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ARBUSCULAR MYCORRHIZAL FUNGI ASSOCIATED WITH THE RHIZOSPHERE OF *Piliostigma reticulatum* AND *Guiera senegalensis* SHRUBS IN SENEGAL

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ABSTRACT

Piliostima reticulatum and *Guiera senegalensis* shrubs constitute “islands of soil fertility” in the rhizosphere, with better availability of water and more intense biological activity in the Sudano-Sahelian agro-ecosystems. There is, however, paucity of information on diversity of arbuscular mycorrhizal fungi (AMF) fungi, which have a wide ecological range of associations with a variety of vegetation. The purpose of this study was to identify the types of AMF in the rhizospheres of *P. reticulatum* and *G. senegalensis* shrubs in Senegal. Soil samples were collected from around the shrubs in Keur Matar Arame and Keur Ndary Ndiaye in 2019 after a rainy season. Arbuscular mycorrhizae fungi spores were isolated by the wet sieving method and identified based on their morphological characteristics (shape, size, colour, attached hyphae, and spore ornamentation). Four types of AMF were identified, namely *Glomus aggregatum*, *Sclerocystis rubiformis*, *Gigaspora margarita* and *Scutellospora gregaria*. In addition, the density of spores was more abundant in the soil outside the shrub canopy compare to the soil beneath the shrub.

Key Words: *Gigaspora margarita*, *Glomus aggregatum*, *Sclerocystis rubiformis*

RÉSUMÉ

Les arbustes *Piliostima reticulatum* et *Guiera senegalensis* constituent des « îlots de fertilité » dans la rhizosphère des sols, avec une meilleure disponibilité en eau et une activité biologique plus intense dans les agro-écosystèmes soudano-sahéliens. Cependant, Il y a peu d'informations sur la diversité des champignons mycorrhiziens arbusculaires (CMA) qui peuvent s'associer avec une large variété de plantes. Le but de cette étude est d'identifier les types de CMA dans les rhizosphères des arbustes *P. reticulatum* et *G. senegalensis* au Sénégal. Des échantillons de sol ont été collectés autour des

arbustes à Keur Matar Arame et Keur Ndary Ndiaye en 2019 après la saison des pluies. Les spores de champignons mycorrhiziens arbusculaires ont été isolées par la méthode de tamisage humide et identifiées en fonction de leurs caractéristiques morphologiques (forme, taille, couleur, hyphes attachés et ornementation des spores). Quatre types de CMA ont été identifiés, à savoir *Glomus aggregatum*, *Sclerocystis rubiformis*, *Gigaspora margarita* et *Scutellospora gregaria*. De plus, la densité des spores était plus abondante dans les sols hors couvert que dans les sols sous-couvert des arbustes.

Mots Clés: *Gigaspora margarita*, *Glomus aggregatum*, *Sclerocystis rubiformis*

INTRODUCTION

The Sudano-Sahelian region of West Africa, like many other arid and semi-arid environments, is characterised by perennial woody shrubs (Diakhaté *et al.*, 2016). Among these shrubs, *Piliostigma reticulatum* (DC) Hochst and *Guiera senegalensis* JF Gmel, are the most common native shrubs found in farmers' fields, where they are traditionally cut and burned as a means of field clearance (Lufafa *et al.*, 2008). *Piliostigma reticulatum* and *G. senegalensis* improves soil quality and promotes crop growth (Bright *et al.*, 2017). They are known as "islands of fertility," also termed "resource islands" under and near the vegetation tufts (Wezel *et al.*, 2000). These "resource islands" created by the shrubs are high in water availability and soil nutrients such as nitrogen, phosphorus and potassium (Wezel *et al.*, 2000; Hernandez *et al.*, 2015). It also creates a favourable environment for microbial population and diversity, hence resulting to high decomposition of organic materials (Diedhiou *et al.*, 2009; Dossa *et al.*, 2010).

According to Kizito *et al.* (2006) and Diakhaté *et al.* (2013), *Piliostigma reticulatum* and *G. senegalensis* surrounding micro-environments showed a high level of water availability and diversity of nematode compared to soil outside their influence. They also promote carbon sequestration in intercropping systems (Bright *et al.*, 2017) and influence the diversity of arbuscular mycorrhizal fungi (AMF) in the soil (Maurer-Troxler *et al.*, 2006; Bender *et al.*, 2016).

AMF play a key role in plant hydro-mineral nutrition and health. Indeed, several studies

have shown the beneficial effects of the AMF on the agro-ecosystems such as improving crop growth, improving soil structure and increasing plant resistance against biotic and abiotic stresses (Gonzalez-Chavez *et al.*, 2009). However, to date, there has not been systematic studies to ascertain the influence of *P. reticulatum* and *G. senegalensis* shrubs on the diversity of AMF. The objective of this study was to characterise the diversity of AMF in the rhizosphere of *P. reticulatum* and *G. senegalensis* shrubs on the abundance of AMF spores.

