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Assessing The Native Arbuscular Mycorrhizal Symbioses To Rehabilitate A Degraded Coastal Sand Dune In Algeria

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ABSTRACT: We examined local arbuscular mycorrhizal fungal (AMF) plant symbioses for their potential for land rehabilitation after sand industrial exploitation in a study site of the coastal sand quarry of Terga (NW Algeria, semi-arid climate). We focused on the mycorrhizal status of five representative plant species (*Acacia saligna, Lotus creticus, Retama monosperma, Pistacia lentiscus* and *Juniperus oxycedrus*) present in the Terga quarry. The arbuscular mycorrhizal (AM) structures showed significant and contrasting rates of root colonization among plant species. Spores density in soil was generally high, but variable depending on soil disturbance and local conditions. AMF diversity study in the rhizospheric soil fraction resulted in the distinction of eleven spore morphotypes affiliated to four genera (*Glomus, Scutellospora, Gigaspora* and *Acaulospora*) with predominance of *Glomus*. The mycorrhizal soil infectivity (MSI) level could be considered as significant except in the rhizosphere of *R. monosperma*. Our results suggest that *A. saligna*, *L. creticus* and *P. lentiscus* are well adapted to Terga local conditions and promote arbuscular mycorrhizal symbiosis. Management of mycorrhizal soil potential by introducing these species is very promising approach to contribute to degraded ecosystem rehabilitation such as in Terga. They may further constitute an important source of AM inoculum in semi-arid ecosystems.
KEY WORDS: Glomales biodiversity; Mycorrhizal soil infectivity; Revegetation strategies; Semi-arid.

INTRODUCTION

The semi-arid ecosystems such as Mediterranean coastal areas are frequently subjected to natural and anthropogenic disturbances (Le Houérou, 2000). This is the case of Terga coastal dunes (NW Algeria) after massive industrial sand mining. Land degradation is further exacerbated by lower rainfall, long periods of drought and high winds causing loss of vegetation and degradation of physical, chemical and biological soil properties (Requina *et al.,* 2001). All these climatic and soil disturbance conditions have severe detrimental effect on the ecosystem restoration, for which a revegetation strategy is needed.

Among successful revegetation strategies widely reported in semi-arid ecosystem, are those including mycorrhizal symbioses (Requina *et al.*,, 1996; Azcon-Aguilar *et al.,* 2003; Sanguin *et al.,* 2013). Two strategies are usually offered based on the level of environmental degradation (Duponnois *et al.,* 2013): (I) management of the native soil mycorrhizal potential via native, drought tolerant and mycotrophic plant species establishment (Ouahmane *et al.,* 2006a), and/or (II) plants inoculation through selected mycosymbiots (Estaún *et al.,* 1997; Caravaca *et al.,* 2003; Duponnois *et al.,* 2007).

Arbuscular mycorrhizal fungi (AMF) can improve plants nutrient uptake efficiency in soils with low fertility by increasing the absorption surface and nutrient sources mobilization (Smith and Read, 2008). They help plants to tolerate biotic (Declerck *et al.,* 2002) and abiotic stress (Mathur and Vyas, 2000; Yano-Melo *et al.,* 2003).They may influence on the structure and activity of microbial Communities in mycorrhizosphere (Dabire *et al.,* 2007) and promote coexistence between plant species (Hart *et al.,* 2003). AMF promote plant settlement, especially in nutrient-poor environments such as sand dunes and contribute to dune fixation by forming aggregates of sand grains (Koske and Polson, 1984).

Although the AMF are important for vegetation persistence in semi–arid Mediterranean ecosystem (Caravaca *et al.,* 2003), understanding the mycorrhizal associations in Terga ecosystem and their distribution in the soil is needed for sound sustainable restoration and management of the exploited site (Requina *et al.,*

1996). Therefore, the objective of this work is to determine the mycorrhizal status of five local plant species and studied the relationship between plant species, mycorrhizal potential and soil fertility.

