Management of the Mycorrhizal Soil Infectivity to Improve Reforestation Program Achievements in Sahelian Ecosystems

Arsene Sanon (1), Fatou Ndoye (2), Ezékiel Baudoin (1), Yves Prin (3), Antoine Galiana (3) and Robin Duponnois (1,*)

(1) IRD. UMR 113 CIRAD/INRA/IRD/SUP-AGRO/UM2. Laboratoire des Symbioses Tropicales et Méditerranéennes (LSTM). TA A-82/J, Campus International de Baillarguet. Montpellier Cedex 5. France
(2) Université Cheikh Anta Diop (UCAD). Laboratoire Commun de Microbiologie IRD/ISRA/UCAD. Centre de Recherche de Bel Air. BP 1386. Dakar. Senegal
(3) CIRAD. UMR 113 CIRAD/INRA/IRD/SUP-AGRO/UM2. Laboratoire des Symbioses Tropicales et Méditerranéennes (LSTM). TA A-82/J, Campus International de Baillarguet. Montpellier Cedex 5. France
* Corresponding author: Present address is IRD. Laboratoire Commun de Microbiologie IRD / ISRA / UCAD. Centre de Recherche de Bel Air. BP 1386. Dakar. Senegal; Tel: + 221 33 849 33 22 Fax : + 221 33 849 33 02; Email: Robin.Duponnois@ird.fr

To reverse the trend of massive degradation of vegetation cover and decline in land productivity in Sahelian regions, important programs aimed at promoting both the revegetalization and rehabilitation of degraded ecosystems have been implemented but, with mitigated results owing, in some cases, to drastic environmental conditions. Due to recent advances in our knowledge in plant and soil biology and ecology, relevant progress has been achieved during reforestation, for instance, with '*biologically improved plants*' (i.e. controlled mycorrhized plants). Besides their beneficial effects on seedlings' early survival and future development, which is profitable both in ecological and economic terms, the mycorrhizal symbiosis could also result in ecological imprints in soil functioning and in plant community dynamics.

In this chapter, we will present and discuss some of the relevant research work that has been implemented in Sahelian ecosystems with an emphasis on studies that have dealt with various monitoring and/or management strategies of the Mycorrhizal Soil Infectivity to sustain the recovery of the vegetation in stressed conditions.

Keywords: Sahelian Ecosystems; Environmental Degradation; Ecological Rehabilitation; Reforestation; Soil Microflora; Mycorrhizae.

1. Introduction

Although vegetation cover is essential for protection of the environment and for the local economy, a dramatic destruction of plant cover has occurred in dry tropical Africa subsequent to an over-exploitation of the natural resources. Also in these regions, drought, climatic variability and other drylands climate characteristics greatly influence human use of these ecosystems. These factors influence vegetation productivity, carrying capacity of the land, susceptibility of the land to erosion, to surface water availability and aquifer recharge [1]. As a result, they complicate the management of drylands and impose limitations on food security and the quality of humans' life [2]. Consequently, the recovery of destroyed vegetation had become an important issue. Many people, not only foresters and environmentalists but also mere citizens, have had an interest in nature conservation. Indeed, tree plantations acquired an increased importance, especially plantings that represent a growing stock of planted trees of value to society. Additionally, large plantations of tree have been encouraged in order to reforest and/or afforest degraded lands. However, the results obtained from these reforestation campaigns remained variable, owing to a set of factors including host site drastic conditions (soil fertility, water availability, other biotic (pathogens) and abiotic (salinity, pollution) stresses), lack of monitoring of the plantations, … [3].

Low-external inputs to improve biomass production have gained attention in many parts of the globe owing to increased interest in the conservation of natural resources, reduction of environmental degradation, and the surging costs of fertilizers [4]. In respect to this, numerous biological, chemical and physical factors could influence soil quality. Among them, rhizosphere microbial communities have been documented to directly affect soil fertility and stability by carrying out essential processes that contribute to nutrient cycling, and enhancing soil structure and ecosystem productivity [4-8]. Of particular interest are mycorrhizal fungi, which are soil microorganisms that establish symbiosis with plants. Mycorrhizal associations are integral, functioning parts of terrestrial ecosystems and are widely recognized to provide a direct physical link between soil and plant roots [7].

Of the seven types of mycorrhizae described in current scientific literature (arbuscular, ecto, ectendo, arbutoid, monotropoid, ericoid and orchidaceous mycorrhizae; [7], the arbuscular mycorrhizal and ectomycorrhizal fungi are the most abundant and widespread in Sahelian ecosystems [5, 9]. Arbuscular mycorrhizal (AM) fungi comprise the most common mycorrhizal association and form mutualistic relationships with over 80% of all vascular plants [10]. AM fungi are obligate mutualists belonging to the phylum Glomeromycota and have a ubiquitous distribution in global ecosystems [11]. Ectomycorrhizal (ECM) fungi are also widespread in their distribution but they associated with only 3-

5% of vascular plant families [7]. These fungi are members of the phyla Ascomycota and Basidiomycota. Differences between AM and ECM symbioses functioning include modifications induced in host root system's morphology, host plant-nutrient acquisition strategies and efficiency, interactions with other rhizosphere biota, … [7, 8, 12, 13].

Owing to the predominant role of AM and ECM symbioses in Sahelian ecosystems, we will focus our discussion on these groups of mycorrhizae.

This chapter will highlight the potential benefits of mycorrhizal associations and major strategies that could be implemented to increase the Mycorrhizal Soil Infectivity (MSI, that is the amount of infective mycorrhizal propagules 'i.e. spores, hyphae and infected root fragments' in a soil) in Sahelian environments. Furthermore, practical applications of mycorrhizal biotechnology for promoting the recovery of the vegetation cover and rehabilitation of degraded sites will be considered.