MATERIALS AND METHODS

Study area. This study was conducted during November to December of 2019 in the peanut Basin in Senegal. The region is semi-arid with a north Sudanian to sahelian climate (Dacosta, 1989). Mean annual precipitation ranges from 540 to 750 mm, distributed from July to October. The mean annual minimum and maximum air temperatures range from 20 °C from December to January and 34 °C from April to June (Diedhiou *et al.*, 2009). Basin soils are sandy, classifying as Calcids and mixed Haplic Ferric Lixisol (FAO, 2006), locally named Dior and Deck-Dior (Badiane *et al.*, 2000). The vegetation of the basin is shrubland with scattered trees (Diouf and Lambin, 2001).

Within the study area, the *G. senegalensis* site was to the west of the study area (in Keur Matar Arame, 14°46'N, 16°51'W, in the Diourbel region); whereas the *P. reticulatum* sites were in the Southeast (in Keur Ndary Ndiaye, 13°45'N, 15°47'W, in the Kaolack

region). For at least 50 years, the area was in crop rotation between peanuts and millet under local farmer management. *Guiera senegalensis* and *P. reticulatum* existed at Keur Matar, and Keur Ndary Ndiaye at densities of 1833 and 1300 shrubs ha⁻¹, respectively (Dossa *et al.*, 2012).

Sample selection. The shrub plots were divided into near or shrub cover (SC) and far or out-cover (HC) to investigate AMF diversities beneath the shrub canopy, which includes both the shrub rhizospheric zone *versus* soils outside the shrub canopy with no direct influence from the shrub canopy (Diedhiou *et al.*, 2013). Soil samples were taken from the rhizospheres beneath the canopies (0-25 cm) of both shrubs plants. Cores were collect from 15 points and the samples were pooled to obtain representative bulk samples.

The soil was passed through a 2-mm sieve to eliminate large particles, homogenised, placed in closed plastic bags, and stored in the room temperature prior to the experiment. Soils analysis and spores characterisation were carried out in the LCM lab (Laboratoire Commun de Microbiologie/IRD/ISRA/UCAD) in the research center of ISRA in Bel Air (Dakar / Senegal).

Isolation and identification of AMF. AMF spores were isolated by wet-sieving and sucrose centrifugation (Gerdemann and Nicolson, 1963). Briefly, 100 g of soil from each plant rhizosphere were suspended in 1000 ml water, stirred with a spatula stirrer for 1 minute and the solutions were passed through a sequences of sieves (400, 200, 50, and 32 µm). The soil fraction in the last sieve was collected in a beaker. Twenty-five milliliter of spore suspensions were transferred into 50 ml centrifugations tubes and centrifuged with 25 ml of 60% sucrose solution for 2 minutes at 1000 rpm. The supernatant was decanted into a 32 µm sieve, washed, and transferred to Petri dishes. Quantification of spores was

carried out in petri dishes under a stereoscopic microscope with 400 times magnification (B³aszkowski, 2012). The spore density was expressed as the total number of spores per 100 g of air-dried soil (McKenney and Lindsey, 1987).

Identification of AMF spores was carried out by observing morphological characters such as shape, size, colour, attached hyphae, and spore ornamentation. For spore identification, the database of AMF specimens by INVAM (2018) (West Virginia University, Morgantown, USA) was used and described as provided by Morton and Benny (1990).

The diversity index was calculated according to Shannon-Weaver for each soil (SC and HC), using the formula:

$$H = - \sum \left(\frac{ni}{N} \right) \ln \left(\frac{ni}{N} \right)$$

Where:

ni represents the density of the spores of the species *i* and *N* the total density of the spores of all the species in a sample.

A low *H* value generally suggests a site with few species and a few dominant species, while a high *H* value suggests considerably more species.

Statistical analysis. The data collected were analysed using a one-way ANOVA. Fisher's test (LSD) was used to compare the means (*P*<0.05). Linear regression was used to clarify the influence of soil chemical parameters on communities of AMF fungi. Statistical analyses were performed using XLSTAT software (Version 2013.1).

Principal Components Analysis (PCA) was performed using Minitab 17 software, to determine relationship between soil chemical properties (C, N and P) and spores abundance. Scores of samples in Axis 1 and Axis 2 were further analysed using permutational multivariate analysis of variance

(PerMANOVA) (Anderson, 2001) to determine the statistical significance of any treatment.

RESULTS

Abundance and diversity of AMF spores.

The abundance of AMF spores was significantly higher ($P < 0.05$) in soil without the shrubs (*P. reticulatum* and *G. senegalensis*) than the soils from the rhizosphere of the shrubs (Table 1). Spore density also displayed a similar pattern, with spores being more diversified in the control soil (without the shrubs) than in the rhizospheric soil of the shrubs (Table 1).