MATERIALS AND METHODS

Study site and samples collection

The study was conducted in Terga coastal sand dunes, located in Northwestern Algeria submitted to semi-arid Mediterranean climate with hot dry summers. The average annual rainfall, occurring mainly in autumn, is 300 mm. A botanical survey was carried out. The study focused on five plant species present in the quarry; *Acacia saligna, Retama monosperma, Lotus creticus, Juniperus oxycedrus* and *Pistacia lentiscus*. Sampling is performed in a preserved area in two locations: (1) on a high dune facing the sea (N40 ° 37 'E0 44'), and (2) in the back of the dune which stretches a plateau characterized by dense natural vegetation (N41 ° 16 E2 ° 05 '). For each target species, ten individual plants were randomly chosen. Roots and soil were collected from the rhizosphere of each plant. The control sample was taken from the bare soil. The physicochemical parameters of different soil composites were analyzed.

AM root colonization detection and evaluation

AM infection was observed after root staining according to Philips and Hayman (1970) under an optical microscope to spot mycorrhizal structures and to estimate the target species AM root infection degree as described by Trouvelot *et al.* (1986).

Spores density assessment

Soil samplings were performed in Spring and Winter. AM fungal spores were extracted from rhizospheric soil of target species and bare soil using the wet sieving method described by Gerdermann and Nicolson (1963). The spore suspension was centrifuged on a sucrose gradient to concentrate the spores and to minimize soil particles and root fragments (Daniels and Skipper, 1982). The mixture obtained after spore extraction was observed under a binocular microscope. The average spore number was expressed as a score per 100 g of dry soil.

Morphological identification of spores

Spores were sorted out manually under a binocular microscope according to color and size. In each homogeneous lot, the morphological characteristics of spores were observed under microscope (Olympus SZ H10 research stereomicroscope, connected to computer digital image analysis software). Slides of each different spore morphotype were prepared using either polyvinyl-alcohol alone or mixed with Melzer's solution (Azcon-Aguilar *et al.,* 2003). Spores identification was mainly based on color, size, wall structure and hyphal attachment, according to the descriptions provided by the International Culture Collection of Arbuscular mycorrhizal Fungi (http:// www.Invam.caf.wvu.edu).

Mycorrhizal soil infectivity (MSI) determination

The method used for MSI determination was described by Plenchette *et al.* (1989). Young mycotrophic plants are cultivated on a series of concentrations of rhirospheric soils and bare soil, diluted with the same sterilized soil. Six dilutions (100, 48, 24, 12, 6 and 3%) were performed in triplicate. The seeds of sorghum (*Sorghum sudanense*) were germinated for two days in Petri dishes on humid filter paper and transplanted into small plastic pots containing 100g of each dilution with ten seeds per pot. Culture was carried out for two weeks with 16h light and 25 ± 1 ° C. The plants were watered daily with sterile distilled water.

At harvest, the whole root system of each seedling was carefully rinsed with water and prepared according to Phillips and Haymann (1970). Mycorrhizal structures were observed under an optical microscope. Each root system showing at least one infection point (hyphal penetration in the root) was considered as mycorrhizal. These results were expressed as the percentage of mycorrhizal plants per pot.

Linear regressions (Y =a X + b) was calculated from the relationship between the percentage of mycorrhizal plants versus the logarithm of the natural soil quantity. Mycorrhizal Soil Infectivity (MSI) is expressed as MSI_{50}units, corresponding to the natural soil quantity required to infect 50% of a plant population under the biological test conditions.

Statistical Analyses

Data were processed with the variance analysis (ANOVA) at $p < 0.05$ using XL Stat software. Means were compared by the Tukey's HSD (Honestly Significant Difference) test ($p < 0.05$). Spearman correlation coefficient was calculated between all variables. The relative abundance of spores was calculated (Johnson *et al.,* 1991). The Shannon diversity index (H) was calculated according to the following equation: $H = -\sum (Pi\ ln\ [Pij])$ where *Pi* is the relative abundance (the number of individuals of the species *i* in relation to the total number

of individuals of all species), and *ln* is the natural log. Pielou's evenness index (E) was obtained by the following equation: E = H/log (S) where S is the total number of species.

RESULTS

Study site characteristics

The preserved area in Terga is characterized by a large plant biodiversity of trees, shrubs and herbaceous plants (Table 1).We chose to further focus our study on *Acacia saligna, Juniperus oxycedrus, Pistacia lentiscus, Retama monosperma,* and *Lotus creticus*. The mined area is totally naked.

The physico-chemical parameter (Table 2) shows that all soils have a sandy soil structure, characterized by an alkaline pH. Nitrogen, Phosphorus and organic matter are generally low.

AM Root colonization

In all plant species, root fragments microscopic examinations revealed the presence of AMF structures like arbuscules and vesicles (Figure 1). The vesicles were widely observed compared to arbuscular structures present only in *A. saligna* and *P. lentiscus*.