2. Benefits of Mycorrhizae

Though parasitic interactions have, sometimes, been evidenced with mycorrhizal partners (see [14, 15]), mycorrhizal fungi have generally been found as essential components of sustainable soil-plant systems. Representing a key interface between host plants and soil (macro- and micro-) nutrients, benefits of mycorrhizae also include an enhanced plant resistance to pathogens and others environmental stresses (i.e. metal and organic pollution, salinity, acidity, …), and improved water relations [7, 13, 16, 17]. Synergistic interactions have been reported between mycorrhizal symbionts development and important other soil microbes termed *Plant Growth-Promoting Rhizobacteria* (PGPR) such as those involved in nutrient cycling processes (nitrogen fixing bacteria, fluorescent pseudomonads, phosphate solubilizing bacteria, …; [18-21], thus enhancing plant growth and sustaining productivity. In addition, the mycorrhizal mycelial network that develops improves the formation and stability of soil aggregates [22] and could strongly influence plant community composition and dynamics [23-25]. For instance, it has been reported that this hyphal network could facilitate the establishment of conspecific as well as interspecific seedlings beneath mature trees by equalizing the distribution of soil resources [7, 24] or could promote the coexistence between dominant canopy (e.g. with allelopathic effect) and underground surbordinates by mitigating the depressive effect [25]. Overall, studies document mycorrhizae as biodiversity and productivity promoter in plant community [23, 26], depending on plants mycorrhizal dependence status and position in the local dominance hierarchy [27, 28]. Finally, other findings evidenced the contribution of mycorrhizal symbioses toward carbon and nutrients sequestration belowground [29, 30].

3. Strategies to Increase Mycorrhizal Inoculum Potential in Soil for Vegetation Recovery

In order to promote environmental-friendly and low cost agriculture and/or sylviculture practices in Sahelian regions, the management of the Mycorrhizal Soil Infectivity (MSI) could be of great relevance toward '*self-sustaining ecosystem'* conditions. Depending on the status of soil degradation and therefore mycorrhizal propagules abundance, two main strategies to increase soil mycorrhizal inoculum potential and sustain vegetation cover could be proposed (Fig 1): (*i*) management of the native soil mycorrhizal potential through the culture of drought-tolerant, native and highly mycotrophic plant species [31, 32] and/or (*ii*) inoculation of plants with selected mycosymbionts [25, 33, 34].

