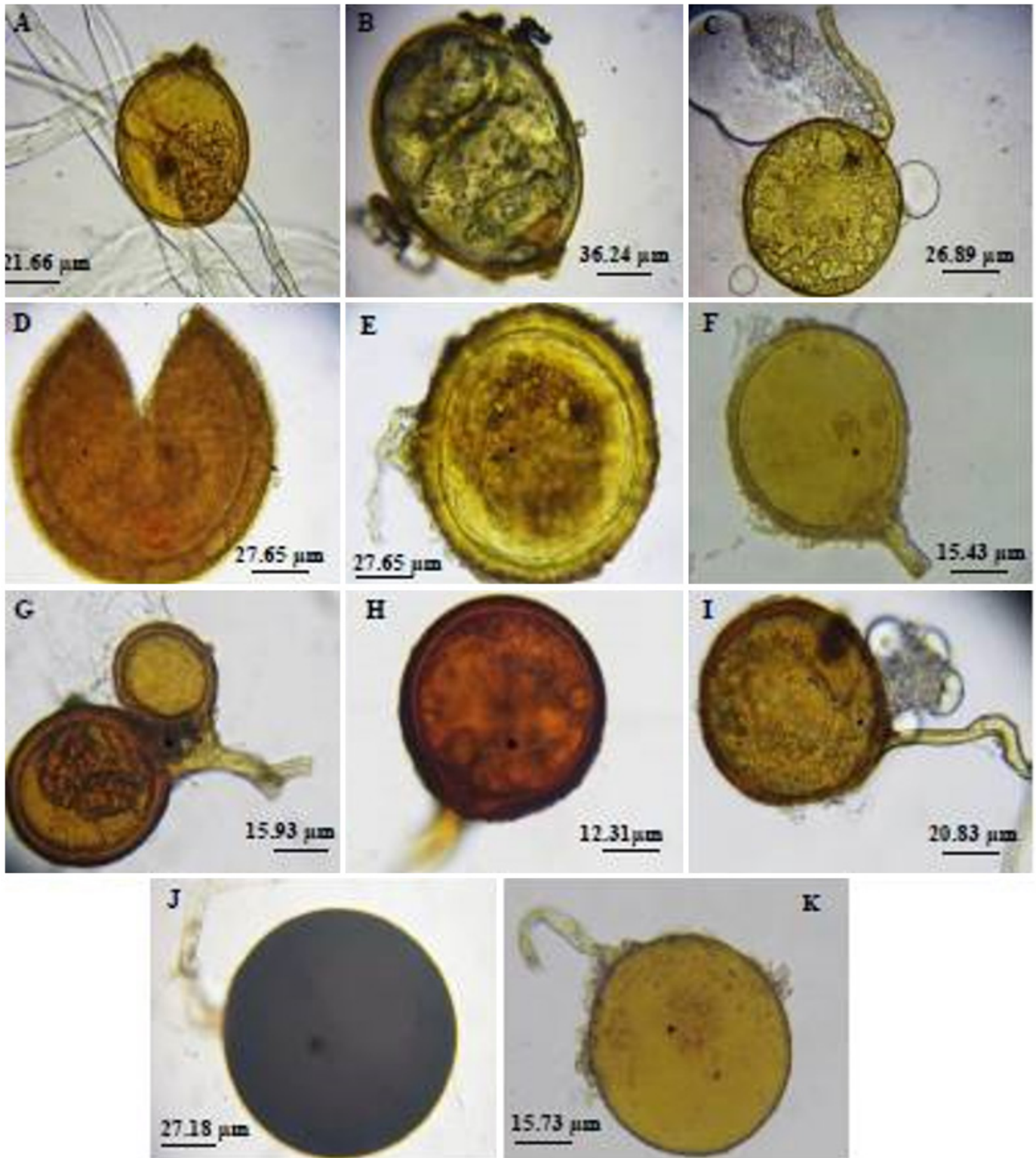


Figure 17: Some species of endomycorrhizal fungi isolated from the rhizosphere of the carob tree (*Ceratonia siliqua*) in Morocco: *Glomus aureum* (A), (F), (K); *Acaulospora* sp 4 (B); *Glomus* sp 3 (C); *Acaulospora denticulate* (D); *Glomus macrocarpum* (E); *Glomus geosporum* (G); *Scutellospora heterogamma* (H); *Acaulospora laevis* (I); *Scutellospora nigra* (I) (Photos LBBPP, Talbi, 2015)