Variance analysis indicates that AM colonization depends on plant species (F = 9.904, P <0.0001). The lowest infection frequency value (F %) was observed for *J. oxycedrus* (54%), while it didn't differ significantly among other species (72% to 82.5%). As regards the intensity of AM colonization in the root system (M %) and in mycorrhizal fragments (m %), the difference among species was significant (Table 3).

Table1. Terga dune floristic survey.

Trees	Shrubs	Herbaceous
Juniperus phoenicea	Calycotome villosa intermedia	Ammophila arenaria
Juniperus oxycedrus	Chamaerops humilis	Asparagus acutifolius
Acacia saligna	Cistus salviifolius	Bellis sylvestris
Tamarix sp	Cistus sericeus	Brassica fruticulosaglabberina
	Ephedra altissima	Calendula tomentosa
	Erica multiflora	Centaurea fragilis
	Genista cephalanta	Centaurium umbellatum
	Halimium halimifolium	Clematis cirrhosa
	Helianthemum origanifolium	Crucianella maritima
	Helianthemum racemosum	Cyperus kalli
	Lonicera implexa	Daphne gnidium
	Lycium intricatum	Echinops spinosus
	Osyris lanceollata	Lagurus ovatus
	Phillyrea angustifolia media	Lavandula dentata
	Pistacia lentiscus	Limonium densiflorum
	Quercurs coccifera	Lobularia maritima
	Retama monosperma bovei	Lotus creticus
	Rosmarinus officinalis	Malcolmia arenaria
		Matthiola tricuspidata
		Medicago littoralis
		Micromeria inodora
		Ononis antennata
		Ononis variegata
		Orlaya maritime
		Pancratium maritimum
		Paronychia argentea
		Prasium majus
		Reicharedia tingitana
		Rubia peregrine
		Rumex bucephaloflorus
		Senecio leucanthemifolius crassifolius
		Silene ramosissima
		Stipa tenacisssima
		Serratula mucronata
		Urginea maritimum

Table 2. Physico-chemical analysis of the target species rhizospheric soil and bare soil

Parameters	Clay	Loam	Sand	pH	Organic matter %	Total Nitrogen%	Total Phosphorus %
Soils origins							
A. saligna	3	5	92	8.87	6.49	0.05	0.037
L. creticus	2	4	94	8.13	0.40	0.01	0.031
R. monosperma	2	4	94	8.37	0.10	0.03	0.033
P. lentiscus	5	3	92	8.45	6.47	0.07	0.035
J. oxycedrus	4	5	91	8.39	6.39	0.05	0.035
Bare soil	2	4	94	9	0.10	0.10	0.037

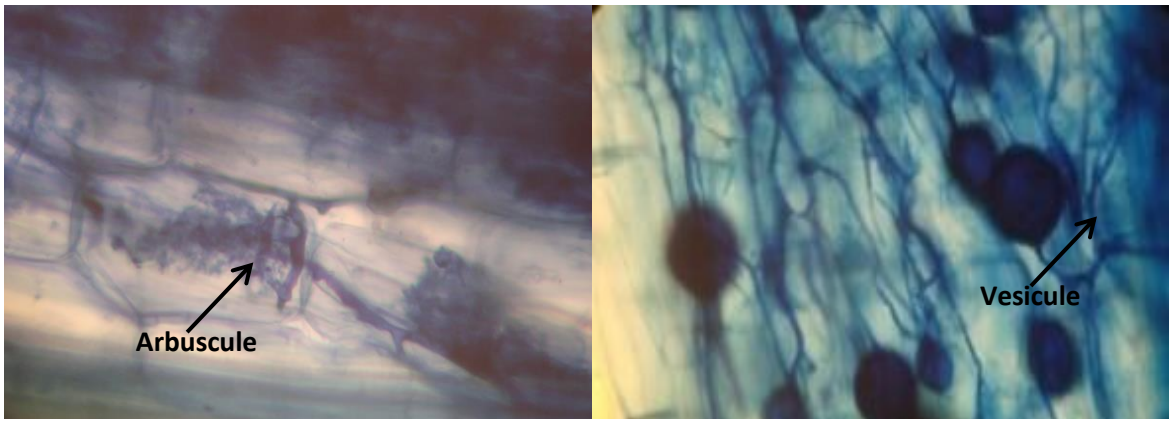

Figure 1. Arbuscular Mycorrhizal Fungi structures in target species roots

Table 3. Arbuscular mycorrhizal colonization in roots.

