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Review

Senegalia senegal (synonym: *Acacia senegal*), its importance to sub-Saharan Africa, and its relationship with a wide range of symbiotic soil microorganisms

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ABSTRACT

Changing environmental conditions in dryland areas exacerbate land degradation and food insecurity in many sub-Saharan African nations. Multi-purpose tree species such as *Senegalia senegal* (L.) Britton, are favored for reforestation and land reclamation as compared to single-use species. A great deal of research has also focused on this tree species due to its ability to fix atmospheric nitrogen into ammonia, which is returned over time to the soil via the recycling of N-rich plant tissue. We review the recent literature on how *S. senegal* contributes to soil fertility and crop production especially in the context of sustainable and ecological agriculture. We also review the current literature on this legume species with regard to its microsymbionts, with the goal of further maximizing the potential of *S. senegal* for agriculture in sub-Saharan Africa. *Senegalia senegal*, which has the potential to restore degraded soils and to be used for agroforestry, is both economically and ecologically important for the dry areas of sub-Saharan Africa because it produces gum arabic, an important commodity crop for smallholder farmers; it succeeds where other crops fail. This tree species also can correct soil fertility loss caused by continuous agriculture and worsened by a reduced or non-existent fallow period. *Senegalia senegal* and its soil microbes are positively associated with this species' ability to survive in harsh conditions. This tree is an important candidate for restoring soil fertility and providing commercial products especially in countries with arid environments.

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1. Introduction

Acacia (mimosoid clade; (LPWG, 2017)) shrubs and trees are common in the savannas and drylands of Africa, Australia, India, and South and North America and are frequently planted in the Sahel region of Africa (Dreyfus and Dommergues, 1981). The genus name *Acacia* was recently changed for the African species because of their polyphyletic nature. They are found not only in Africa, but also in Central and South America, and Asia and comprise more than 60 species. Kyalangalilwa et al. (2013) separated *Acacia* sensu *lato* into two new genera, namely *Senegalia* and *Vachellia*. *Senegalia senegal* is now the accepted name of what was formerly called *Acacia senegal*.

Senegalia senegal is a multipurpose agroforestry tree species (Raddad and Luukkanen, 2007), and this small tree or shrub species (Fig. 1) is one of the most commercially exploited (Fagg and Allison, 2004). This legume produces gum arabic, which is used for foods, beverages, pharmaceuticals, and cosmetics, and other applications. *Senegalia senegal* also supports dryland ecosystems in tropical Africa (Fagg and Allison, 2004; Gray et al., 2013; Odee et al., 2011; Omondi et al., 2010; Sprent et al., 2010). Agroforestry systems based on *S. senegal* and a variety of crops produce combined yields that are larger than when the trees or agricultural crops are grown separately. It accumulates a large biomass when given sufficient water (Gaafar et al., 2006). In Sudan, a traditional rotation with agricultural crops and *S. senegal* was shown to maintain soil fertility (Ballal et al., 2005; Barbier, 1992) and has a low input production cycle (Raddad et al., 2006). Despite *S. senegal's* commercial, industrial, agricultural, and ecological importance, this tree still remains under-utilized in African drylands. This under-utilization is attributed to a lack of knowledge of production systems and also to the fact that there are relatively few seed sources (Omondi et al., 2010). Nonetheless, *S. senegal* has been a successful crop in agroforestry systems in the Sudan and several West African nations (Anderson, 1988).

Senegalia senegal is symbiotic with soil microorganisms, especially rhizobia and Arbuscular Mycorrhizal Fungi (AMF). Rhizobia contribute to the global nitrogen cycle (Sprent, 1994), and a number of different rhizobial taxa and strains establish nitrogen-fixing nodules on *S. senegal* roots (Bakhoum et al., 2014; de Lajudie et al., 1998; Fall et al., 2008; Nick et al., 1999; Njiti and Galiana, 1996; Odee et al., 1995, 1997). AMF are widespread and are critical to establishing a healthy soil microbiome. They establish symbiotic phosphate (P)-acquiring mutualisms with their host plants that improve both water and nutrient uptake. They also protect their hosts against plant pathogens (Smith and Read, 2008). Although *S. senegal* plays both economic and ecological roles and is used for agroforestry, information regarding the species is scattered and up to now, very little data integration has taken place.