The presence of AMF is essential to explore the soil in search of phosphorus to satisfy the nutritional needs of plants. To access soil P pools inaccessible to plants, AMF would be able to hydrolyze organic P into inorganic P to make it available in the soil to the plant or even transfer it directly to the host plant (Joner, 2000; Koide and Kabir, 2000; Feng, 2003; Shibata and Yano, 2003). Phosphatase activity increases in the rhizosphere in the presence of endomycorrhizal plants (Rubio, 2002). AMFs exhibit strong alkaline and acid phosphatase activities in intra- and extra-root hyphae (Smith and Gianinazzi-Pearson, 1990; Ezawa, 2001; Van Aarle, 2001, 2002; Olsson, 2002).

Indeed, it has been shown, thanks to the use of compartment devices and P labeled ^{32}P or ^{33}P that the extra-root hyphae of the fungus are able to take up and transport P to the roots (Cooper et Tinker, 1978; Jakobsen, 1992; Pearson et Jakobsen, 1993; Cui and Caldwell, 1996; Smith, 2003, 2004). In addition, it has been noted that even when a supply of P is added to the matrix where the roots develop, the plants still seek to obtain a transfer of this P via the AMF (Smith, 2003, 2004).

The AM fungus can store a greater amount of phosphorus than the roots, allowing a continuous flow of phosphorus into the hypha. Phosphorus can be stored in three