Three morpho-species were found in the rhizosphere of the shrubs (*P. reticulatum* and *G. senegalensis*) and one more in the control (without the shrubs) (Table 1). These species belonged to three genera; with two species belonging to the *Glomeraceae* family (*Glomus aggregatum* and *Sclerocystis rubiformis*), and two to *Gigasporaceae* family (*Gigaspora margarita* and *Scutellospora gregaria*) (Fig. 1). *Sclerocystis rubiformis* was found exclusively in the control (without the presence of the shrubs).

With regard to the density, *Glomus aggregatum* and *Gigaspora margarita* had a relatively higher density of spores compared to *Sclerocystis rubiformis* and *Scutellospora gregaria* (Table 1). A comparison of the soils showed that the Diversity Index was higher in the soil outside the shrubs canopies ($H = 1.00$) than in the soil beneath the shrubs canopies ($H = 0.71$) (Table 1).

For *P. reticulatum*, the comparison of the means also showed that the number of spores of AMF was significantly higher in the control (300 ± 84 per 100 g of dry soil) than in the presence of the shrubs (201 ± 42 per 100 g of dry soil) $P < 0.01$. A similar trend was observed for *G. senegalensis*.

Soil chemical properties and abundance of AMF. It was clear that the abundance of AMF spores was negatively correlated with the quantity of soil organic C ($r = -0.28$, $P < 0.001$),

TABLE 1. Number of spores per 100 g of soil per fungal type and soil type (\pm standard error)

Shrubs	Treatments	<i>Gigaspora margarita</i>	<i>Glomus aggregatum</i>	<i>Sclerocystis rubiformis</i>	<i>Scutellospora gregaria</i>	Mean	Species number	Shannon Index (H)
<i>P. reticulatum</i>	SC	65 ± 30 a	131 ± 76 a	0 ± 0 a	7 ± 2 a	201 ± 87 a	3	0.71 a
	HC	73 ± 24 a	171 ± 55 a	54 ± 14 b	3 ± 2 a	300 ± 84 b	4	1.00 b
<i>G. senegalensis</i>	SC	43 ± 16	75 ± 25	0 ± 0 a	5 ± 2 a	123 ± 42 a	3	0.71 a
	HC	154 ± 43	183 ± 58	172 ± 44	5 ± 2 a	524 ± 93 b	4	1.00 b

* = Different letters within a row indicate significant difference between treatments according to the Turkey test at $P < 0.05$ different

organic N ($r = -0.47$, $P < 0.001$) and available P ($r = -0.67$, $P < 0.01$). The three elements (C, P and N) had a negative influence on the abundance of AMF spore (Table 2).

Multivariate analysis of all data showed a strong clustering by soil location ($P < 0.01$) (Fig. 2). Principal component analysis of the abundance of the spore of AMF showed a

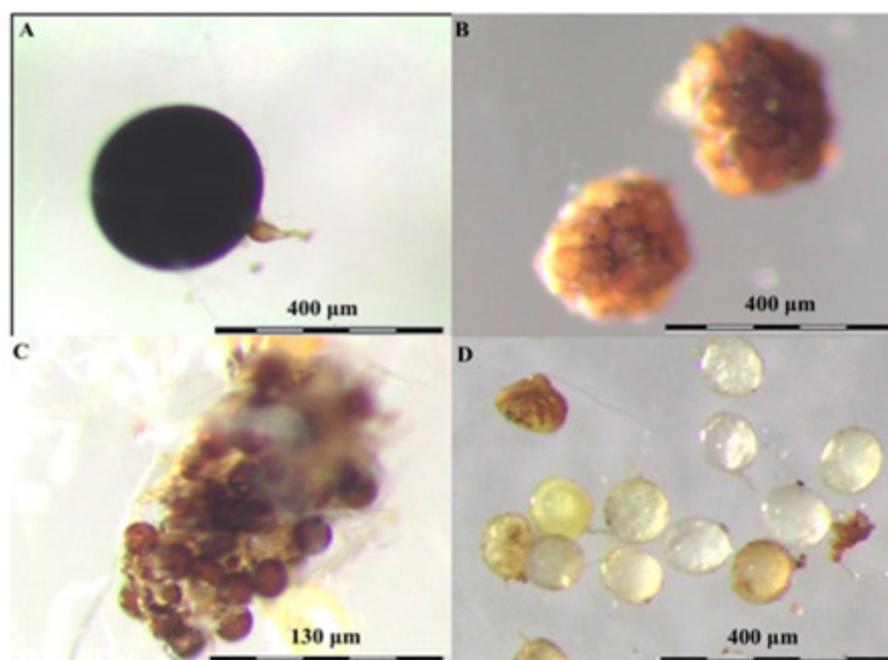


Figure 1. Spore diversity in soil within and outside the influence of *P. reticulatum* shrub. A: Spore of *Scutellospora gregaria* is found in all soils. Its spores are large and visible to naked eye, black and have a suspending bulb. B: *Sclerocystis rubiformis* is the species characteristic of soil outside the influence of *P. reticulatum*. The spores are inseparable cluster and brown. C: Spore of *Glomus aggregatum*, is present in all soils. It forms spores in brown clusters. D: Spore of *Gigaspora margarita* is found in all soils. The spores are medium-sized, whitish and yellowish with a suspending bulb.