Fig. 1. *Senegalia senegal* trees growing in a plantation (Dahra sylvopastoral zone, Latitude, 15°21′N; Longitudinal 15°29′W).

Our objectives in this review are to: (1) highlight the diversity within *S. senegal*; (2) assess the chemical quality and factors influencing gum arabic; (3) describe the microsymbionts associated with *S. senegal* and the impact of their inoculation on the plant and the rhizosphere; and (4) lastly, summarize the effects of *S. senegal* on soil fertility and reclamation of soil damaged by salinity.

2. Diversity within *S. senegal* trees

Senegalia senegal can be divided into four different varieties based on morphology: *senegal*, *kerensis*, *rostrata*, and *leiorhachis* (Fagg and Allison, 2004). The variety *senegal* is established in West Africa and also East Africa, as are the *leiorhachis* and *kerensis* varieties (Fig. 2).

Previously range-wide genetic studies of *S. senegal* revealed differences among varieties and provenances, especially between West Africa and eastern and southern Africa (Chevallier and Borgel, 1998; Odee et al., 2012, 2015). For example, the variety *senegal* exhibits a different population structure in Senegal (Chevallier et al., 1994). Isoenzyme electrophoresis demonstrated low genetic variability in *S. senegal* var. *senegal* populations, which indicated that the differences between provenances were low although rare alleles were sometimes observed (Sall, 1997). In contrast, Omondi et al. (2010) observed a high genetic diversity and low inter-population genetic differentiation in the *kerensis* variety in Kenya. In a large *S. senegal* genetic diversity study that used ITS and chloroplast DNA (cpDNA) analysis, Odee et al. (2012) observed genetic variation based on geography, such that the eastern and southern African populations were separated from western and central Africa within the Sudano-Sahelian region.

Based on cytology, *S. senegal* was reported to consist of diploids only (Atchison, 1948; Bukhari, 1997a, 1997b; Oballa and Olng'otie, 1993). However, Assoumane et al. (2013) observed tetraploids in three different populations from the Sudano-Sahelian region. Recently, Odee et al. (2015) reported that *S. senegal* is principally diploid, but other ploidy levels were detected. Together, these authors have concluded that the incidence of diploid–polyploid complexes in the northern range overlaps with phylogenetic and phylogeographic parameters. They hypothesized that the recent arrival and the expansion of *S. senegal* in this region could be explained by polyploidy. Thus, polyploidy is expected

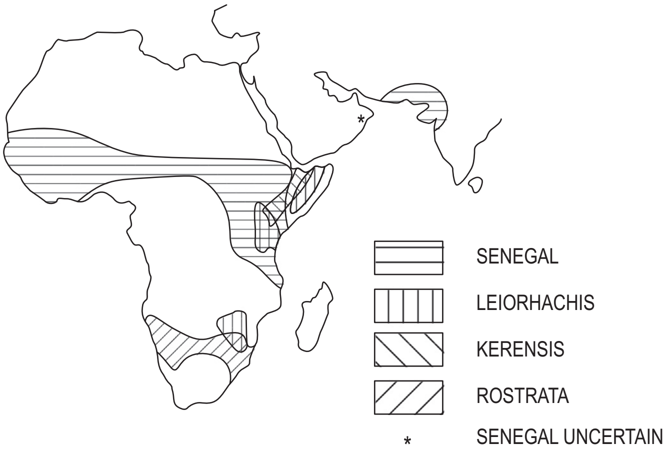

Fig. 2. Map showing approximate distribution of *Senegalia* species and varieties. Redrawn from an illustration in: Food and Agriculture Organization of the United Nations, [1983], [J. P.M. Brenan], [FAO:Handbook on the Taxonomy of *Acacia* Species].

to be encountered mainly in trees of the Sudano-Sahelian region and in the native range.