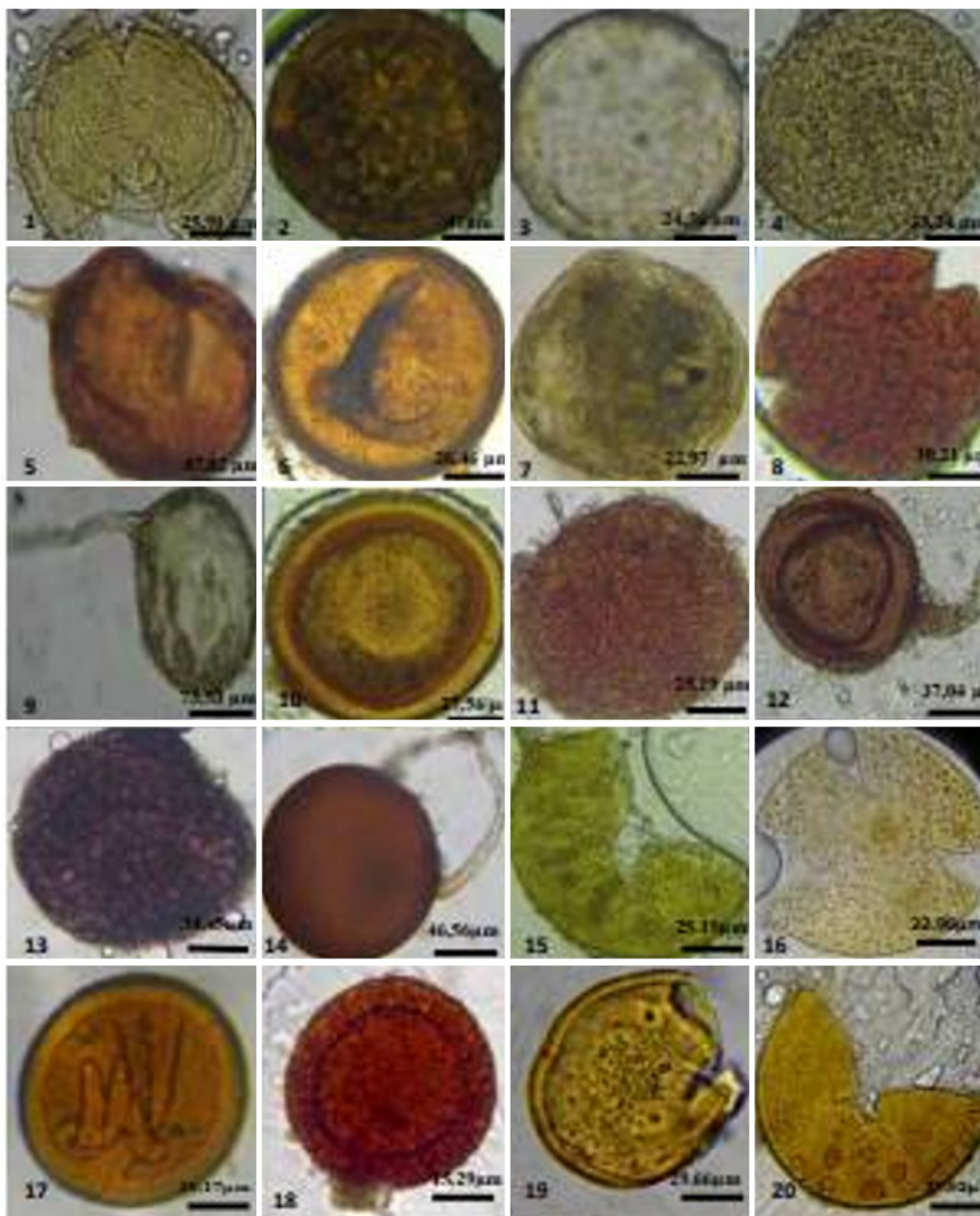


Figure 18: Some spores of endomycorrhizal fungi isolated from the rhizosphere of sugarcane (1) *Acaulospora morrowiae*; (2); *Pacispora scintillans*; (3) et (4): *Gigaspora* sp; (5); *G. sp*; (6); *Glomus macrocarpum*; (7); *Gigaspora* sp; (8); *Acaulospora spinosa*; (9); *Ambispora Appendicula*; (10); *Acaulospora excavate*; (11); *Acaulospora* sp1; (12); *Gigaspora*.sp; (13); *E. infrequens*; (14); *Glomus versiforme*; (15); *Pacispora scintillans*; (16); *Pacispora* sp.1; (17); *Glomus globiferum*; (18); *Scutellopora heterogamma*, (19); *Glomus fasciculatum*; (20); *Acaulospora dilatata* ($\times 400$) (Photos LBBPP, Selmaoui, 2017)

forms: soluble orthophosphate, soluble polyphosphate and polyphosphate granules. These correspond to more than 40% of the total phosphorus of the fungus and are stored in the vacuole (Bolan, 1991).

The uptake of P by the extra-root mycelium takes place against a concentration gradient (passive transport). As the uptake process is energy dependent, P enters the cytoplasm via high affinity Pi/H⁺ symports (Harrison and Van Buuren, 1995; Karandashov and Bucher, 2005; Javot, 2007b). There are three P transporters, GvPT, GiPT and GmosPT, identified in *Glomus versiforme*, *G. intraradices* and *G. mosseae* respectively (Harrison and Van Buuren, 1995; Maldonado-Mendoza, 2001; Benedetto, 2005).

The P is then rapidly condensed into polyphosphate (poly-P) (Ezawa, 2004). These poly-Ps have been shown to account for more than 60% of the total P accumulated in AMFs (Hijikata, 2010). Poly-Ps are polymers made up of 3 to thousands of Ps linked by high-affinity phosphoanhydride bonds (Kornberg, 1999). In the extra-root mycelium of AMFs, the average length of poly-P reaches 13 to 15 P connected (Rasmussen, 2000; Viereck, 2004). The majority of the poly-P thus formed is then stored in the acid compartments, probably vacuolar, in the extra-root hyphae of the AMF (Viereck, 2004). The poly-P would be very mainly transported in the intra-root hyphae by a system of tubular vacuoles connected between them, while another part of the transport would take place via the cytoplasmic current (Uetake, 2002; Van Aarle and Olsson, 2008). This transfer takes place at the level of the exchange surfaces which can theoretically be located at two levels: at the level of the intercellular hypha and at the level of the arbuscule. The arbuscular organization develops a large exchange surface, so it is supposed to be the privileged place for the flow of phosphorus to the root. Poly-P length is less in intra-root hyphae compared to extra-root hyphae (Solaiman, 1999; Viereck, 2004; Ohtomo et Saito, 2005). This lower length seems to confirm the active hydrolysis of poly-P in the intra-root hyphae in order to produce orthophosphates that can be released in the apoplast at the plant/AMF interface (Ezawa, 2001). The exact mechanism of hydrolysis of poly-P groups is not fully understood. However, the intense enzymatic activity of phosphatases near arbuscules compared to other intra-root structures seems to indicate a role of these enzymes in this function (Tisserant, 1993; Ezawa, 1995; Van Aarle, 2005).

