Environmental and Experimental Biology (2022) 20: 119–126
http://doi.org/10.22364/eeb.20.12

Original Paper

Taxonomic diversity and morphological types of arbuscular mycorrhizal fungal communities symbiotic with Atlas pistachio along an aridity gradient in Algeria

ISSN 2255-9582

Abdelkrim Limane*, Noria Saadoun

Department of Biology, Faculty of Biologic Sciences and Agronomic Sciences, Mouloud Mammeri University, Route de Hasnaoua, 15000, Tizi Ouzou, Algeria

*Corresponding author, E-mail: abdelkrim.limane@ummto.dz

Abstract

Because of the global warming threat, multidisciplinary studies of arid environment ecology are highly expected. In four populations of Atlas pistachio (*Pistacia atlantica* Desf.) located in Algeria along an aridity gradient, both the taxonomic diversity and the morphological types of communities of arbuscular mycorrhizal fungi (AMF) in rhizospheric soil were assessed. AMF taxonomic richness was low in all sampled populations, with a dominance of the Glomeraceae family. The AMF morphological *Arum* type was identified in fine roots of all sampled individuals, and the *Paris* type only in those sampled in the two less arid sites. Along the increasing aridity gradient, climatic conditions would be a determining factor in the decrease of the AMF taxonomic richness within Atlas pistachio rhizospheric soils; it could also indirectly influence the expression of both morphological types (*Arum* and/or *Paris*) within Atlas pistachio fine roots.

Key words: aridity, Atlas pistachio, arbuscular mycorrhizal fungi, taxonomic richness, *Arum* type, *Paris* type, rhizosphere.
Abbreviations: AMF, arbuscular mycorrhizal fungi.

Introduction

Studies dealing with adaptations of living communities to arid environments are important due to the global warming trend, as they help scientists to anticipate suitable responses to the increasing aridity crisis that threatens life on Earth. Algeria is naturally appropriate for such studies, as it is the tenth-largest country in the world and the largest in Africa (Entelis 2016), with 95% of its surface located in arid areas (Halitim 1988). Only a limited number of tree plant species are adapted to such xeric biotopes. Of these tree species, Atlas pistachio (*Pistacia atlantica* Desf.) can serve as an interesting model. Indeed, several publications have reported the high adaptability of Atlas pistachio to increasing aridity (from semi-arid to hyperarid ecoclimatic conditions) by leaf morphological and histological (Belhadj et al. 2007; Belhadj et al. 2008), root architecture (Limane et al. 2014; Limane 2018), and leaf biochemical traits (Hadj Aissa 2004; Ait Saïd et al. 2011). However, publications concerning its mycorrhizal status are scarce (Limane et al. 2016).

Arbuscular mycorrhizal fungi (AMF) are of high interest regarding their proven efficiency in increasing the fitness of vascular plants and thus their productivity (Klironomos et al. 2000; Allen et al. 2003). They optimize plant development via two main pathways: (i) facilitation of mineral nutrition (more particularly for phosphorus, considered as one of the main mineral deficiencies in Mediterranean and tropical soils) and, (ii) better tolerance or resistance of the plant to biotic stresses (impact of fungal pathogenic microorganisms, bacteria or plant-parasitic nematodes), and/or abiotic stresses (water stress, saline stress, heavy metals). Therefore, in arid areas it might be likely to expect strong and diverse symbiotic relationships between plants and AMF that benefit both communities. Studies from semi-arid and arid areas show that globally the AMF species richness of plants varies from three to 32 species (Yang et al. 2010; Alguacil et al. 2012; Pagano et al. 2013). Furthermore, the diversity of AMF species decreases in water-deprived soils with a dominance for taxa that form glomoid spores (Bahadur et al. 2019).

The aim of the present study was to characterize the taxonomical and morphological diversity of AMF communities associated with Atlas pistachio, along an aridity gradient, ranging from semiarid to hyperarid ecoclimate.

Materials and methods

Selection of Atlas pistachio populations

In Algeria, aridity increases from the north (Mediterranean littoral) to the south (Sahara). The spontaneous populations

of Atlas pistachio (*Pistacia atlantica* Desf.), located along the north-south transect were the same as those used in previous studies (Fig. 1, Limane et al. 2014; Limane 2018).

Climatic conditions

There are no weather stations within the sampled populations, so climatic data from the nearest stations were extrapolated. Table 1 summarizes the main climatic variables measured and those calculated for the four weather stations near the studied populations of Atlas pistachio.

The locations of the studied populations range gradually from the semi-arid zone (Sidi Naamane –Médéa), arid zones (Daya el Mergueb – M'sila, Daya Lekhneg – Laghouat) and to the hyperarid zone (Béni Ounif – Béchar). The length of dry seasons ranges from 4.5 months per year in the semi-arid zone to 12 months per year in the hyper-arid zone.

Sampling and processing of rhizospheric soils and fine roots

The sampled populations and individuals were those of previous studies (Limane et al. 2014; Limane 2018).

Atlas pistachio is a dioecious species (the male and the female flowers are located on different trees), and thus, it is necessary to carry out sampling "in clusters". This method involved subdividing the population into two groups (clusters), one comprised of male individuals and the second of females. In each subgroup, simple random sampling was performed to obtain equal numbers of each sex.. The number of samples in each population was even except that of Daya el Mergueb because it contained a young immature individual.