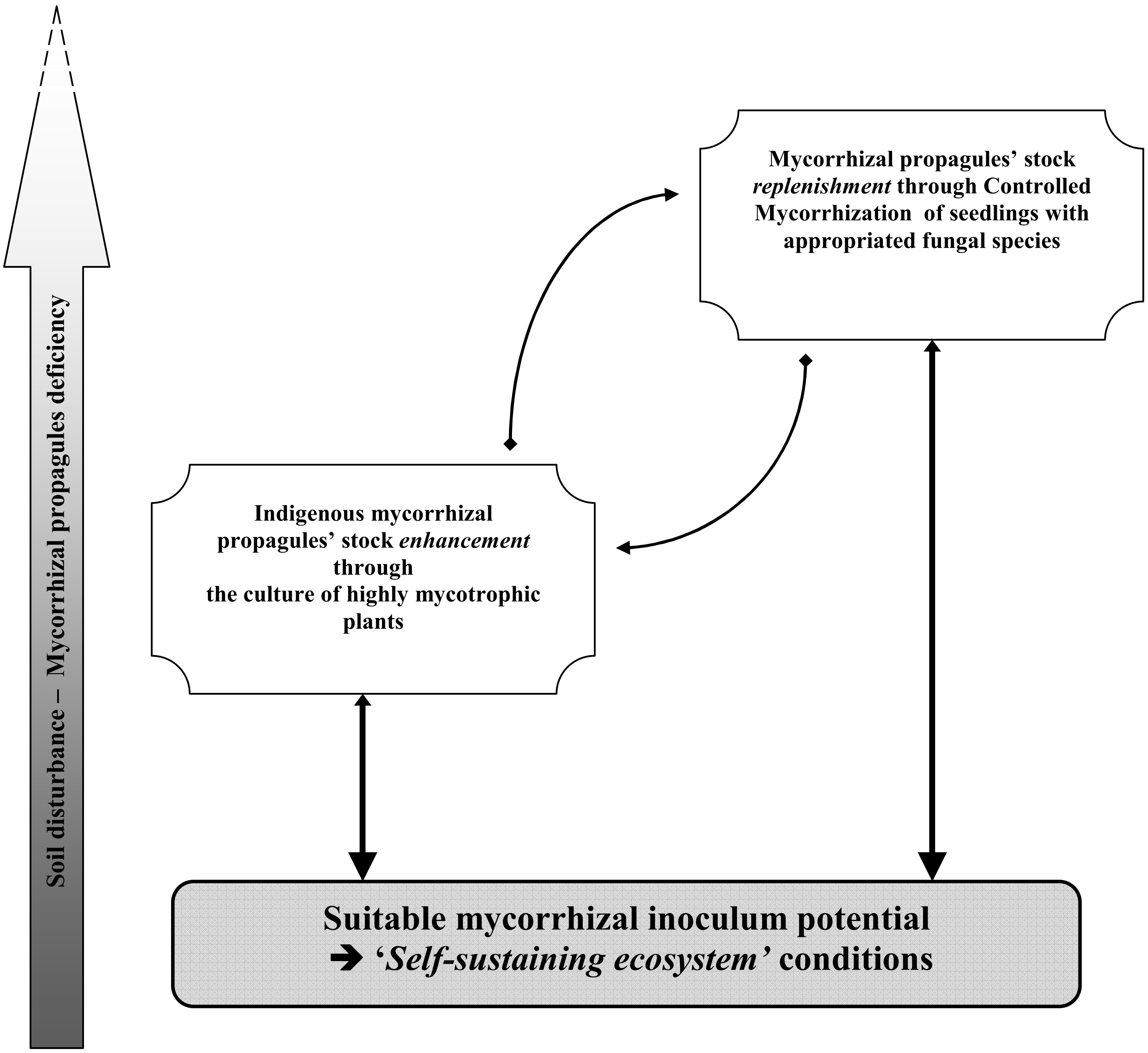

Fig. 1 Conceptual diagram illustrating important approaches that could enable to increase soil mycorrhizal inoculum in revegetation schemes in Sahelian ecosystems.

Importantly, when decision is made to inoculate seedlings before plantation, it is important to mention that the best strategy will be to screen for effective mycosymbionts in the recipient biotope instead of introducing exotic fungal species, which could fail to adapt and establish or to achieve the needed benefits [35]. Though some results evidenced interesting results subsequent to seedlings' inoculation with exotic mycorrhizal fungi [25, 36], contrastingly, several other studies demonstrated that native AM could perform better in soils from which they are originated from [37-39], highlighting that locally collected field inoculum may be more effective than commercial inocula for establishing vegetation cover [40]. Also, note that it will be relevant to select stressed site-adapted mycorrhizal fungi, which we expect could survive and be more effective to rehabilitate disturbed biotopes [35, 41]; and inoculating seedlings with a consortium of fungal species might be envisaged as different fungi are thought to show different effect on the same host [27, 42]. Furthermore, massive inoculation with selected fungal species thus rises the question of the need to monitor the species used as inoculants (e.g. through, for instance, molecular tools such as micro satellite or simple sequence repeat (SSR) markers, …; [43, 44]) in order to acquire knowledge concerning their persistence and, importantly, their potential ecological effects as certain research works pointed out that mycorrhizal inoculation could alter soil composition in the recipient biotope [34, 45].

4. Practical Applications of Mycorrhizal Biotechnology in Revegetation and Rehabilitation of Degraded Lands in Sahelian Ecosystems

The lack of mycorrhizal associations on plant root systems is one of the major reasons for failure of vegetation establishment and growth in various soils with low inoculum potential. Therefore, increase in mycorrhizal propagules may be beneficial for revegetation of variety of degraded sites and may be of great importance to rehabilitate natural ecosystems [6, 46, 47].

4.1. Management of the indigenous mycorrhizal fungi community to sustain vegetation recovery

Most of soils in Sahelian regions are P- and/or N-deficient [6, 13, 48] and the yields of crops are found to be largely dependant on their symbiotic (mycorrhizae and/or N-fixing bacteria) status [6, 49, 50]. Therefore, farmers generally intercrop with legumes or include them in crop rotations. In this respect, Duponnois et al. [51] carried out in glasshouse conditions an experiment to determine the endomycorrhizal status of seventeen indigenous fallow legumes (herb and tree species) in Senegal. They observed variations in the species' mycorrhizal dependency, ranging from 92.7 to 26.2%. Their findings thus provided relevant information regarding the species that could constitute potential candidates when screening plant species for intercrop or rotation purposes in farmlands in order to restore lands sustainable productivity.

Additionally, in Sahelian ecosystems, fallow is a common practice to regenerate soil fertility [52, 53]. The duration of fallow is a compromise between agronomic requirements and human needs [31] and generally, people tend to keep it as short as possible. Since the herbaceous and woody plants that grow during the fallow constitute the main agents to rehabilitate soil fertility [54] through, *inter alia*, their rhizosphere microbial communities (e.g. mycorrhizal symbionts, …; [31]) by carrying out essential processes that contribute to nutrient cycling and plant growth and health, it might be possible to act to improve soil rehabilitation by favoring the recovery of plant species with competitive advantages. In this concern, Duponnois et al. [31] carried out in field conditions a survey to assess the MSI and arbuscular mycorrhizal fungal spore communities in soil of different aged fallows in Senegal. Importantly, their results did not provide evidence of a beneficial effect of increased length of fallowing on the MSI, but they did suggest that particular attention must be paid to plant species displaying high mycorrhizal dependency (e.g. legumes), which could greatly enhance the indigenous AM fungal communities and the mycorrhizal infectivity of soil within a short delay.

4.2. Controlled mycorrhization of seedlings to improve their survival and establishment in degraded lands

Disturbance of natural plant communities is generally the first visible symptom of desertification of terrestrial ecosystems, but it is often accompanied or preceded by loss of key physicochemical and biological soil properties [4, 6, 47]. These properties largely determine soil quality and fertility, and thus plant establishment and productivity. Hence, their degradation results in a loss of sustainability. Soil degradation limits the potential for reestablishment of plants, and erosion and desertification are accelerated. These disturbances reduce the inoculum potential of mutualistic microbial symbionts that are key ecological factor governing the cycles of major plant nutrients and hence in sustaining vegetative covers in natural habitats [4, 6]. Therefore in many situations, it becomes a necessity to help plants to face these hazards, and one of the most effective, low cost and nature-friendly alternative remains to '*biologically improve*' plants through their controlled mycorrhization with selected fungal species before outplanting in the field.

A set of results do exist where experimentations have been carried out in Sahelian ecosystems to assess the effect of mycorrhizal inoculations on plant growth parameters and on soil biofunctioning in nursery, as well as, in field conditions.