Interaction mycorrhizes-bactéries

The interaction between the mycelium of arbuscular mycorrhizal fungi (AMF) and bacteria has been studied by several mechanisms to know the transport of carbon in fungal tissues (Andrade, 1997; Bago, 2002; Trépanier, 2005), change in soil structure (Tisdall and Oades, 1979), competition for available nutrients (Ravnskov, 1999) and physiological changes in root exudates (Söderberg, 2002). Bending (2006) noted that some information regarding the composition of AM fungal exudates, and their availability in soil for the benefit of microbial communities has not been very well studied.

Various studies have reported the influence of bacterial populations present in the soil on the colonization of the root system of plants by AMF (Taktek, 2015). Some soil bacteria colonize the hyphae of dead or living AMFs, they use the exudates released by the living fungal hyphae, while other bacterial species use the hyphae themselves as a substrate (Toljander, 2006). The study by Fillion (1999) on the effect of fungal exudates on the growth of some bacterial strains present in the soil showed that these extracts could sometimes have an antagonistic effect, but in most cases stimulatory effects on the growth of microorganisms, suggesting that the products exuded by the mycelium may play an important role in the direct interactions between AMFs and other soil microorganisms.

Some bacteria of the genus *Paenibacillus* can be intimately associated with the mycelium of *Glomus intraradices* (Mansfeld-Giese, 2002). Artursson and Jansson (2003) found that *Bacillus cereus*, isolated from soil, has higher levels of attachment to *Glomus dussii* hyphae compared to other bacterial strains. Scheublin (2010) reported that the colonization of the hyposphere of two AMFs (*Glomus intraradices* and *Glomus proliferum*) is specific to certain groups of bacteria. The analysis of bacterial communities attached or not to the fungal mycelium showed the abundance of a group of bacteria from the Oxalobacteraceae family, intimately attached to the hyphae, thus suggesting the presence of a specific dialogue between these microorganisms (Scheublin, 2010). Indeed, it seems that some bacteria are more specific to a particular type of AMF, which could be due to the secretion of specific exudates by the fungal species (Artursson and Jansson, 2003). *Bacillus pabuli* has the ability to improve root colonization by arbuscular mycorrhizae (Xavier and Germida, 2003) and can also improve plant growth (Artursson, 2006).

This phenomenon could be linked to the solubilization of rock phosphate by phosphate-solubilizing bacteria (BSP) and the release of P, part of which will be taken up by the AMF and will ensure its development and the other will be transported to the plant by the intermediary of the mycelial network (Taktek, 2015).

In addition, AMFs can influence the diversity and structure of bacterial communities in the rhizosphere (Linderman, 1988; Meyer and Linderman, 1986; Paulitz and Linderman, 1991; Toljander, 2006; Offre, 2007). PSBs (Phosphate Solubilizing Bacteria) have already been proposed as a viable solution to solve the problem of precipitation of soluble superphosphate fertilizers (Khan, 2007; Narula, 2000).

Many genera of PSBs have shown good potential for use as biofertilizers for improving plant nutrition P, as they mobilize P from low inorganic and organic P sources in the soil (Calvo, 2014). Several reports have also highlighted the importance of the beneficial interaction between PSB and AMF in mobilizing phosphorus and improving plant uptake (Calvo, 2014; Sharma, 2013).

CONCLUSION

Through this bibliographic study, we noted the diversity of ectomycorrhizal and endomycorrhizal fungi related to plant species. The important role of these fungi in the functionality of ecosystems has also been noted. In Morocco, studies carried out on endomycorrhizae have shown the importance of inocula based on these fungi in stimulating the growth of plant species and their protection against various pathogens. The use of these fungi in the nursery will make it possible to obtain vigorous plants capable of developing once transferred to different biotopes, with various climatic conditions. Mycorrhization of plants at the nursery level will gain momentum in the coming years and will be widely accepted as a component of an integrated approach to ecosystem management.

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