Species	Mycorrhizal frequency (F%)	Mycorrhizal intensity in root system (M%)	Mycorrhizal intensity in mycorrhizal fragment (m%)	Arbuscules content in mycorrhizal fragment (a%)	Arbuscules content in root system (A%)
A. saligna	82.50[a]	36.25[b]	44.17[b]	24.86	9.00
R. monosperma	80.00[a]	27.30[d]	34.12[d]	0.00	0.00
L. creticus	72.00[a]	28.40[c]	39.44[c]	0.00	0.00
P. lentiscus	80.00[a]	37.26[a]	46.57[a]	5.09	1.90
J. oxycedrus	54.00[b]	14.80[e]	27.40[e]	0.00	0.00

For each column, values followed by the same letter are not significantly different at P <0.05

Spore density

The average spore density (Table4) varies very significantly among species (F= 34.98, P <0.0001) with largest spore scores for *R. monosperma* soil (123.6 spores /100g soil) and *J. oxycedrus* (111.6 spores/100g soil) and close scores for *A. saligna*, *P. lentiscus* and *L. creticus* (65.5, 80.8, 76.6 spores/100g soil respectively). Bare soil had very poor spore score (12.16 spores /100g soil).

Winter and Spring samples (Table 4) showed a negative correlation (r= -0.623, α= 0.05) and a highly significant variation between seasons (F= 33.42, P <0.0001). Thus the maximum spore score was recorded in *R. monosperma* Spring soil (123.6 spores/100g soil) then decreasing to 44.8 spores /100g soil in winter. Similar trends were also observed for the four other plant species.

Table 4. Spore densities across seasons

	spores number /100g soil	
Soils Origins	Winter	Spring
A. saligna	36.33±4.16[a]	67.33±8.02[b]
L. creticus	32.33±11.01[a]	76.33±14.36[b]
R. monosperma	45.00±11.53[a]	123.33±27.53[a]
P. lentiscus	32.00±8.88[a]	80.33±4.50[b]
J. oxycedrus	41.33±5.50[a]	110.00±18.02[a]
Bare soil	12.00±1.00[b]	12.33±3.05[c]

For each column, values followed by the same letter are not significantly different at P <0.05

Spores diversity

Spore morphotypes observed according to shape, color and size; vary from 4 in bare soil to 11 in rhizospheric soil (Table 5). Most of the morphotypes are common in all soils and some are specific. The relative abundance of the different spore types is shown in Table 5. Presence of characteristic structures (hyphae, saccule and walls) on some spores observed allows their allocation to a genus. These spores belong to four genera: *Glomus, Scutellospora, Gigaspora* and *Acaulospora*. The genus *Glomus* is the most frequent in the five studied plant species. It varies colors among spores (black, dark brown, light brown, hyaline and orange). The genus *Gigaspora* spores has yellowish white whose *Gigaspora margarita* (Figure 2). Brown spores and brown with dark outline characterized by the saccule, correspond to *Acaulospora* (Figure 2).

Table 5. Morphological characteristics and relative abundance of spores

Spore Color	Morphotypes diameter (µm)	Relative abundance (%) of spores morphotypes					
		A. saligna	L. creticus	R. monosperma	P. lentiscus	J. oxycedrus	Bare soil
Black	60-100	19	14	9	4	8	32
Black	250-400	3	5	11	-	4	16
light brown	40-100	10	11	10	10	10	-
light brown	240-450	23	4	11	6	8	-
dark brown	40-100	8	7	13	4	16	3
dark brown	160-450	10	1	13	2	12	-
Cream to yellowish	240-400	6	-	6	-	2	-
Hyaline to pale yellow	40-80	12	9	15	9	17	49
Brown dark wall	80-120	7	19	12	3	23	-
orange	60-80	2	4	-	-	-	-
oval brown	20-30	-	-	-	29	-	-
irregular brown	200-360	-	15	-	26	-	-
Irregular brown yellow	200-360	-	11	-	7	-	-