In spring (March, April), for each selected individual in each population, samples of rhizospheric soil were collected at 20-cm depth intervals, starting from the surface (0 cm) to 80 cm under each pistachio tree. The collected soil samples (four from each individual) were homogenized to obtain one composite sample representative of the rhizospheric soil.

Fine roots with a diameter of less than 1 cm were extracted from each sample. Fine roots less than this diameter have not yet developed secondary structures (Drénou 2006). The fine roots were those located in the terminal ramifications of the root system. Given their fragility, as a precaution care was taken to extract a few thick pre-terminal roots with an appreciable density of terminal fine roots coated with their rhizospheric soils, to maintain their tissue integrity during transport, especially in these arid environments.

In the laboratory, the rhizospheric soil particleswere gently eliminated by rinsing with tap water. Then, fine roots were selected and were coarsely cut into a suitable number of fragments of 2-cm length (Table 2) before processing.

AMF spore extraction and identification

Spores were separated from rhizospheric soil by wet sieving and decanting (Gerdemann, Nicolson 1963). Under a stereomicroscope, the spores were manually extracted and sorted by morphotypes. They were then mounted on microscope slides in polyvinyl alcohol-lactic acid-glycerol mounting medium (Omar 1979) mixed with Melzer's reagent (1:1) to identify dextrose. Description of size, shape, colour, parietal architecture, ornamentation, and characteristics of the suspending hyphae by microscopic examination of spores (Nikon Eclipse) at 400 – 600 × magnification was used for morphological characterization, and in several cases to species identification using species descriptions and identification keys of Blaszkowski (2012), as well as internet resources (http://www.amf-phylogeny.com). The estimation of the number of spores for the different morphotypes and species encountered allowed the estimation of AMF species richness in Atlas pistachio rhizospheric soils.

Bleaching and coloration of fine roots

The protocol of Brundrett et al. (1996) adapted to Atlas pistachio roots was used: bleaching with 10% KOH (w/v) at 90 °C for 1 h; the roots of Atlas pistachio are very rich in tannins, and therefore several bleaching cycles were necessary. After passage in acidified water (2% HCl for

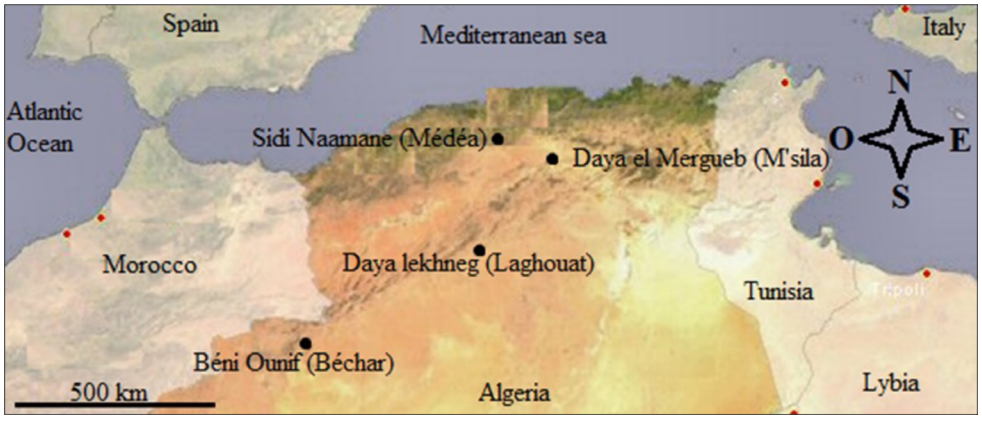

Fig. 1. Geographic location of the four Atlas pistachio populations.

Table 1. Climatic data of the four weather stations according to the north-south transect (Limane et al. 2014; Limane 2018)

Population	Geographical coordinates, altitude (m)	Weather station	Precipitation (mm year^{-1})	Average annual temperature (°C)	Potential of evapotranspiration (mm year^{-1})	Aridity index	Ecoclimatic zonation (UNEP 1992)	Length of dry season (Bagnouls, Gaussen 1953) (months year^{-1})
Sidi Naamane	35°11'354"N 3°1'248"E (765)	Médéa	627.6	15.43	1597.38	0.39	Semiarid	4.5
Daya El Mergueb	35°33'177"N 3°56'214'E (584)	M'sila	216.42	19.47	1573.86	0.14	Arid	10
Daya Lekhneg	33°41'400"N 2°39'761"E (837)	Hassi R'mel	110.29	19.8	2168.03	0.05	Arid	11
Béni Ounif	31°48'728"N 1°44'871"E (760)	Béchar	75.92	21.62	2365.57	0.03	Hyperarid	12

30 min), the roots were stained with trypan blue [0.05% (w/v) in lactoglycerol] at 90 °C for 4 h and the excess dye was diluted in a glycerol-water solution (50%), in which solution the roots were kept until microscopic observation.

Identification of mycorrhizal structures and morphological types expressed in fine roots

The bleached and colored fine roots were mounted on a microscope slide in fresh lactoglycerol. They were carefully crushed to separate the tissues. Microscopic examination (FinePix J38) at 100 – 400 × magnification was performed to verify the occurrence of endomycorrhizal symbiosis in roots by presence of arbuscules, vesicles, intra and intercellular hyphae and others, and to identify the "*Arum*" and "*Paris*" morphological types of AMF, based on the host plant colonization pattern (Dickson 2004).