TABLE 2. Chemical properties of the rhizospheric soils beneath the shrubs and the soil without the shrubs in Senegal (\pm standard error)

Soil parameters	<i>P. reticulatum</i>		<i>G. senegalensis</i>	
	Control (HC)	Rhizospheric soil (SC)	Control (HC)	Rhizospheric soil (SC)
Total C (mg C g ⁻¹)	2.50 \pm 0.77 a*	4.00 \pm 0.40 b	1.50 \pm 0.14 a*	3.44 \pm 0.48 a*
Total N (mg N g ⁻¹)	0.22 \pm 0.01 a	0.36 \pm 0.01 b	0.20 \pm 0.01 a	0.40 \pm 0.02 b
Total P (μ g P g ⁻¹)	42.30 \pm 3.23 a	59.50 \pm 5.77 b	13.30 \pm 0.33 a	95.0 \pm 7.32 b
pH (H ₂ O)	5.5 \pm 0.1 a	5.5 \pm 0.1 a	5.4 \pm 0.1 a	5.2 \pm 0.1 a

*= Means followed by different letter within a row indicate significant difference between treatments (HC/SC) at $P < 0.05$

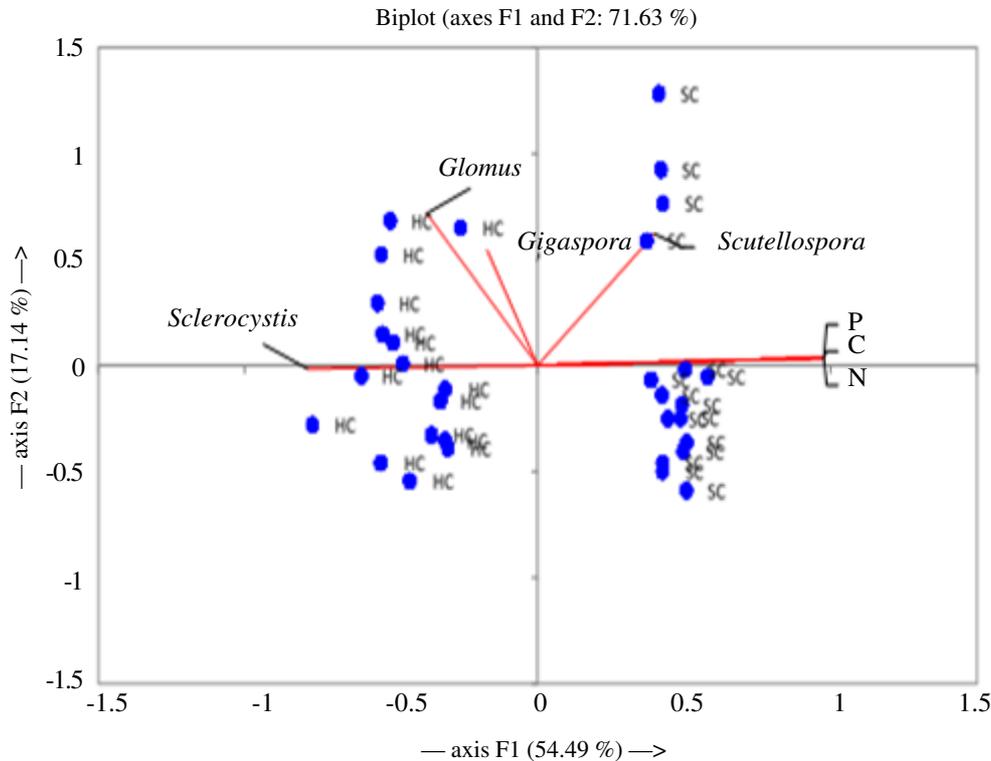


Figure 2. Principle component analysis of the abundance of AMF spore from soil beneath and outside the shrubs canopy influence. HC = outside beneath of canopy, SC = beneath canopy C = carbon; P = phosphorus and N = nitrogen.

distinct separation of clusters along the first axis (54.5% of the total variance) based on the soil chemical properties. The second axis accounted for only 17.1% of the variability. Samples were clustered separately between data from beneath and outside the canopy influence. Total N, P and C were negatively correlated with the abundance of spores of *Glomus*, *Sclerocystis* and *Gigaspora* ($P < 0.01$).