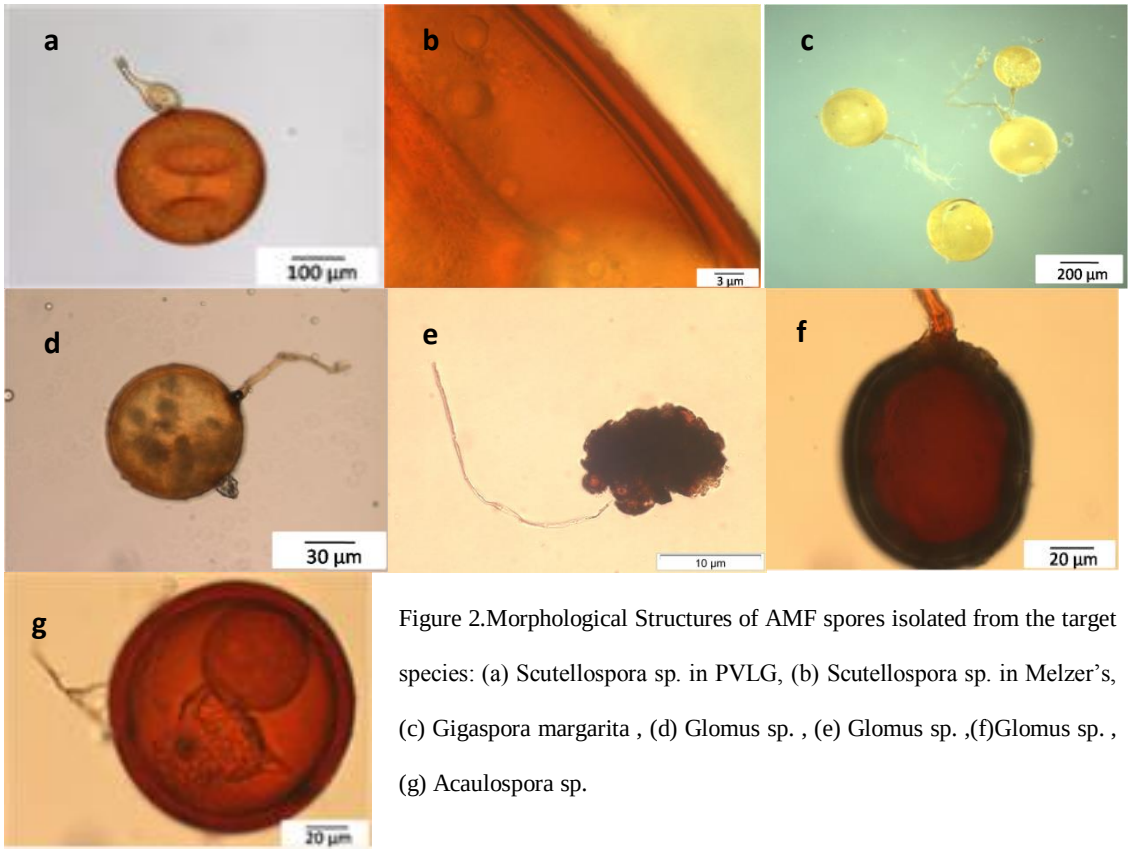

Figure 2.Morphological Structures of AMF spores isolated from the target species: (a) Scutellospora sp. in PVLG, (b) Scutellospora sp. in Melzer's, (c) Gigaspora margarita , (d) Glomus sp. , (e) Glomus sp. ,(f)Glomus sp. , (g) Acaulospora sp.

The Shannon diversity index (H) and the Pielou's evenness index (E), are parameters that express AMF diversity (Table 6). H index ranged from 2.02 to 2.28 and follow the gradient *L. creticus>R. monosperma> A. saligna> P. lentiscus>J. oxycedrus*. E index vary from 0.43 to 0.53 following the gradient *L. creticus> A. saligna> P. lentiscus> R. monosperma> J. oxycedrus.*

Mycorrhizal Soil Infectivity

The MSI_{50} characterizes the amount of rhizospheric soil required to infect 50% of a plant population under bioassay conditions. Here it varied significantly depending on the soil (F= 10.277, P < 0.001). *Tukey* test showed three groups of rhizospheric soils compared to the level of infectivity (Table 7). A low value of MSI_{50} indicates high soil infectivity. Concerning *A. saligna* soil, only 16.22 g of rhizospheric soil is sufficient to infect 50% of plants. In comparison, the necessary amount of *R. monosperma* soil is 29.50 g and over to 100 g for bare soil. This means that there were not enough propagates of mycorrhizal fungi in 100 g of bare soil to obtain

50% of mycorrhizal seedlings. The number of MSI_{50}units per 100 g soil is calculated by dividing 100 by MSI_{50} value (g). More the number of units MSI_{50} is higher, more the soil is rich in mycorrhizal propagates.