Results

Taxonomic richness of AMF communities in rhizospheric soil

Only six species belonging to four genera of AMF were identified in the rhizospheric soils (Table 3). The AMF species richness per population was low (varied from three to five species per population) and tended to decrease along the aridity gradient. The majority of identified species had formed glomoid spores. Only one species in the population of Sidi Naamane and that of the Daya Lekhneg had gigasporoid spores. Three species were dominant and common to the four populations: *Rhizophagus irregularis, Septoglomus constrictum* and *Funneliformis mosseae*. These species seem to constitute an invariable "trio" along the gradient of increasing aridity.

Occurrence of endomycorrhizal structures in fine roots

A sufficient number of fine roots per population were examined (Table 2). Their microscopic observation allowed the identification of different structures indicative of mycorrhizal activity, as shown in Fig. 3. These observations showed that the species was naturally infected by AMF. However, no root fragments among the 518 observed showed ectomycorrhizal structures, which confirms the endomycotrophic nature of this species.

AMF morphological types in fine roots along the increasing gradient of aridity

The AMF morphological structures observed in Atlas pistachio fine roots confirmed the presence of inter-cellular hyphae and vesicles (Fig. 3A, 3C, 3F) characteristic of *Arum* type. Fig. 3D illustrates intracellular coils and Fig. 3B and 3E show arbusculated coils characteristic of the *Paris* type. The proportions of these structures within fine roots of the four populations are shown in Table 3. The *Arum* type dominated in all the sites, whereas the *Paris* type was not detected in the most arid sites.

Table 2. Percentage of morphological types of AMF per population of Atlas pistachio

Population	Number of sampled individuals	Total number of root fragments observed	Morphological type of AMF	
			Paris type (% of individuals)	*Arum* type (% of individuals)
Sidi Naamane	8	147	≈ 30	100
Daya el Mergueb	7	140	100	100
Daya Lekhneg	6	114	0	100
Béni Ounif	6	117	0	100

Table 2. AMF genera and species identified in rhizospheric soils of the four sampled populations of Atlas pistachio

Population	Number of sampled individuals	Identified genera	Total number of genera	Identified species	Total number of species
Sidi Naamane	8	*Rhizophagus* *Septoglomus* *Funneliformis* *Scutellospora*	4	*Rhizophagus irregularis* *Rhizophagus fasciculatum* *Septoglomus constrictum* *Funneliformis mosseae* *Scutellospora* sp1.	5
Daya el Mergueb	7	*Rhizophagus* *Septoglomus* *Funneliformis*	3	*Rhizophagus irregularis* *Septoglomus constrictum* *Funneliformis mosseae* *Funneliformis geosporus*	4
Daya Lekhneg	6	*Rhizophagus* *Septoglomus* *Funneliformis* *Scutellospora*	4	*Rhizophagus irregularis* *Septoglomus constrictum* *Funneliformis mosseae* *Scutellospora* sp2.	4
Béni Ounif	6	*Rhizophagus* *Septoglomus* *Funneliformis*	3	*Rhizophagus irregularis* *Septoglomus constrictum* *Funneliformis mosseae*	3
Total	27		4		6

Discussion

Taxonomic richness of AMF communities

It was demonstrated that taxonomical identification of AMF based only on morphological characters of spores for many reasons might not allow correct estimatation of the number of AMF species due to damaged spores as well as low sporulation intensity of some species (Sanders 2004). In addition, seasonal variation related to the sporulation of species present in the soil, the number of sample replicates, and losses during the procedure are among factors affecting detection of AMF species by spores (Dalpé, personal communication). However, data from semi-arid and arid areas show that globally the AMF species richness varies from three to 32 species (Yang et al. 2010; Alguacil et al. 2012; Pagano et al. 2013). In seven sites located in semi-arid areas in Morocco, seven distinct phylotypes belonging to the genus *Glomus* (dominant), *Scutellospora* and *Gigaspora* were identified (Abbas 2014). Seven species of AMF, all forming glomoid spores, were identified in Tunisia (Jmal et al. 2015). Within rhizospheric soils of the Atlas pistachio population in Daya el Gouffa (located in the same region as Daya Lekhneg), five genera of AMF were identified, in order of abundance: *Acaulospora* (45%), *Glomus* (18.18%), *Gigaspora* (7.43%), *Scutellospora* (3.85%), *Ambispora* (3%) and unidentified genera (22.54%) (Mechiah 2015). More recently, in populations of Atlas pistachio in different regions (except the one in Sidi Naamane), also few morphotypes were identified from rhizospheric soil, with the majority of spores belong to the Glomeraceae and Gigasporaceae families (Bouabdelli et al. 2018).