In a glasshouse experiment, Diédhiou et al. [55] assessed the effects of four ECM fungi on the growth and mineral nutrition of five caesalpinioid legumes and one Euphorbiaceae species seedlings and they tested for the hypothesis that plants having smaller seeds show greater ECM dependency than those with large seeds. They observed that effects on plant growth and nutrition after inoculation with ECM fungi varied with tree species and that positive effects were recorded on *Afzelia bella*, *Cryptosepalum tetraphyllum*, *Paramacrolobium coeruleum* and *Uapaca somon* seedlings whereas no effect was recorded on *Afzelia macrophylla*. Interestingly, these authors also reported that seed mass was negatively correlated with the relative mycorrhizal dependency, indicating that large seed reserve is probably important for seedling nutrition and initial growth [55]. These findings may therefore be of great relevance when selecting candidates for the association (plant and fungal species to associate).

In the same line of idea, Sanon et al. [56] and Kisa et al. [25] investigated in container experiments, in Sahelian conditions (Burkina Faso and Senegal), the influence of AM inoculation or chemical fertilization on the growth of exotic plants, *Gmelina arborea* and *Eucalyptus camaldulensis* respectively, on the structure of soil microbial communities (MSI and total bacteria) and on the development of underground herbs. In particular, after 4 months of culture in a disinfected soil, AM inoculation significantly increased the growth of the exotic plant. In particular for *E. camadulensis* seedlings, the growth was multiplied by factors of 1.40, 1.79 and 1.83 for height, shoot and root dry weight respectively, compared with the control ([25]; Table 1). In addition, these results indicated a similar growth pattern of AM fungal inoculation with that observed when chemical fertilizer was added to the culture soil. After 12 months' further culture in containers filled with the same soil but not autoclaved, the stimulating effect of the AM inoculation was still recorded, AM colonization of plant root systems and the length of external mycorrhizal hyphae were significantly greater with AM-inoculated seedlings than with the controls and pre-fertilized seedlings ([25]; Table 1), suggesting a sustainable effect of the previous AM inoculation. Moreover, their results showed that the mycorrhizal inoculation tended to return the soil to its initial conditions (prior to the exotic tree plantation) and this was revealed by a similar bacterial community structure and higher catabolic evenness and soil mycorrhizal inoculum potential between treatment with inoculated seedlings and that with containers kept without trees [25]. Finally, Sanon et al. [56] and Kisa et al. [25] found that the inoculation of *G. arborea* or *E. camaldulensis* seedlings with an appropriate AMF (e.g. *Glomus intraradices*) significantly reduced the depressive effect of exotics on annual herbs that naturally grow in the containers. These results underlined the crucial role that mycorrhizal symbioses could have in reforestation with non-native tree species that target preservation of native plant diversity. However, field-based experiments are required to fully understand the impact of AM networks on interactions between plant species, with an especial emphasis on allelopathic interferences between plants.

Table 1 Growth response of *Eucalyptus camaldulensis* seedlings in soils inoculated with *Glomus intraradices* or fertilized after 4 months culture in a disinfected soil ; and growth response, AM colonization of the seedlings of *E. camaldulensis* transplanted in a non-desinfected soil, soil microbial catabolic evenness, total above- and belowground biomasses, plant species richness, and Shannon index of the herbaceous cover recorded in each treatment after 12 months' culture (adapted from [25])

	WEC(1)	Control	Fertilized(2)	*G. intraradices*(3)
	Plants development after 4 months culture in a disinfected soil			
Height (cm)		32.3 a(4)	45.3 b	43.6 b
Shoot biomass (mg dry weight)		852 a	1532 b	1499 b
Root biomass (mg dry weight)		326 a	598 b	624 b
	Plants development after 12 months culture in a non-disinfected soil			
Height (cm)		144 a	196 b	166 b
Total shoot biomass (g dry weight)		121 a	179 b	168 b
Root biomass (g dry weight)		50.5 a	82.9 b	73.1 b
AM colonization (%)		38.1 a	37.7 a	52.1 b
Hyphal length (m g^{-1} soil)	3.9 b	2.3 a	2.8 a	4.2 b
Catabolic evenness	16.9 b	17.8 b	9.6 a	20.7 c
Herbs aboveground biomass (g dry weight)	21.3 c	1.94 a	1.04 a	9.51 b
Herbs belowground biomass (g dry weight)	4.2 d	0.25 b	0.09 a	0.85 c
Herb species richness	4.8 c	2.8 b	1.2 a	3.0 b
Herbs Shannon index	0.97 c	0.63 b	0.11 a	0.57 b

(1)Without Eucalyptus camaldulensis seedlings.
(2)Preplanting fertilizer application.
(3)Soil inoculation with the AM fungus Glomus intraradices.
(4)Data in the same line followed by the same letter are not significantly different according to Newman-Keuls test ($P<0.05$).

In another experiment carried out by Duponnois et al. [33], the authors studied the influence of several strains of ECM fungi on the growth of *Acacia holosericea* in glasshouse conditions and their short-term effect on indicators of ecosystem soil conditions (microbial biomass, MSI) after outplanting. Results pointed out that ectomycorrhizal inoculation significantly enhanced the growth (shoot and root biomasses) of seedlings after 4 months culture in nursery. In field conditions, the transplanting shock had less effect on the ectomycorrhized trees. After two years, the inoculated trees had a better growth than that recorded in the control treatment. Ectomycorrhizal inoculation had modified the leaf nutrient content for P, N and phenols. Also, microbial biomass and MSI were both stimulated when plants were previously inoculated [33].