Table 6. AMF diversity as reflected by Shannon diversity and Pielou's evenness indexes

Species	H (Shannon)	E (Pielou)
A. saligna	2.10	0.50
R. monosperma	2.17	0.45
L. creticus	2.28	0.53
P. lentiscus	2.05	0.47
J. oxycedrus	2.02	0.43

Table 7. Mycorrhizial soil infectivities in target species rhizospheric soil and bare soil

soils origins	Regression coefficients	MSI_{50}units g per 100g	Nb MSI_{50} units g per 100g
A. saligna	0.94	16.22^{b}	6.17^{b}
R. monosperma	0.68	29.50^{a}	3.39^{a}
L. creticus	0.88	18.15^{b}	5.51^{b}
P. lentiscus	0.88	18.09^{b}	5.53^{b}
J. oxycedrus	0.94	19.74^{b}	5.07^{b}
Bare soil	-	$>100^{c}$	<1

Correlation between spore density Root colonization and soil fertility

Table 8 presents the correlations between the density of spores, mycorrhizal intensity (M %) and soil fertility in total nitrogen (N), total phosphorus (P) and organic matter (OM). The Pearson correlation coefficient is denoted by *r*. Negative correlations could be observed between spore density and the content of P and between spore density and M%.

Table 8. Correlation coefficient (*r*) between spore density and mycorrhiza intensity and soil fertility

	Organic matter%	Total Nitrogen %	Total Phosphorus%	Mycorrhiza intensity (M%)	Nb MSI_{50} units /100 g
spore density	-0.281	-0.091	-0.551	-0.570	-0.566
Mycorrhiza intensity (M%)	0.107	0.261	0.262	1	0.290

Values in blod are different from 0 at signification level alpha=0,05

DISCUSSION

The arbuscular mycorrhizal fungi are geographically widely distributed (Öpik et al., 2006) and almost generally present in the plant kingdom (Trappe, 1987).Many reports showed that most plant species of semi-arid Mediterranean environments are mycorrhized (Requena et al.,, 1996 Ferrol et al., 2004; Maremmani et al., 2003).Here we detected the presence of arbuscular mycorrhizal fungi in roots of all target species (A. saligna, L. creticus, R. monosperma, P. lentiscus and J. oxycedrus). Such symbiotic associations were reported previously (Ducousso and Thoen, 1991; Escaray et al., 2010; Hatimi and Tahrouch, 2007; Ferrol et al., 2004; Caravaca et al., 2006). AMF infection rates were high and vary depending on the studied species. Our results are consistent with those reported by Requina et al., (1996) in South Spain. According to Diagne and Ingleby (2003) mycorrhizal infection is affected by soil disturbances but not by the climate or the vegetation.

Despite current adverse conditions, dune soils may harbor rich and varied bacterial and fungal microflora (Hatimi and Tahrouch 2007). Despite the total absence of vegetation in the Terga exploited area and poor nutrients and limited water, spores could be detected in soil. The spore density is known to vary considerably among ecosystems. Values range from a few dozen to 10,000 spores per 100 g soil (Frioni et al., 1999; Zhao and Li, 2005; Abbas et al., 2006; Camprubí et al., 2010). Spore densities found in this study in rhizospheric soils can be considered as relatively large compared to densities reported in semi-arid coastal dunes (Hatimi and Tahrouch 2007; Camprubí et al., 2010), but remain relatively low compared to those reported in other semi -arid soils (Ouahmane et al., 2006b; Abbas et al., 2006).

The spore densities observed in rhizospheric soils of R. monosperma and J. oxycedrus are substantially higher than those of A. saligna, L. creticus and P. lentiscus. Nicolson (1960) reported that the factors affecting the distribution of AM fungi in sand dunes are plant species, degree of dune stability, organic matter and soil microbiological activity. Soil disturbance affect spore formation in these dunes. Indeed R. monosperma and J. oxycedrus were found in a fixed dune protected from the wind and surrounded by dense vegetation ; in comparison the other colonizing species were subjected to severe climatic disturbances and limited canopy. Spore density is higher in older dunes than in the mobile and the younger dunes located near the sea (Koske, 1975). Soil disturbance affect the AM fungi community in sand dunes systems (Beena et al., 2000).