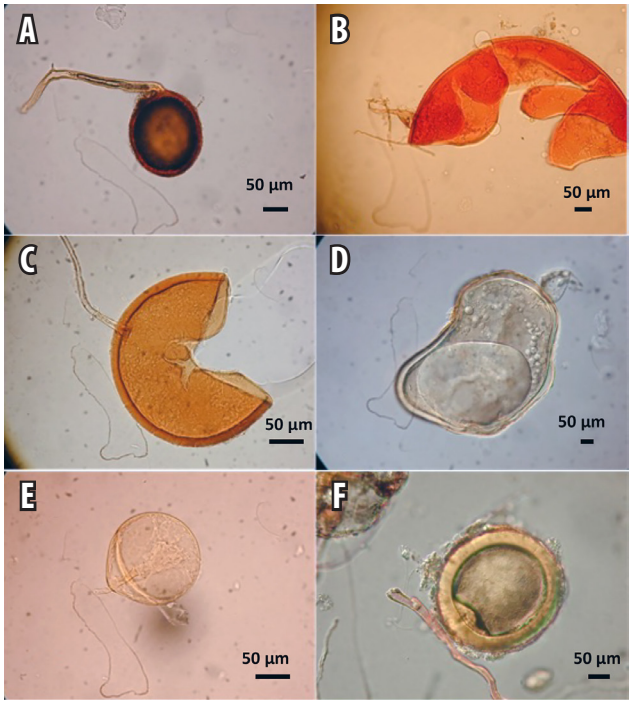

Fig. 2. Some of spores identified in the rhizospheric soils of Atlas pistachio. A, *Septoglomus constrictum*; B, *Funneliformis mosseae*; C, *Funneliformis geosporus*; D, *Scutellospora* sp.; E, *Rhizophagus irregularis*; F, *Rhizophagus fasciculatum*.

Despite the importance of AMF in plant physiology and nutrition, as well as in formation of plant communities, the factors affecting the presence, diversity, and density of spores in the soil and root colonization are not well understood (Van der Heijden et al. 2006). The main reason for this is the difficulty in establishing a causal relationship between soil factors, plants, and AMF populations (Vyas, Gupta 2014). Noverheless, there is evidence that AMF populations within soils can be affected by a variety of

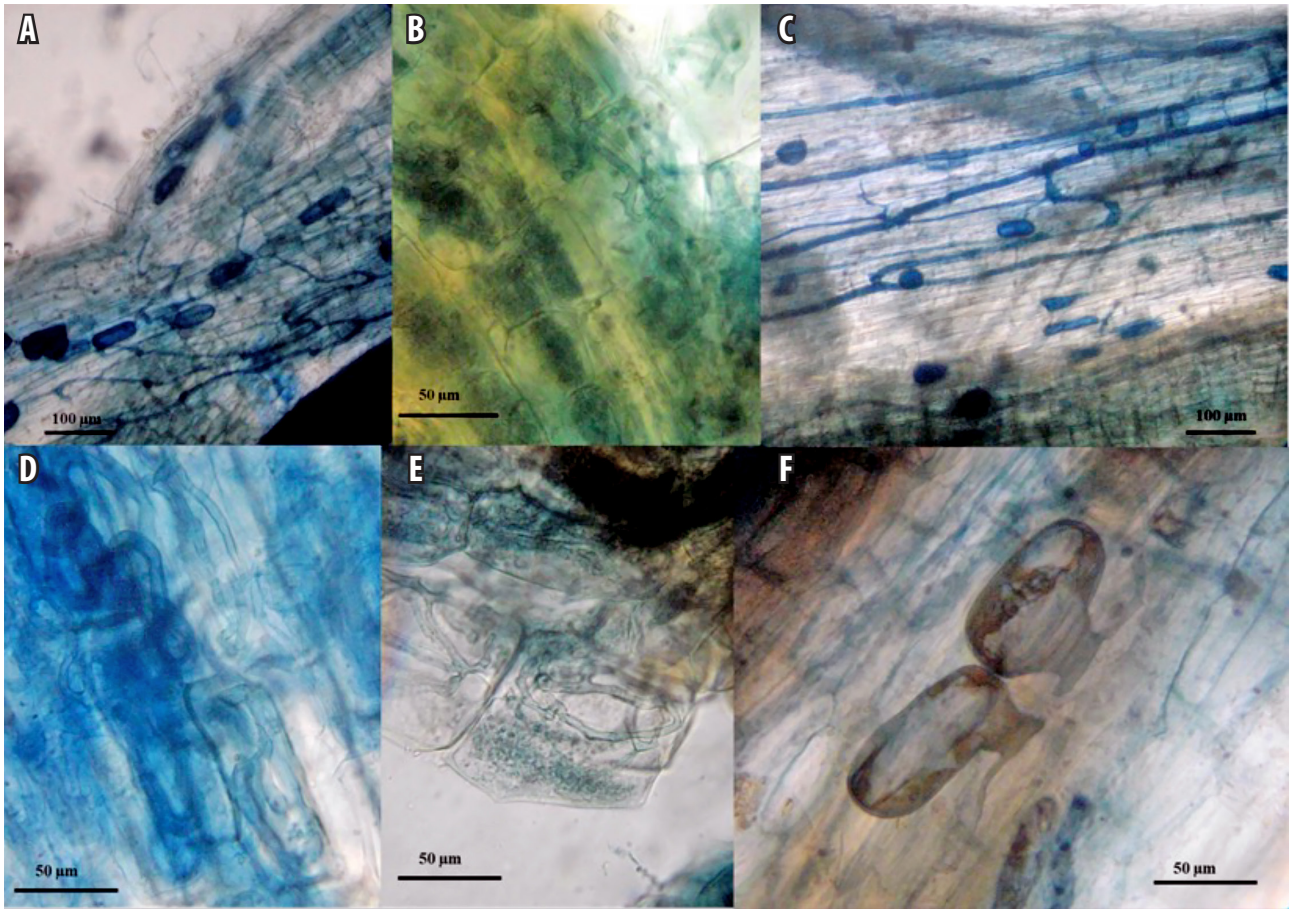

Fig. 3. Occurrence of different AMF structures within fine roots of Atlas pistachio. A, C and F, inter-cellular hyphae and vesicles; B and E, arbusculed coils; D, intracellular coils.

biotic and abiotic factors and various soil disturbances (Boddington, Dodd 2000; Egerton-Warburton, Allen 2000; Carvalho et al. 2003; Jmal et al. 2015).