Furthermore, the stimulating effect of nursery inoculation of *A. holosericea* seedlings was kept after 7 years of culture in field conditions ([34]; Table 2). Nevertheless, additional research work carried out in the 7-year plantation reported alterations in recipient soil microbial communities' structure (e.g. in AM fungal and N-fixing bacterial communities) subsequent to *A. holosericea* seedlings' inoculation with the ECM fungus *Pisolithus albus* IR100 ([34, 45]; Table 2).

Table 2 Effect of the ECM fungus *Pisolithus albus* IR100 inoculation (***a***) on the growth of *Acacia holosericea* seedlings and on nitrogen fixative symbiosis after 4 months of culture under glasshouse conditions; and (***b***) on the growth of *A. holosericea*, on soil chemical characteristics and microbial biomass and, on AM fungi community after 7 years of plantation in the field (adapted from [34])

	Crop soil(1)	Un-inoculated trees	Trees inoculated with *P. albus* IR100
	A. holosericea seedlings' growth after 4 months of culture in glasshouse conditions		
Shoot biomass (mg dry weight)		650 a(2)	1,545 b
Root biomass (mg dry weight)		341 a	795 b
Total nodule biomass (mg dry weight)		2.8 a	10.5 b
ECM colonization index (%)		-	30.5
	A. holosericea seedlings' growth after 7 years of plantation in the field		
Height (m)		4.84 a	6.43 b
Stem diameter (cm)		11.8 a	23.2 b
Litter biomass (kg m^{-2})		1.98 a	6.19 b
Total aboveground biomass (kg per tree)		63.1 a	310.9 b
Soil total nitrogen (%)	0.032 a	0.024 a	0.046 a
Soil total carbon (%)	0.398 a	0.338 a	0.600 b
Soil soluble phosphorus (%)	4.6 a	4.9 a	7.1 b
Soil microbial biomass (µg C g^{-1} soil)	278.7 b	227.5 a	231.2 a
AM spores number (100 g^{-1} soil)	104 a	112 a	253 b
AM spores diversity (Simpson indices)	7.66	5.2	4.7

(1) Soil samples collected from the crop soil surrounding the *A. holosericea* plantation

(2) Data in the same line followed by the same letter are not significantly different according to Newman-Keuls test (P<0.05).

Interestingly, we will also discuss here the experimental work we carried out in Dakar, Senegal, that aimed at examining the potential for soil-mediated effects resulting from the invasion of *Amaranthus viridis*, to affect the growth of several Sahelian *Acacia* species. *A. viridis* is an annual herb native to Central America [57] and, in Senegal it is reported in agrosystems, and increasingly invades fallow lands, areas of pasture and domestic waste deposit areas. *Amaranthus*, by invading large soil patches in these areas, severely compromised native plant (grass-, shrub- and woodland) growth [58]. Our results thus indicated that the invasive exotic, *A. viridis*, decreases the growth of native *Acacia* species by altering both soil community diversity and global activities. Indeed, we observed an overall increase in soil nutrients availability, in bacterial abundance and in microbial activities upon the invasion by *Amaranthus viridis*. In contrast, symbiotic organisms (AM fungi and rhizobia) development were severely reduced, probably owing to the fact that *Amaranthus* is not an effective host of that microbes but also, probably owing to additional phytochemical interference [58]. These alterations in soil ecology due to the exotic plant might have therefore generated a '*novel ecological niche*', which might have favored the exotic invasive plant own fitness relative to that of native species. However, soil inoculation with the AM fungus, *Glomus intraradices*, significantly improved the growth and nodulation of *Acacia* species in invaded soil [58], thus increasing indigenous plants' competitive performance. Over all, these results thus highlighted the role of AM symbiosis in the processes involved in soil biological functioning and plant coexistence.

As both endo- and ectomycorrhizae have been reported on certain plant species, such as *Acacia* species [59], these symbiotic fungi have been used in combination in controlled mycorrhization experiments. Though certain results did report possible competition between fungal species [46], important other findings contrastingly revealed significant improvement of seedlings growth and development, as well as a synergistic effect on the root system colonization pattern by the symbionts [60, 61]. For instance, it has been documented that AM and ECM fungi might access distinct pools of soil nutrients [13, 62], thus suggesting more efficient exploration and uptake of nutrients during a tripartite symbiosis (plant, endo- and ectomycorrhizae).

Importantly, synergistic interactions, resulting in positive effects on beneficial microbes' development on plant root system and on plant growth, were recorded subsequent to mycorrhizal inoculation in combination with PGPR inoculants (N-fixing bacteria, fluorescent pseudomonads, Mycorrhiza Helper Bacteria (MHB), …; [63-65]), with soil amendment with rock phosphate [20, 66], … In addition, some results provided evidence that inoculation with mycosymbionts could drastically mitigate the depressive effect of plant parasitic nematodes [67, 68], and such beneficial effect could increase the performances of inoculated seedlings to face this cosmopolitan and important problem affecting the production of subtropical and tropical crops.

5. Conclusion

The importance of microbial manipulation, in particular mycorrhizal biotechnology, for the rehabilitation and revegetalization of degraded lands is well appreciated by the scientific community and effort is in progress for its large utilization by potential beneficiaries. A set of studies has demonstrated that plant-microbes symbioses and their feedbacks in the rhizosphere constitute essential drivers of plant productivity and soil quality and fertility. As man-made disturbances ultimately resulted in the destruction of mycorrhizal networks and other microbial activities in the soil systems, their promotion and/or re-establishment are essential steps for successful reforestation and soil rehabilitation. Therefore, effort must continue in sylviculture and reforestation schemes to determine the best compromise between symbiotic compatibility and efficiency of both partners under local soil conditions [36] to achieve optimum benefits from these microorganisms and their associations.