DISCUSSION

Diversity and abundance of AMF spores. The density of AMF spores in the rhizosphere of the shrubs (*P. reticulatum* and *G. senegalensis*) was relatively low (on average 201 and 109 spores per 100 g of dry soil for *P. reticulatum* and *G. senegalensis*, respectively), compared to the AMF spores from the control (on average 300 and 144

spores per 100 g of dry soil for *P. reticulatum* and *G. senegalensis*, respectively). These results are in accordance with those obtained by Dabiré *et al.* (2007), who showed that the absence of vegetation (bare soil) is hardly conducive to the development of fungi; hence the presence of a high quantity of spores which is the form of resistance of fungi to unfavourable environmental conditions. Indeed, AMF being obligatory symbionts, need host plants to maintain themselves in the soil.

The rhizospheric soil had fewer spores than the control soil (Table 1) perhaps because of the presence of the shrubs, which accelerated spore germination to rapidly infect new roots and the mycorrhizae sporulate continuously (Hamid and Renard, 2003). Overall, the density of spores in rhizosphere of the shrubs was lower than that found in plantations of *Acacia holosericea* and *Acacia*

mangium in the southern and northern regions of Sudan in Burkina Faso (Bâ *et al.*, 1996); and that of *Acacia albida* in different regions from Senegal (Diop *et al.*, 1994). The density of *Glomeromycota* spores was generally higher in the control in the present study than in rhizosphere of the shrubs (Table 1).

Using morphological identification, four morphotypes were found in all soils (Table 1), yet Diallo *et al.* (1999) found nine morphotypes in the semi-arid regions of Senegal. Morphological identification does not allow assessment of the real diversity in terms of fungal species. However, the morphotypes were related to the genera *Glomus*, *Gigaspora*, *sclerocistys* and *Scutellospora*. The morphotypes of *Glomeraceae* family were dominant in both soils (rhizosphere and nonrhizosphere) and spores of the genus *Glomus* were more abundant.

The predominance of *Glomeraceae* has also been reported in some studies based on AMF morphotypes in various tropical soils (Bâ *et al.*, 1996; Diallo *et al.*, 1999; Houngnandan *et al.*, 2009) and in certain agricultural soils of temperate zones (Mathimaran *et al.*, 2005). Indeed, in the semi-arid zones in Senegal, *Glomus* is numerically more important than others genus (Diop, 1995; Diallo *et al.*, 1999). According to Bourou (2012), in arid areas of Africa, the best-known AMF belongs to the genus *Glomus* and *Gigaspora*. Indeed, the genus *Glomus* is considered to be the most associated with woody plants in dry areas of Africa (Bouamri *et al.*, 2006). Hatimi and Tahrouch (2007) reported that *Glomus* was the most ubiquitous AMF.

Our results have revealed that at morphological level of the spores, there are dismal differences in the composition of AMF from rhizosphere of the shrubs and in the soil control. The same morphotypes are found on both treatment conditions, but only in different quantities. The absence of the shrubs significantly ($P = <0.05$) favoured the abundance of spores of AMF (Table 1). The results confirm the assertion by Bogie *et al.*

(2018) that the beneficial effects of the shrubs through hydraulic redistribution for the benefit of the crops may not favor the presence of AMF spores.

Sclerocystis rubiformis is a characteristic species of the control. This species is not found in the rhizosphere of the shrubs. *Glomus aggregatum* has been reported from the rhizosphere of palm-oil in Java (Widiastuti and Kramadibrata, 1992) and *Chrysophyllum cainito* (Destifani, 2013). *Sclerocystis rubiformis* has been reported in Cordoba from the rhizosphere of poacea (Lugo and Cabello, 2002). In Mexico, *S. rubiformis* has been reported from the rhizosphere of *cocos nucifera* in a coconut-growing area along the coastline and the inland in the tropical forest of Yucatan (Lara-Perez *et al.*, 2020). *Gigaspora margarita* on the other hand, has been identified from the rhizosphere of *Vigna unguiculata* in Senegal (Diop *et al.*, 2021). *Scutellospora gregaria* has been also reported from the rhizosphere of *Borreria articularis* in west coast of India (Beena *et al.*, 2001).

Soil chemical properties and diversity of AMF. This study has revealed that richness and abundance in fungal are negatively influenced by the richness of P, C and nitrogen in the rhizosphere soil (Fig. 2). When the concentration of N, P, and C in the soil is low, the richness of AMF increases.