Taxonomically, AMF species diversity decreases in water-deprived soils with a dominance of taxa that form glomoid spores (*Glomus, Claroideoglomus, Funneliformis, Septoglomus* etc.) (Bahadur et al. 2019). These genera account for more than 38% of those described so far (http://www.amf-phylogeny.com). Many studies have reported their good adaptation to variable physical and chemical conditions (Schenck, Kinloch 1980; Blaszkowski et al. 2002), and their ubiquity (Strullu 1990; Schwarzott et al. 2001).

The Glomeraceae family has been described as the most common group all similar studies. Their efficiency of infection is due to their speed of colonization, before that of Acaulosporaceae and Gigasporaceae; the fastest colonizers are also the most abundant (Hart, Reader 2002). However, AMF community assembly is not a matter of chance, but is favoured by the host (Gao et al. 2019). The coexistence of several AMF species is common and taxonomic diversity is a prerequisite for "functional complementarity". This concept suggests that a set of differently specialized species contribute better to a (given) function than each alone (e.g., one fungus provides aridity resistance, while another fungus is responsible for nutrient acquisition) – a direct positive effect of biodiversity on ecosystem functioning (Loreau et al. 2001). Nevertheless, physiological studies showing that different fungi provide different services are rare, although there are observations that fungal diversity increases plant productivity (Van der Heijden et al. 1998; Hart, Reader 2002; Gustafson, Casper 2006; Lekberg et al. 2007).

When the cooperation between plants and fungal partners is experimentally manipulated, it is possible to show that the plant can detect, discriminate, and reward the fungal partner with more carbohydrates; in turn, their fungal partners enhance their cooperation by increasing nutrient transfer only to the roots that provide more carbohydrates (Kiers and al. 2011). It can be hypothesized that the "trio" of AMF species (*Rhizophagus irregularis, Septoglomus constrictum* and *Funneliformis mosseae*), ubiquitous in all pistachio populations sampled in this study, is selected by the host, considering its potential competence and efficiency to cope with the requirements of arid environmental conditions.

AMF morphological types

Gallaud (1905) was the first to describe the two main morphological characteristics expressed during AMF root colonization, based on the identity of the plant. The *Arum* type was observed for the first time in the genus *Arum* (Araceae family), and the *Paris* type in the genus *Paris* (Liliaceae family). Most crop plants have characteristic *Arum* type mycorrhizal colonization with inter-cellular hyphae, arbuscules, and vesicles, while trees and herbaceous plants in forest habitats are associated with the *Paris* type with intra-cellular hyphae, coils, and arbusculated coils (Smith, Smith 1997; Dickson 2004).

The species of the Anacardiaceae family (to which *Pistacia atlantica* belongs) are classified as plants that exhibit only the *Arum* morphological type (Smith, Smith 1997). Previous studies (Hawley, Dames 2004; Bouabdelli et al. 2018) and the present observations confirm the expression of the *Paris* type within fine roots of Atlas pistachio.

The mechanisms controlling the expression of the *Arum* and *Paris* types are not fully understood. Both types of root colonization depend on the presence of inter-cellular spaces within the root cortex of the host plant (Brundrett, Kendrick 1988; Brundrett, Kendrick 1990; Menoyo et al. 2007). The *Arum* type grows in the cortex of roots with large inter-cellular spaces. These spaces constitute a pathway of less physical resistance for hyphal growth compared to the intracellular pathway (case of the *Paris* type) (Menoyo et al. 2007), which provides an opportunity for a rapid sequential penetration through cortical cells for the formation of arbuscules and inter-cellular vesicles (Smith, Smith 1997). It was demonstrated that intra-cellular hyphal growth during the expression of the *Paris* type was relatively slow compared to that of the *Arum* type (Brundrett, Kendrick 1990).

However, a strain of AMF isolated from a colonized *Arum*-type root can produce *Paris*-type structures in a different host (Smith, Smith 1997). A detailed study with *Lycopersicon esculentum* (tomato) confirmed that the type of colonization is not only under plant control, but that fungal identity plays an important role (Cavagnaro et al. 2001). In tomato grown in controlled culture, three fungal species (*Rhizophagus intraradices, Funneliformis mosseae*, and *Diversispora versiformis*) formed *Arum* structures, while three others (*Funneliformis coronatus, Gigaspora margarita*, and *Scutellospora calospora*) formed *Paris* structures without a visible inter-cellular phase. It seems that the morphology of AMF depends on both the individual plant species and the fungus colonizing them (Dickson 2004).

By comparing the morphological and functional differences of the two types, it could be deduced that each could provide advantages for the host. The *Arum* type would have the advantage of its rapid colonization and operationality, while the *Paris* type would have the advantage of having a larger surface and volume of coils (Dickson, Kolesik 1999). Arbuscular branches can be also formed on hyphal coils (i.e. producing arbusculate coils), like those observed in the present study (Fig. 3B, 3E) – these structures have a large surface area, which may also be highly important in nutrient transfer via this morphological type (Dickson et al. 2007).

In light of these results showing the apparent exclusivity of the *Arum* type in sites with the most arid conditions, it seems that environmental factors would be the determining factor. Under the hyperarid conditions of Béni-Ounif and the aridity of the Daya Lekhneg (aridity index 0.03 and 0.05, respectively), the optimal relative conditions for growth are met only during a short season when the roots of Atlas pistachio can develop rapidly. Indeed, it was reported that elongation of its root system can reach up to 1.5 m in one season (Ozenda 1977). Thus, in this race for survival, the young roots of Atlas pistachio would exclusively favour the morphological type *Arum*, which is quicker to establish and then quickly becomes functional.