References

[1] Williams AJ, Balling Jr RC. *Interactions of Desertification and Climate.* Nairobi and Geneva: WMO & UNEP; 1994.
[2] Darkoh MBK. The deterioration of the environment in Africa's drylands and river basins *Desertification Control Bulletin*. 1994;24:35-41.
[3] Diouf D, Sougoufara B, Neyra M, Lesueur D. Le reboisement au Sénégal: Bilan des réalisations de 1993 à 1998. CIRAD-IRD-DEFCCS Project Report; 2000.
[4] Siddiqui ZA, Pichtel J. Mycorrhizae : an overview. In: Siddiqui ZA, Akhtar MS, Futai K, eds. (2008). *Mycorrhizae : Sustainable Agriculture and Forestry*. Dordrecht, The Netherlands : Springer ; 2008 :1-35.
[5] Gobat JM, Aragno M, Matthey W, eds. *Le sol vivant*. Lausanne : Presses Polytechniques Universitaires Romandes ; 2003.
[6] Cardoso IM, Kuyper TM. Mycorrhizas and tropical soil fertility. *Agriculture, Ecosystems and Environment*. 2006;116:72-84.
[7] Smith SE, Read DJ, eds. *Mycorrhizal Symbiosis*. London : Academic Press ; 2008.
[8] Bonfante P, Anca I-A. Plants, Mycorhizal Fungi, and Bacteria : A Network of Interactions. *Annual Review of Microbiology*. 2009; 63:363-383.
[9] Read DJ. Mycorrhiza in ecosystems. *Experientia*. 1991;47:376-391.
[10] Brundrett MC, Coevolution of roots and mycorrhizas of land plants. *New Phytologist*. 2002 ; 154: 275–304.
[11] Redecker D, Morton JB, Bruns TD. Ancestral lineages of arbuscular mycorrhizal fungi (*Glomales*). *Molecular Phylogenetics and Evolution*. 2000;14:276–284.
[12] Moyersoen B, Alexander IJ, Fitter AH. Phosphorus nutrition of ectomycorrhizal and arbuscular mycorrhizal tree seedlings from a lowland tropical rain forest in Korup National Park, Cameroon. *Journal of Tropical Ecology*. 1998;14:47-61.
[13] Lambers H, Raven JA, Shaver GR, Smith SE. Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology and Evolution*. 2008;23:95-103.
[14] Johnson NC, Graham JH, Smith FA. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist*. 1997;135: 575-585.
[15] Purin S, Rillig MC. Parasitism of arbuscular mycorrhizal fungi : reviewing the evidence. *FEMS Microbiology Ecology*. 2008;279: 8-14.
[16] St-Arnaud M, Hamel C, Vimard B, Caron M, Fortin JA. Inhibition of *Fusarium oxysporum* f.sp. *dianthi* in the non-VAM species *Dianthus caryophyllus* by co-culture with *Tagetes patula* companion plants colonized by *Glomus intraradices*. *Canadian Journal of Botany*. 1997;75:998-1005.
[17] Joner EJ, Leyval C. Rhizosphere gradients of polycyclic aromatic hydrocarbon (PAH) dissipation in two industrial soils and the impact of arbuscular mycorrhiza. *Environmental Science and Technology*. 2003;37:2371-2375.
[18] Founoune H, Duponnois R, Meyer JM, Thioulouse J, Masse D, Chotte JL, Neyra M. Interactions between ectomycorrhizal symbiosis and fluorescent pseudomonads on *Acacia holosericea*: isolation of Mycorrhiza Helper Bacteria (MHB) from a Soudano-Sahelian soil. *FEMS Microbiology Ecology*. 2002;41: 37-46.
[19] André S, Galiana A, Le Roux C, Prin Y, Neyra M, Duponnois R. Ectomycorrhizal symbiosis enhanced the efficiency of two *Bradyrhizobium* inoculated on *Acacia holosericea* plant growth. *Mycorrhiza*. 2005:15:357–364.
[20] Duponnois R, Colombet A, Hien V, Thioulouse J. The Mycorrhizal fungus *Glomus intraradices* and rock phosphate amendment influence plant growth and microbial activity in the rhizosphere of *Acacia holosericea*. *Soil Biology and Biochemistry*. 2005;37:1460-1468.
[21] Ramanankierana N, Rakotoarimanga N, Thioulouse J, Kisa M, Randrianjohany E, Ramaroson L, Duponnois R. The Ectomycorrhizosphere effect influences functional diversity of soil microflora. *International Journal of Soil Sciences*. 2006;1:8-19.

[22] Rillig MC, Mummey DL. Mycorrhizas and soil structure. *New Phytologist.* 2006;171:41-53.

[23] van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*. 1998;396:69-72.

[24] Simard SW, Durall DM. Mycorrhizal networks: a review of their extent, function, and importance. *Canadian Journal of Botany*. 2004;82:1140-1165.

[25] Kisa M, Sanon A, Thioulouse J, Assigbetse K, Sylla S, Spichiger R, Dieng L, Berthelin J, Prin Y, Galiana A, Lepage M, Duponnois R. Arbuscular mycorrhizal symbiosis can counterbalance the negative influence of the exotic tree species *Eucalyptus camaldulensis* on the structure and functioning of soil microbial communities in a Sahelian soil. *FEMS Microbiology Ecology*. 2007;62:32-44.

[26] van der Heijden MGA, Boller T, Wiemken A, Sanders IR. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology*. 1998;79:2082-2091.