The results of the PCA (Fig. 2) confirm those of the Pearson correlation with regard to the abundance of spores in relation to the soil chemical properties. In addition, we found that the variation in AMF community structure according to soil type was mainly explained by N, P and C levels. These results are consistent with those of Cuenca and Meneses (1996) and Isobe *et al.* (2007), who indicated that the abundance and diversity of AMF communities associated with cocoa, were negatively correlated with the available P in the soils. According to Johnson *et al.* (2013), certain morpho-species are more sensitive to available P and become less frequent and

undetectable in soils with high level of available P. The low species richness in both soils (with and without shrubs) could be due to limited or non-existent sporulation in the soils of certain species since many AMF species can end their life cycle with sporulation only towards the end of the wet season, to survive during the dry season. Another reason is, the previous crop grown in the sites was pearl millet, which has a low mycorrhizal dependency (Rao *et al.*, 1985)

CONCLUSION

This study has shown that *P. reticulatum* and *G. Senegalensis* shrubs are naturally associated with a range of AM fungi in the soils of the Sudano-Sahelian agro-ecosystems of Senegal. Four species (*Glomus aggregatum*, *Sclerocystis rubiformis*, *Gigaspora margarita* and *Scutellospora gregaria*) were identified in the rhizosphere of the shrubs from two sites. *Glomus* is the most represented genus; followed by *Gigaspora* in the different soils. Our results also revealed that AMF communities were clustered according to soil chemical properties (N, P and C). Future research should focus on the use of soil these AMF species in order to develop highly effective and competitive inoculants for pearl millet and groundnut cultivation in these different and sites.

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REFERENCES

- Anderson, M.J. 2001. A new method for non parametric multivariate analysis of variance. *Austral Ecology* 26(1):32-46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Bâ, A.M., Dalpé, Y. and Guissou, T. 1996. Les Glomales d'Acacia holosericea et d'Acacia mangium. *Bois & Forêts des Tropiques* 250:5-18.
- Badiane, A. N., Khouma, M. and Sene M. 2000. Region de Diourbel: Gestion des sols. Drylands Research Working Paper 15. Drylands Research, Somerset, England, p. 25. <https://doi.org/10.19182/bft1996.250.a19862>
- Beena, K.R., Arun, A.B., Raviraja, N.S. and Sridhar, K.R. 2001. Association of arbuscular mycorrhizal fungi with plants of coastal sand dunes of west coast of India. *Tropical Ecology* 42(2):213-222.
- Bender, S.F., Wagg, C. and van der Heijden, M.G. 2016. An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. *Trends in Ecology & Rvolution* 31(6):440-452. <https://doi.org/10.1016/j.tree.2016.02.016>
- Blaszkowski, J. 2012. *Glomeromycota*. W. Szafer Institute of Botany, Polish Academy of Sciences.
- Bogie, N.A., Bayala, R., Diedhiou, I., Conklin, M.H., Fogel, M.L., Dick, R.P. and Ghezzehei, T.A. 2018. Hydraulic redistribution by native sahelian shrubs: bioirrigation to resist in-season drought. *Frontiers in Environmental Science* 6:98 <https://doi.org/10.3389/fenvs.2018.00098>
- Bouamri, R., Dalpé, Y., Serrhini, M.N. and Bennani, A. 2006. Arbuscular mycorrhizal fungi species associated with rhizosphere of Phoenix dactylifera L. in Morocco. *African Journal of Biotechnology* 5(6):10-516.
- Bourou, S. 2012. Étude éco-physiologique du tamarinier (*Tamarindus indica* L.) en milieu tropical aride. Doctoral dissertation, Ghent University, Belgium. 193pp.
- Bright, M.B., Diedhiou, I., Bayala, R., Assigbetse, K., Chapuis-Lardy, L., Ndour, Y. and Dick, R.P. 2017. Long-term *Piliostigma reticulatum* intercropping in the Sahel: Crop productivity, carbon