However, and despite the fact that the Daya el Mergueb and the Daya Lekhneg are both located in arid ecoclimate sites, nevertheless their respective populations have different root colonization profiles. The *Arum* and *Paris* types are both expressed within the roots of some individuals of Daya el Mergueb whereas only the *Arum* type is found in those of Daya Lekhneg. The rainfall and aridity index at Daya Lekhneg were by 49 and 65% lower than those of Daya el Mergueb, respectively. In addition, the soil of the population of Daya lekhneg was swamped by seasonal flood water for a while before feasible sampling (Limane, unpublished results). Soil flooding can affect the diameter of aerial spaces in the roots (Cavagnaro et al. 2001). It was reported that seasonally flood-tolerant plants can survive under these conditions because of the interaction between structural and functional adaptations; important structural adaptations that facilitate O_2 diffusion include aerenchyma formation (Justin, Armstrong 1987). It can be hypothesized that in response to the risk of hypoxia, the roots of Atlas pistachio under the conditions at Daya Lekhneg would increase their aerenchyma surface, which would "indirectly" favour the *Arum* morphological type over the *Paris* type. This might explain the differences in the AMF morphological type, compared with the population of Daya el Mergueb that was also classified as an arid site.

Regarding the populations in the northern habitats of the transect (Sidi Naamane and Daya el Mergueb), their relatively less extreme conditions would allow the roots to be colonized by both AMF morphological types (*Arum* and *Paris*), which would complement each other with their respective advantages, as discussed earlier. The differences between the populations in the numbers of individuals that hosted the *Paris* type could be the subject of future research on the potential intra-population factors controlling these communities.

Acknowledgements

Acknowledgement: All our gratitude to Prof. Yolande Dalpé and her team for welcoming us in their laboratory (at the Eastern Cereal and Oilseed Research Centre (ECORC), Ottawa, Canada) and providing us with their valuable resources and expertise to achieve this works.

References

Abbas Y. 2014. Microorganismes de la rhizosphère des Tetraclinaies: un outil pour optimiser la régénération assistée du *Tetraclinis articulata* Vahl. Master. Thèse de doctorat. Université Mohamed V N° d'ordre 2751, Maroc.

Alguacil M.M., Torrecillas E., Roldán A., Díaz G., Torres M.P. 2012. Perennial plant species from semiarid gypsum soils support higher AMF diversity in roots than the annual *Bromus rubens*. *Soil Biol. Biochem*. 49: 132–138.

Allen M.F., Swenson W., Querejeta J.I., Egerton-Warburton L.M., Treseder K.K. 2003. Ecology of mycorrhizae: a conceptual framework for complex interactions among plants and fungi. *Annu. Rev. Phytopathol.* 41: 271–303.

Azcón-Aguilar C., Palenzuela J., Roldán A., Bautista S., Vallejo R., Barea J.M. 2003. Analysis of the mycorrhizal potential in the rhizosphere of representative plant species from desertification-threatened Mediterranean shrublands. *Appl. Soil Ecol.* 14: 165–175.

Bagnouls F., Gaussen H. 1953. Saison sèche et indice xérothermique. *Bull. Soc. Hist. Nat. Toulouse* 88: 193–239.

Bahadur A., Batool A., Nasir F., Jiang S., Mingsen Q., Zhang Q., Pan J., Liu Y., Feng H. 2019. Mechanistic insights into arbuscular mycorrhizal fungi-mediated drought stress tolerance in plants. *Int. J. Molec. Sci.* 20: 4199.

Belhadj S., Derridj A., Aigouy T., Gers C., Gauquelin, T., Mevy J.P. 2007. Comparative morphology of leaf epidermis in eight populations of Atlas pistachio (*Pistacia atlantica* Desf., Anacardiaceae). *Microsc. Res. Techn.* 70: 837–846.

Belhadj S., Derridj A., Auda Y., Gers C., Gauquelin T. 2008. Analyse de la variabilité morphologique chez huit populations spontanées de *Pistacia atlantica* en Algérie. *Botany* 86: 520–532.

Błaszkowski J. 2012. *Glomeromycota*. W. Szafer Institute of Botany Polish Academy of Sciences, Kraków, p. 304.

Błaszkowski J., Adamska I., Czerniawska B. 2002. Arbuscular mycorrhizal fungi (Glomeromycota) of the Vistula Bar. *Acta Mycol.* 37: 39–62.

Boddington C.L., Dodd J.C. 2000. The effect of agricultural practices on the development of indigenous arbuscular mycorrhizal fungi. II. Studies in experimental microcosms. *Plant Soil* 218: 145–157.

Bouabdelli Z., Belhadj S., Smail-Saadoun N., Mévy J.P., Notonnier R. et al. 2018. Influence de l'aridité sur la variation de la colonisation mycorhizienne arbusculaire chez cinq populations naturelles algériennes du pistachier de l'atlas (*Pistacia atlantica* Desf.). *Rev. Ecol. Terre et Vie* 73: 330–344.

Brundrett M.C. 2002. Coevolution of roots and mycorrhizas of land plants. *New Phytol.* 154: 275–304.