[27] Hart MM, Reader RJ, Klironomos JN. Plant coexistence mediated by arbuscular mycorrhizal fungi. *Trends in Ecology and Evolution*. 2003;18:418-423.

[28] Urcelay C, Diaz S. The mycorrhizal dependence of subordinates determines the effect of arbuscular mycorrhizal fungi on plant diversity. *Ecology Letters*. 2003;6:388-391.

[29] Rygiewicz PT, Andersen CP. Mycorrhizae alter quality and quantity of carbon allocated belowground. *Nature*. 1994;369:58–60.

[30] Wilson GWT, Rice CW, Rillig M, Springer A, Hartnett DC. Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. *Ecology Letters*. 2009;12:452-461.

[31] Duponnois R, Plenchette C, Thioulouse J, Cadet P. The mycorrhizal soil infectivity and arbuscular mycorrhizal fungal spore communities in soils of different aged fallows in Senegal. *Applied Soil Ecology*. 2001;17:239-251.

[32] Azcon-Aguilar C, Palenzuela J, Roldan A, Bautist S, Vallejo R, Barea JM. Analysis of the mycorrhizal potential in the rhizosphere of representative plant species from desertification-threatened Mediterranean shrublands. *Applied Soil Ecology*. 2003;22:29-37.

[33] Duponnois R, Founoune H, Masse D, Pontanier R. Inoculation of *Acacia holosericea* with ectomycorrhizal fungi in a semi-arid site in Senegal: growth response and influences on the mycorrhizal soil infectivity. *Forest Ecology and Management*. 2005;207:351-362.

[34] Remigi P, Faye A, Kane A, Deruaz M, Thioulouse J, Cissoko M, Prin Y, Galiana A, Dreyfus B, Duponnois R. The exotic legume tree species *Acacia holosericea* alters microbial soil functionalities and the structure of the arbuscular mycorrhizal community. *Applied and Environmental Microbiology*. 2008;74:1485-1493.

[35] Gaur A, Adholeya A. Prospect of arbuscular mycorrhizal fungi in phytoremediation of heavy metal contaminated soils. *Current Science*. 2004;86:528–534.

[36] Bâ AM, Diédhiou AG, Prin Y, Galiana A, Duponnois R. Management of ectomycorrhizal symbionts associated to useful exotic tree species to improve reforestation performances in tropical Africa. *Annals of Forest Science*. 2010; *in press*. doi: 10.1051/forest/2009108.

[37] Enkhtuya B, Rydolvá J, Vosátka M. Effectiveness of indigenous and non- indegenous isolates of arbuscular mycorrhizal fungi in soils from degraded ecosystems and man-made habitats. *Applied Soil Ecology*. 2000;14:201–211.

[38] Caravaca F, Barea JM, Palenzuela J, Figuerosa D, Alguacil MM, Roldan A. Establishment of shrub species in a degraded semiarid site after inoculation with native or allochthonous arbuscular mycorrhizal fungi. *Applied Soil Ecology*. 2003;22:103-111.

[39] Göhre V, Paszkowski U. Contribution of the arbuscular mycorrhizal symbiosis to heavy metal phytoremediation. *Planta*. 2006;223:1115-1122.

[40] Rowe HI, Brown CS, Claassen VP. Comparisions of mycorrhizal responsiveness with field soil and commercial inoculum for six native Montane species and *Bromus tectorum*. *Restoration Ecology*. 2007;15:44-52.

[41] Oliveira RS, Vosátka M, Dodd JC. Studies on the diversity of arbuscular mycorrhizal fungi and the efficacy of two native isolates in a highly alkaline anthropogenic sediment. *Mycorrhiza*. 2005;16:23–31.

[42] Kernaghan G, Hambling B, Fung M, Khasa DP. *In vitro* selection of Boreal ectomycorrhizal fungi for use in reclamation of saline–alkaline habitats. *Restoration Ecology*. 2002;10:1-9.

[43] Jany JL, Bousquet J, Khasa DP. Microsatellite markers for *Hebeloma* species developed from expressed sequence tags in the ectomycorrhizal fungus *Hebeloma cylindrosporum*. *Molecular Ecology*. 2003;3: 659-661.

[44] Jany JL, Bousquet J, Gagné A, Khasa DP. Simple sequence repeat (SSR) markers in the ectomycorrhizal fungus *Laccaria bicolor* for environmental monitoring of introduced strains and molecular ecology applications. *Mycological Research*. 2006;110:51-59.

[45] Faye A, Krasova-Wade T, Thiao M, Thioulouse J, Neyra M, Prin Y, Galiana A, Ndoye I, Dreyfus B, Duponnois R. Controlled ectomycorrhization of an exotic legume tree species *Acacia holosericea* affects the structure of root nodule bacteria community and their symbiotic effectiveness on *Faiderbia albida*, a native Sahelian *Acacia*. *Soil Biology and Biochemistry*. 2009;41:1245-1252.

[46] Janos DP. Mycorrhizae influence tropical succession. *Biotropica*. 1980;12: 56-64.

[47] Requena N., Perez-Solis E, Azcon-Aguilar C, Jeffries P, Barea JM. Management of indigenous Plant-Microbe Symbioses aids restoration of desertified ecosystems. *Applied and Environmental Microbiology*. 2001;67:495-498.

[48] Bationo A, Mugbogho SK, Mokwunye AU. Agronomic evaluation of phosphate fertilizers in Tropical Africa. In: Mokwunye AU, Vleck PLG, eds. *Management of nitrogen and phosphorus fertilizers in sub-saharian Africa*. Netherlands: Martinus Nijhoff Dordrech; 1986:283-318.