3. *Senegalia senegal* gum production

Gum arabic is used in numerous industries and for a variety of purposes worldwide (Fagg and Allison, 2004). The European Union is one of the major consumers of gum arabic (200,000 tons, which is equivalent to approximately US$432 million; MNS, 2008). Sixty per cent (60%) of gum arabic product comes from Sudan, 24% from Chad, 6% from Nigeria, and 8% from other countries (Couteaudier, 2007; Touré, 2009), including 1% from Senegal.

Gum production generally begins during the first tapping period, when the tree is 4 or 5 years old. The quality of the gum depends on the site of the population, the recorded rainfall, soil moisture, temperature, and the date on which tapping is practiced (Sall, 1997). The period of production is also highly dependent on climatic conditions. Other studies showed a correlation between the amount of water in the soil and gum arabic production (Vassal and Dione, 1993; Wekesa et al., 2009). Previous investigations demonstrated that gum arabic quality is also affected by origin, soil type, and/or climatic factors (Chikamai and Odera, 2002). Moreover, each variety, *senegal*, *kerensis*, *rostrata*, and *leiorhachis*, differs in gum quality (Lelon et al., 2010). Lastly, it takes between 8 and 13 years before sufficient gum arabic is produced by a tree, and the amount of gum produced fluctuates greatly from one tree to another and from one year to another, varying between 100 and 1000 g per tree. The annual average production per ha is about 200 to 300 kg in Sudan and 240 kg in Senegal (Sall, 1997).

Gum arabic fractionated by hydrophobic affinity chromatography detects a broad spectrum of arabinogalactans, arabinogalactan-proteins, and/or glycoproteins (Osman et al., 1993; Renard et al., 2006). Diallo et al. (2015) reported that provenances as well as certain families of polyploids had a different nitrogen content in their gum arabic. However, provenances, families, or plant ploidy levels appeared to have only a minor effect on carbon content. On average, the nitrogen content obtained in these studies was higher in diploids (0.39%) than in polyploids (0.34%). Gashua et al. (2015), in comparing physicochemical characteristics of *S. senegal* gum arabic samples from Nigeria and Sudan, found similar characteristics, but interestingly, the Nigerian samples had more protein. These authors concluded that the protein difference could be attributed to genotypic differences or to the influence of biotic/abiotic stress conditions, or a combination of the two. Thus, like nitrogen content, protein quantity in *S. senegal* gum arabic changes with environmental conditions, but it may also be affected by ploidy level. Research by Diallo et al. (2015) showed that for both diploid and polyploidy trees, plant growth and gum yield/quality differed among ploidy levels, and in populations and progenies.

In Kenya, interest is developing in improving local *S. senegal* resources to benefit the large silvopastoral dryland community (Omondi et al., 2010). Kenya is also developing a new market for gum arabic variety *kerensis*, which is widely distributed and also prized for its quality. Gum production forms the foundation of an active international market (Booth and Wickens, 1988; Chretin et al., 2008; Fagg and Allison, 2004).

4. Microsymbionts associated with *S. senegal*

Rhizobia that establish nitrogen-fixing nodules on *S. senegal* are very diverse. *S. senegal* was previously believed to be nodulated by *Rhizobium* strains exclusively (Dreyfus and Dommergues, 1981). Later, several authors (Supplementary Table 1) reported that the legume-nodulating bacteria that associate with *S. senegal* are members of genera belonging to the *Alphaproteobacteriaceae*, mainly *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium,* and *Ensifer* (Ba et al., 2002; de Lajudie et al., 1994, 1998; Dreyfus and Dommergues, 1981; Nick et al., 1999; Njiti and Galiana, 1996; Odee et al., 1995, 1997; Sarr et al., 2005a; Zhang et al., 1991).