- sequestration, nutrient cycling, and soil quality. *Agriculture, Ecosystems & Environment* 24(2):9-22.
- Cuenca, G. and Meneses, E. 1996. Diversity patterns of arbuscular mycorrhizal fungi associated with cacao in Venezuela. *Plant and Soil* 83(2):315-322. <https://doi.org/10.1007/BF00011447>
- Dabiré, A.P., Hien, V., Kisa, M., Bilgo, A., Sangare, K.S., Plenchette, C., Galiana, A., Prin, Y. and Duponnois, R. 2007. Responses of soil microbial catabolic diversity to arbuscular mycorrhizal inoculation and soil disinfection. *Mycorrhiza* 17(6):537-545.
- Dacosta, H. 1989. Précipitations et écoulements sur le bassin de la Casamance. Dakar: ORSTOM, multigr. Doctoral dissertation, Thèse 3e cycle, Université Cheikh Anta Diop de Dakar, Sénégal.
- Destifani, Y.F. 2013. Arbuscular mycorrhizal fungi on star apple (*Chrysophyllum cainito*) at IPB Darmaga Campus. Undergraduate Thesis, Bogor Agricultural University, Indonesia.
- Diakhaté, S., Gueye, M., Chevallier, T., Diallo, N.H., Assigbetsé, K., Abadie, J., Diouf, M., Masse, D., Sembène, M., Ndour, Y.B. and Dick, R.P. 2016. Soil microbial functional capacity and diversity in a millet-shrub intercropping system of semi-arid Senegal. *Journal of Arid Environments* 12(9):71-79. <https://doi.org/10.1016/j.jaridenv.2016.01.010>
- Diakhaté, S., Villenave, C., Diallo, N.H., Ba, A.O., Djigal, D., Masse, D., Sembène, P.M. and Chapuis-Lardy, L. 2013. The influence of a shrub-based intercropping system on the soil nematofauna when growing millet in Senegal. *European Journal of Soil Biology* 5(7):35-41. <https://doi.org/10.1016/j.ejsobi.2013.04.003>
- Diallo, A.T., Samb, P.I. and Ducousso, M. 1999. Arbuscular mycorrhizal fungi in the semi-arid areas of Senegal. *European Journal of Soil Biology* 35(2):65-75. [https://doi.org/10.1016/S1164-5563\(99\)00110-7](https://doi.org/10.1016/S1164-5563(99)00110-7)
- Diedhiou, S., Dossa, E.L., Badiane, A.N., Diedhiou, I., Sene, M. and Dick, R.P. 2009. Decomposition and spatial microbial heterogeneity associated with native shrubs in soils of agroecosystems in semi-arid Senegal. *Pedobiologia* 52(4):273-286. <https://doi.org/10.1016/j.pedobi.2008.11.002>
- Diedhiou-Sall, S., Dossa, E.L., Diedhiou, I., Badiane, A.N., Assigbetsé, K.B., Ndiaye Samba, S.A., Khouma, M., Sène, M. and Dick, R.P. 2013. Microbiology and macrofaunal activity in soil beneath shrub canopies during residue decomposition in agroecosystems of the Sahel. *Soil Science Society of America Journal* 77(2):501-511. <https://doi.org/10.2136/sssaj2012.0284>
- Diop, T.A., Gueye, M., Dreyfus, B.L., Plenchette, C. and Strullu, D.G. 1994. Indigenous arbuscular mycorrhizal fungi associated with *Acacia albida* Del. in different areas of Senegal. *Applied and Environmental Microbiology* 60(9):3433-3436.
- Diop, T. 1995. Ecophysiologie des champignons mycorhiziens à vésicules et arbuscules associés à *Acacia albida* dans les zones Sahéliennes et Soudano-Guinéenne du Sénégal (Doctoral dissertation).
- Diop, I., Ndoeye, F., Diédhiou, A. and Krasova-Wade, T. 2021. Diversity and spore density of arbuscular mycorrhizal fungi in the rhizosphere of cowpea (*Vigna unguiculata* [L.] Walp.) cultivated in different soils in Senegal.
- Diouf, A. and Lambin, E.F. 2001. Monitoring land-cover changes in semi-arid regions: remote sensing data and field observations in the Ferlo, Senegal. *Journal of Arid Environments* 48(2):129-148.
- Dossa, E.L., Diedhiou, I., Khouma, M., Sene, M., Lufafa, A., Kizito, F., Samba, S.A.N., Badiane, A.N., Diedhiou, S. and Dick, R.P.