The seasonal variation in spore abundance has been reported by several authors (Hayman, 1970; Sutton and Barron, 1972; Giovanetti et al., 1985; Hatimi and Tahrouch 2007). It may be attributed to the

process of spore formation, germination and degradation (Smith, 1980). Our results show that there is a seasonal dynamics with increase spore density during Spring, consistent with Smith (1980) observation.

In Terga ecosystem, spore density is negatively correlated to the rate of AM root colonization. Thus, the impact of disturbances on spore production appears to be higher than on root colonization of host plants. In arid areas, few or no sporulation is observed although roots are clearly colonized (Morton et al., 1993). Several studies showed that there is no correlation between spore density and intensity of root infection (Mukerji and Kapoor, 1986; Clapp et al.,, 1995;Merryweather and Fitter, 1998). In controlled conditions correlation between spore population and root infection is often positive (Jensen and Jakobsen, 1980). The weak relationship between the formation of endomycorrhizae and density of spores may be due to the mortality, dormant spores (Jasper et al., 1991) and discontinuous sporulation of some Glomeromycota members (Schüßler et al., 2001). However, the spores don't seem to be the only ones able to infect plants but also mycorrhizal roots and extraradical mycelia in the soil (Klironomos and Hart, 2002).

This study evidences the rich diversity of AM fungi in the sandy soil of Terga coastal dunes with eleven spore morphotypes belonging to four genera Glomus, Acaulospora, Scutellospora, and Gigaspora. The Shannon diversity index indicates that some fungal species are more frequent than others. Moreover this index increases; the plant species is favorable to all fungal species, offering same survival opportunities. Therefore L. creticus rhizospheric soil exhibit high diversity of AM species; previously observed by Camprubí et al. (2010) in Spanish Mediterranean dunes. The values of the evenness index being in the medium of [0, 1], indicate a variable species distribution. A high value of this index (tends to 1) would show an equitable distribution of species. In contrast, a low value (tends to 0) means that there are in the middle several rare species and there is disproportionate distribution of species, which therefore translates into a very selective vegetation.

Fungi belonging to the genus Glomus were predominant in samples, with the highest number of morphotypes. According Turrini et al. (2008), the diversity of species other than Glomus in highly disturbed ecosystems is low. This can be explained by the ability of Glomus species to initiate a colonization process from spores, infected roots and hyphae unlike genera as Gigaspora and Scutellospora, able to initiate new root infection only from spores (Biermann and Linderman 1983).

MSI_{50}values in rhizospheric Terga soils are similar to those found in cultivated soils in France (Plenchette et al., 1989b) and higher than those found in the fallows of Senegal (Duponnois et al., 2001). R. monosperma rhizospheric soil shows the lowest mycorrhizal soil infectivity although it is the richest in spores. Soils in disturbed ecosystems contain very few viable spores (Diop et al., 1994) which may explain the negative correlation found between MSI_{50} units and spore density in Terga soils. Other rhizospheric soils have an important mycorrhizal soil intensity compared to the infectivity potential estimated in the rhizosphere soil of the Spanish Mediterranean dunes (Camprubí et al., 2010).

The spore density in the rhizosphere soil is negatively correlated between the phosphorus content. Frioni et al. (1999) found a negative correlation between AM colonization and P content. Mycorrhizae have an important role in the survival and growth of plants in soils poor in nutrient particularly phosphorus (Smith and Read, 1997).

The overall results (soil fertility, root colonization, MSI, spores' diversity and density) suggest that L. creticus, A. saligna and P. lentiscus are most suitable for the rehabilitation of Terga degraded soils. Several studies have suggested that legume with mycorrhizal dependency can improve the fertility restoration of disturbed soils and AMF biodiversity (Duponnois et al., 2001). Ferrol et al. (2004) suggested that the mycelial network AM colonized P. lentiscus soil could be a major source of AM inoculum.

CONCLUSION

The management of soil mycorrhizal potential by the introduction of A. saligna, L. creticus and P. lentiscus is very promising and may validly contribute to Terga ecosystem rehabilitation, since they are adapted to these ecosystem local conditions and have the ability to promote arbuscular mycorrhizal symbioses which plays a key role in the ecosystem productivity and stability. They can also be an important source of AM inoculum in semi-arid ecosystems.

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