Brundrett M.C., Bougher N., Dell B., Grove T., Malajczuk N. 1996. *Working with Mycorrhizas in Forestry and Agriculture.* ACIAR Monograph 32. Australian Centre for International Agricultural Research, Canberra.

Brundrett M.C., Kendrick B. 1988. The mycorrhizal status, root anatomy and phenology of plants in a sugar maple forest. *Can. J. Bot.* 66: 1153–1173.

Brundrett M.C., Kendrick B. 1990. The roots and mycorrhizas of herbaceous woodland plants. II. Structural aspects of morphology. *New Phytol.* 114: 469–479.

Carvalho L.M., Correia P.M., Caçador I., Martins-Loução M.A. 2003. Effects of salinity and flooding on the infectivity of salt marsh arbuscular mycorrhizal fungi in *Aster tripolium* L. *Biol. Fertil. Soils* 38: 137–143.

Cavagnaro T.R., Gao L.L., Smith F.A., Smith S.E. 2001. Morphology of arbuscular mycorrhizas is influenced by fungal identity. *New Phytol.* 151: 469–475.

Dickson S. 2004. The *Arum-Paris* continuum of mycorrhizal symbioses. *New Phytol.* 163: 187–200.

Dickson S., Kolesik P. 1999. Visualization of mycorrhizal fungal structures and quantification of their surface area and volume using laser scanning confocal microscopy. *Mycorrhiza* 9: 205–213.

Dickson S., Smith F.A., Smith S.E. 2007. Structural differences in arbuscular mycorrhizal symbioses: more than 100 years after Gallaud, where next? *Mycorrhiza* 17: 375–393.

Drénou C. 2006. *Les racines: Face cachée des arbres.* Institut pour le développement forestier CNPPF, Paris, 335 p.

Egerton-Warburton L.M., Allen E.B. 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecol. Applic.* 10: 484–496.

Entelis J.P. 2016. *Algeria: the Revolution Institutionalized*. Routledge. London, 252 p.

Gai J.P., Christie P., Cai X.B., Fan J. Q., Zhang J.L., Feng G., Li L. 2009. Occurrence and distribution of arbuscular mycorrhizal fungal species in three types of grassland community of the Tibetan Plateau. *Ecol. Res.* 24: 1345–1350.

Gallaud I. 1905. Études sur les mycorrhizes endophytes. *Revue Générale de Botanique* 17: 5–48, 66–83, 123–136, 223–239, 313–325, 425–433, 479–500.

Gao C., Montoya L., Xu L., Madera M., Hollingsworth J., Purdom E., Hutmacher R.B., Dahlberg J.A., Coleman-Derr D., Lemaux P.G., Taylor J.W. 2019. Strong succession in arbuscular mycorrhizal fungal communities. *ISME J.* 13: 214–226.

Gerdemann J.W., Nicolson T.H. 1963. Spores of mycorrhizal Endogone species extracted from soil by wet sieving and decanting. *Transact. British Mycol. Soc.* 46: 235–244.

Gillman L.N., Wright S.D. 2014. Species richness and evolutionary speed: the influence of temperature, water and area. *J. Biogeogr.* 41: 39–51.

Gustafson D.J., Casper B.B. 2006. Differential host plant performance as a function of soil arbuscular mycorrhizal fungal communities: experimentally manipulating co-occurring *Glomus* species. *Plant Ecol.* 183: 257–263.

Hadj Aissa F.Z. 2004. Etude de l'évolution de l'activité antioxydante de feuilles et de fruits du pistachier de l'atlas (*Pistacia atlantica* Desf. Doctoral dissertation, Laghouat, Centre Universitaire Amar Telidji. Laboratoire des sciences fondamentales.

Halitim A. 1988. *Sols des régions arides d'Algérie.* O.P.U., Alger, 384 p.

Hart M.M., Reader R.J. 2002. Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. *New Phytol.* 153: 335–344.

Hawley G.L., Dames J.F. 2004. Mycorrhizal status of indigenous tree species in a forest biome of the Eastern Cape, South Africa. *South Afr. J. Sci.* 100: 633–637.

Jmal Z., Labidi S., Dalpé Y., Slim S., Sahraoui A.L.H., Jeddi F.B. 2015. Diversité des champignons mycorhiziens arbusculaires d'un bas fond halomorphe en Tunisie. *J. New Sci.* 18: 648–657.

Justin S., Armstrong W. 1987. The anatomical characteristics of roots and plant response to soil flooding. *New Phytol.* 106: 465–495.

Kadi-Bennane S., Ait Said S., Smail Saadoun N. 2005. Etude adaptative de trois populations de *Pistacia atlantica* Desf. subsp atlantica (Ain Oussera- Messaad-Taissa), par le biais du complexe stomatique. *Options Méditerranéennes Série A* 63: 365–368.

Kiers E.T., Duhamel M., Beesetty Y., Mensah J.A., Franken O. et al. 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* 333: 880–882.

Klironomos J. N., McCune J., Hart M., Neville J. 2000. The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity. *Ecol. Lett.* 3: 137–141.

Lekberg Y., Koide R.T., Rohr J.R., Aldrich-Wolfe L., Morton J.B. 2007. Role of niche restrictions and dispersal in the composition of arbuscular mycorrhizal fungal communities. *J. Ecol.* 95: 95–105.

Limane A. 2018. Réponses architecturales racinaires et stratégies d'absorption hydrominérale chez *Pistacia atlantica* en fonction d'un gradient d'aridité croissante: cas d'un transect Nord-Sud en Algérie. Doctoral dissertation, Université Mouloud Mammeri, Tizi-Ouzou, Algeria.