[49] Howlever RH, Sieverding E, Saif SR. Practical aspects of mycorrhizal technology in some tropical crops and pastures. *Plant and Soil*. 1987;100:249–283.

[50] Duponnois R, Founoune H, Lesueur D. Influence of the dual ectomycorrhizal and rhizobial symbiosis on the growth of *Acacia mangium* provenances, the indigenous symbiotic microflora and the structure of plant parasitic nematode communities. *Geoderma*. 2002;109:85-102.

[51] Duponnois R, Plenchette C, Bâ AM. Growth stimulation of seventeen fallow leguminous plants inoculated with *Glomus aggregatum* in Senegal. *European Journal of Soil Biology*. 2001;37:181-186.

[52] Greenland DJ, Nye PH. . Increases in carbon and nitrogen contents of tropical soils under natural fallow. *Journal of Soil Science*. 1959;10:284–299.

[53] Feller C, Lavelle P, Albrecht A, Nicolardot B. La jachère et le fonctionnement des sols tropicaux. Rôle de l'activité biologique et des matières organiques. Quelques éléments de réflexions. In : ORSTOM, ed. *La jachère en Afrique de l'Ouest, Montpellier, 2-5 décembre 1991*. 1993:15–32.

[54] Piéri C. Les bases agronomiques de l'amélioration et du maintien de la fertilité des terres des savanes au sud Sahara. In: ORSTOM, ed. *Savanes d'Afrique, terre fertile? Actes des Rencontres Internationales. Montpellier , 10–14 Décembre 1990.* 1991:43–74.

[55] Diédhiou AG, Guèye O, Diabaté M, Prin Y, Duponnois R, Dreyfus B, Bâ AM. Contrasting responses to ectomycorrhizal inoculation in seedlings of six tropical African tree species. *Mycorrhiza*. 2005;16:11-17.

[56] Sanon A, Martin P, Thioulouse J, Plenchette C, Spichiger R, Lepage M, Duponnois R. Displacement of an herbaceous plant species community by mycorrhizal and non-mycorrhizal *Gmelina arborea*, an exotic tree, grown in a microcosm experiment. *Mycorrhiza*. 2006;16:125-132.

[57] USDA Plant Database (2010) Plant Profile : *Amaranthus viridis*. Available at :
http://plants.usda.gov/java/profile?symbol=AMVI. Accessed April 13, 2010.

[58] Sanon A, Beguiristain T, Cébron A, Berthelin J, Ndoye I, leyval C, Sylla S, Duponnois R. Changes in soil diversity and global activities following invasions of the exotic invasive plant, *Amaranthus viridis* L., decrease the growth of native sahelian *Acacia* species. *FEMS Microbiology Ecology*. 2009; 70:118-131.

[59] Cornet F, Diem HG, Dommergues YR. Effet de l'inoculation avec *Glomus mosseae* sur la croissance d'*Acacia holosericea* en pépinière et après transplantation sur le terrain. In : INRA, ed. Les mycorhizes : biologie et utilisation. Dijon;1982:287-293.

[60] Founoune H, Duponnois R, Bâ AM, El Bouami F. Influence of the dual arbuscular endomycorrhizal/ectomycorrhizal symbiosis on the growth of *Acacia holosericea* (A. Cunn. ex G. Don) in glasshouse conditions. *Annals of Forest Science*. 2001;59:93-98.

[61] Duponnois R, Diédhiou S, Chotte JL, Sy MO. Relative importance of the endomycorrhizal and/or ectomycorrhizal associations in *Allocasuarina* and *Casuarina* genera. *Canadian Journal of Microbiology*. 2003;49:281-287.

[62] Michelsen A, Quarmby C, Sleep D, Jonasson S. Vascular plant ^{15}N natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia.* 1998;115:406-418.

[63] Founoune H, Duponnois R, Meyer JM, Thioulouse J, Masse D, Chotte JL, Neyra M. Interactions between ectomycorrhizal symbiosis and fluorescent pseudomonads on *Acacia holosericea*: isolation of Mycorrhiza Helper Bacteria (MHB) from a Soudano-Sahelian soil. *FEMS Microbiology Ecology*. 2002;41:37-46.

[64] Duponnois R, Plenchette C. A mycorrhiza helper bacterium (MHB) enhances ectomycorrhizal and endomycorrhizal symbiosis of Australian *Acacia* species. *Mycorrhiza*. 2003;13:85-91.

[65] Lesueur D, Sarr A. Effects of single and dual inoculation with selected microsymbionts (rhizobia and arbuscular mycorrhizal fungi) on field growth and nitrogen fixation of *Calliandra calothyrsus* Meissn. *Agroforestry Systems*. 2008;73:37-45.

[66] Guissou T, BA AM, Guinko S, Plenchette C, Duponnois R. Mobilisation des phosphates naturels de Kodjari par des jujubiers (*Ziziphus mauritiana* Lam.) mycorhizés dans un sol acidifié avec de la tourbe. *Fruits*. 2001;56:261–269.

[67] Duponnois R, Cadet P. Interactions of *Meloidogyne javanica* and *Glomus* sp. on growth and N_2 fixation of *Acacia seyal*. *Afro-Asian Journal of Nematology*. 1994;4:228-233.

[68] Duponnois R, Founoune H, Bâ A, Plenchette C, El Jaafari S, Neymar M, Ducousso M. Ectomycorrhization of *Acacia holosericea* A. Cunn. ex G. Don by *Pisolithus* spp. in Senegal : effect on plant growth and on the root-knot nematode *Meloidogyne javanica*. *Annals of Forest Science*. 2000;57:345-350.