2012. Crop productivity and nutrient dynamics in a shrub (*Guiera senegalensis*)–based farming system of the Sahel. *Agronomy Journal* 104(5):1255-1264. <https://doi.org/10.2134/agronj2011.0399>
- Dossa, E.L., Diedhiou, S., Compton, J.E., Assigbetse, K.B. and Dick, R.P. 2010. Spatial patterns of P fractions and chemical properties in soils of two native shrub communities in Senegal. *Plant and Soil* 327(1):185-198. <https://doi.org/10.1007/s11104-009-0044-8>
- FAO, I. 2006. ISRIC: World Reference Base for soil resource in World Soil Resource Report no. 103. FAO, Rome, Italy.
- Gerdemann, J.W. and Nicolson, T.H. 1963. Spores of mycorrhizal endogone species extracted from soil by wet sieving and decanting. *Transactions of the British Mycological Society* 46(2):235-244.
- Gonzalez-Chavez, M.C., Carrillo-Gonzalez, R. and Gutierrez-Castorena, M.C. 2009. Natural attenuation in a slag heap contaminated with cadmium: The role of plants and arbuscular mycorrhizal fungi. *Journal of Hazardous Materials* 161(2-3):1288-1298. <https://doi.org/10.1016/j.jhazmat.2008.04.110>
- Hamid, A. and Renard, A. 2003. Statuts des mycorhizes à arbuscules. Etude de la mycorhization de quelques espèces végétales présentant un intérêt pour la restauration écologique, Université de la Nouvelle Calédonie, Rapport n° 5. 36pp.
- Hatimi, A. and Tahrouch, S. 2007. Caractérisations chimique, botanique et microbiologique du sol des dunes littorales du Souss-Massa. *Biomatec Echo* 2(5):85-97.
- Hernandez, R.R., Debenport, S.J., Lewis, M.C.C., Ndoye, F., Soumare, A., Thuita, M., Gueye, M., Miambi, E., Chapuis-Lardy, L., Diedhiou, I. and Dick, R.P. 2015. The native shrub, *Piliostigma reticulatum*, as an ecological “resource island” for mango trees in the Sahel. *Agriculture, Ecosystems & Environment* 20(4):51-61. <https://doi.org/10.1016/j.agee.2015.02.009>
- Houngnandan, P., Yemadje, R.G.H., Kane, A., Boeckx, P. and Van Cleemput, O. 2009. Les glomales indigènes de la forêt claire à Isoberlinia doka (Craib et Stapf) à Wari-Marou au centre du Bénin. *Tropicultura* 27(2):83-87.
- INVAM, 2018. International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi. West Virginia University. <https://invam.wvu.edu/>
- Isobe, K., Aizawa, E., Iguchi, Y. and Ishii, R. 2007. Distribution of arbuscular mycorrhizal fungi in upland field soil of Japan I. Relationship between spore density and the soil environmental factor. *Plant Production Science* 10(1):122-128. <https://doi.org/10.1626/pp.s.10.122>
- Johnson, J.M., Houngnandan, P., Kane, A., Sanon, K.B. and Neyra, M. 2013. Diversity patterns of indigenous arbuscular mycorrhizal fungi associated with rhizosphere of cowpea (*Vigna unguiculata* (L.) Walp.) in Benin, West Africa. *Pedobiologia* 56(3):121-128. <https://doi.org/10.1016/j.pedobi.2013.03.003>
- Kizito, F., Dragila, M., Sene, M., Lufafa, A., Diedhiou, I., Dick, R.P., Selker, J.S., Dossa, E., Khouma, M., Badiane, A. and Ndiaye, S. 2006. Seasonal soil water variation and root patterns between two semi-arid shrubs co-existing with Pearl millet in Senegal, West Africa. *Journal of Arid Environments* 67(3):436-455. <https://doi.org/10.1016/j.jaridenv.2006.02.021>
- Lara-Pérez, L.A., Oros-Ortega, I., Córdova-Lara, I., Estrada-Medina, H., O’Connor-Sánchez, A., Góngora-Castillo, E. and Sáenz-Carbonell, L. 2020. Seasonal shifts of arbuscular mycorrhizal fungi in Cocos nucifera roots in Yucatan, Mexico. *Mycorrhiza* 30(2):269-283.
- Lufafa, A., Diédhiou, I., Samba, S.A.N., Séné, M., Khouma, M., Kizito, F., Dick, R.P., Dossa, E. and Noller, J.S. 2008. Carbon stocks and patterns in native shrub

- communities of Senegal's Peanut Basin. *Geoderma* 146(1-2):75-82. <https://doi.org/10.1016/j.geoderma.2008.05.024>
- Lugo, M.A. and Cabello, M.N. 2002. Native arbuscular mycorrhizal fungi (AMF) from mountain grassland (Córdoba, Argentina) I. Seasonal variation of fungal spore diversity. *Mycologia* 94(4):579-586.
- Mathimaran, N., Ruh, R., Vullioud, P., Frossard, E. and Jansa, J. 2005. *Glomus intraradices* dominates arbuscular mycorrhizal communities in a heavy textured agricultural soil. *Mycorrhiza* 16(1):61-66. <https://doi.org/10.1007/s00572-005-0014-9>
- Maurer-Troxler, C., Chervet, A., Ramseier, L., Sturny, W.G. and Oberholzer, H.R. 2006. Soil biology after ten years of no-and conventional tillage. *Revue Suisse d'Agriculture* 38:89-94.
- McKenney, M.C. and Lindsey, D.L. 1987. Improved method for quantifying endomycorrhizal fungi spores from soil. *Mycologia* 79(5):779-782. <https://doi.org/10.1080/00275514.1987.12025458>
- Morton, J.B. and Benny, G.L. 1990. Revised classification of arbuscular mycorrhizal fungi (Zygomycetes): A new order, Glomales, two new suborders, Glomineae and Gigasporineae, and two new families, *Acaulosporaceae* and *Gigasporaceae*, with an emendation of Glomaceae. *Mycotaxon* 37:471-491.
- Rao, N.S., Tilak, K.V.B.R. and Singh, C.S. 1985. Effect of combined inoculation of *Azospirillum brasilense* and vesicular-arbuscular mycorrhiza on pearl millet (*Pennisetum americanum*). *Plant and Soil* 84(2):283-286.
- Wezel, A., Rajot, J.L. and Herbrig, C. 2000. Influence of shrubs on soil characteristics and their function in Sahelian agroecosystems in semi-arid Niger. *Journal of Arid Environments* 44(4):383-398. <https://doi.org/10.1006/jare.1999.0609>
- Widiastuti, H. and Kramadibrata, K. 1992. Vesicular-arbuscular mycorrhizal fungi on selected acid soil of West Java. *Menara Perkebunan* 60(1):9-19.