Limane A., Smail-Saadoun N. 2016. *Pistacia atlantica*, a spontaneous hypermycotrophic phanerophyte: could be a natural tool to enhance the potential of mycorrhizal infectivity (PMI) of soils in arid regions? *Options Méditerranéennes Série A Séminaires Méditerranéens* 119: 267–271.

Limane A., Smail-Saadoun N., Belkebir-Boukais A., Kissoum-Hamdini K. 2014. Root architecture adaptation of *Pistacia atlantica* subsp. *atlantica* according to an increasing climatic and edaphic gradient: case of a north-south transect in Algeria. *Turkish J. Bot.* 38: 536–549.

Loreau M., Naeem S., Inchausti P., Bengtsson J., Grime J.P. et al. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294: 804–808.

Mechiah F. 2015. Approche des symbioses racinaires de Pistacia atlantica desf. de dayate el gouffa (laghouat, Algerie). Doctoral dissertation, Tizi Ouzou- Mouloud Mammeri. Algeria.

Menoyo E., Becerra A.G., Renison D. 2007. Mycorrhizal associations in *Polylepis* woodlands of Central Argentina. *Botany* 85: 526–531.

Monjauze A. 1968. Répartition et écologie de *Pistacia atlantica* Desf. en Algérie. *Bull. Soc. Hist. Afr. du Nord* 56: 128.

Omar M.B. 1979. A permanent mounting medium for fungi. *Bull. British Mycol. Soc.* 13: 31–32.

Ozenda P. 1977. *Flore du Sahara.* Ed. C.N.R. S, 622 p.

Pagano M.C., Zandavalli R.B., Araújo F.S. 2013. Biodiversity of arbuscular mycorrhizas in three vegetational types from the semiarid of Ceará State, Brazil. *Appl. Soil Ecol.* 67: 37–46.

Quézel P., Médail T. 2003. *Écologie et biogéographie des forêts du bassin méditerranéen*. Environmental Series. Elsevier.

Redecker D., Morton J.B., Bruns T.D. 2000. Ancestral lineages of arbuscular mycorrhizal fungi (Glomales). *Molec. Phylogen. Evol.* 14: 276–284.

Said S.A., Fernandez C., Greff S., Derridj A., Gauquelin T., Mevy J.P. 2011. Inter-population variability of leaf morpho-anatomical and terpenoid patterns of *Pistacia atlantica* Desf. ssp. atlantica growing along an aridity gradient in Algeria. *Flora* 206: 397–405.

Sanders I.R. 2004. Plant and arbuscular mycorrhizal fungal diversity: are we looking at the relevant levels of diversity and are we using the right techniques? *New Phytol.* 164: 415–418.

Schenck N.C., Kinloch R.A. 1980. Incidence of mycorrhizal fungi on six field crops in monoculture on a newly cleared woodland site. *Mycologia* 72: 445–456.

Schwarzott D., Walker C., Schuβler A. 2001. *Glomus*, the largest genus of the arbuscular mycorrhizal fungi (Glomales), is non-monophyletic. *Molec. Phylogen. Evol.* 21: 190–197.

Smith F.A., Smith S.E. 1997. Structural diversity in (vesicular)-arbuscular mycorrhizal symbioses. *New Phytol.* 137: 373–388.

Staddon P.L., Gregersen R., Jakobsen I. 2004. The response of two *Glomus* mycorrhizal fungi and a fine endophyte to elevated atmospheric CO_2, soil warming and drought. *Global Change Biol*. 10: 1909–1921.

Strullu D.G. 1990. *Les mycorhizes des arbres et plantes cultivées*. Collection TEC & DOC, Lavoisier, Paris, 250 p.

Stutz J.E., Morton J.B. 1996. Successive pot cultures reveal high species richness of arbuscular endo-mycorrhizal fungi in arid ecosystems. *Can. J. Bot.* 74: 1883–1889.

UNEP. 1992. *World Atlas of Desertification. United Nations Environment Program*. London, Baltimore. Edward Arnold Ed.

Van Der Heijden M.G., Streitwolf-Engel R., Riedl R., Siegrist S., Neudecker A., Ineichen K., Boller T., Wiemken A., Sanders I.R. 2006. The mycorrhizal contribution to plant productivity, plant nutrition and soil structure in experimental grassland. *New Phytol.* 172: 739–752.

Van Der Heijden M.G.A., Klironomos J.N., Ursic M., Moutoglis P., Streitwolf-Engel R., Boller T., Wiemken A., Sanders I.R. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396: 72–75.

Vyas D., Gupta R.K. 2014. Effect of edaphic factors on the diversity of VAM fungi. *Tropical Plant Res.* 1: 14–25.

Yang F.Y., Li G.Z., Zhang D.E., Christie P., Li X.L., Gai J.P. 2010. Geographical and plant genotype effects on the formation of arbuscular mycorrhiza in *Avena sativa* and *Avena nuda* at different soil depths. *Biol. Fertil. Soils* 46: 435–443.

Yang H., Yuan Y., Zhang Q., Tang J., Liu Y., Chen X. 2011. Changes in soil organic carbon, total nitrogen, and abundance of arbuscular mycorrhizal fungi along a large-scale aridity gradient. *Catena* 87: 70–77.

Received 26 May 2022; received in revised form 22 July 2022; accepted 15 July 2022