Studies performed in Senegal have shown that even though *S. senegal* is nodulated by the genus *Rhizobium*, its main symbionts are strains phylogeneticaly related to *Mesorhizobium plurifarium* (Bakhoum et al., 2014; Fall et al., 2008; Sarr et al., 2005b,a). However, some of the strains that nodulate *S. senegal* and previously described as *M. plurifarium* belong to a new species (Diouf et al., 2015). In contrast, Nick et al. (1999) investigated rhizobia isolated from *S. senegal* in Sudan and showed that all were *Ensifer*. The data suggested that the rhizobia that associate with *S. senegal* are characterized by the soil from which they were collected, and studies performed in Senegal support these conclusions. Further support comes from investigations where the diversity of nodulating bacteria associated with *S. senegal* was found to be high when the soil physical and chemical parameters were favorable (Bakhoum et al., 2014). These authors also reported that nodulating bacteria for *S. senegal* appeared to be selected by seed provenance. However, although 16S–23S rDNA data indicated diversity, the symbiotic genes (*nod*A, *nod*C, and *nif*H) were identical in sequence to the comparable genes of *Mesorhizobium plurifarium* (Bakhoum et al., 2015), strongly suggesting horizontal gene transfer.

Compared to rhizobia, fewer studies have been performed on AMF associations with *S. senegal*, even though these fungi are critical components of soil microbiomes, both engineered and natural (Finlay, 2008). Plant community diversity as well as productivity are mediated by AMF species richness and diversity (Van Der Heijden et al., 1998). Ndoye et al. (2012b) used the large subunit region of the nuclear rDNA to study AMF diversity in the rhizosphere of *S. senegal* in plantations and natural populations. They showed that the AMF morphotypes present were most closest related to the genera *Rhizophagus* and *Funneliformis* (see: www.speciesfungorum.org for genus name changes from earlier published literature).

5. Inoculation of *S. senegal* with rhizobia

Previous studies demonstrated that inoculating *S. senegal* seedlings with efficient rhizobial strains stimulated their growth both in vitro and in the greenhouse (Badji et al., 1988; Bakhoum et al., 2012; Colonna et al., 1991; Ndoye et al., 2012a; Räsänen et al., 2001). In Senegal, Fall et al. (2012) found that *S. senegal* positively influenced rhizospheric microbial biomass and inorganic N content (Supplementary Table 2), two markers of soil fertility (Adrover et al., 2011). Using a mixture of four different *Ensifer* strains (CIRADF 300, CIRADF 301, CIRADF 302, and CIRADF 303), Fall et al. (2007) and Faye et al. (2006) reported that gum arabic production of 10- and 13-year-old *S. senegal* trees growing under natural conditions was enhanced. It will be interesting to expand this experiment to environmentally contrasting sites. However, after using the same combination of *Ensifer* strains to inoculate mature *S. senegal* trees, Herrmann et al. (2012) determined that rhizobial inoculation increased gum arabic production in Niger, but not in Burkina Faso, suggesting that other factors are likely involved (Supplementary Table 2). Later, Fall et al. (2016a) showed that gum arabic production positively correlated to soil microbial biomass, mineral nitrogen content, and rainfall. Thus, if conditions for tree growth are optimal, rhizobial inoculation becomes the deciding factor for improving not only plant growth and soil fertility, but also for enhancing gum production.

Research performed in Senegal, Niger, and Burkina Faso revealed an interaction among rhizobial strains, soil types, and *S. senegal* genotypes with respect to competitiveness, nodulation, and symbiotic nitrogen fixation under both greenhouse (Bakhoum et al., 2012) and natural conditions (Herrmann et al., 2012). It will be crucial in future studies to identify the best strains and plant provenances/species with regard to soil type. Although *Ensifer* inoculation increased gum arabic production, Herrmann et al. (2012) found no correlation between microbial biomass, inorganic N content, and gum arabic yield following the inoculation of mature trees. Fall et al. (2016a) demonstrated that rhizobial inoculation significantly increased soil microbial biomass, soil microbial activity, and acid phosphatase activities in the rhizosphere of mature trees, but they observed no major effect on either C mineralization or mineral N content. In addition, experiments that target microbial communities critical for the N, P, and K cycles need to be pursued in the future to help us understand the tangible effects of rhizobial inoculation on *S. senegal* mature trees in terms of gum production and microbial community interactions.

6. Inoculation of *S. senegal* with mycorrhiza

Colonna et al. (1991) and Ndiaye et al. (2011) associated the growth of *S. senegal* trees in nutrient-poor soil with their ability to establish AMF symbioses in soils deficient in P. Ndiaye et al. (2011) found that *S. senegal* seedlings that were cultivated in sterilized soils showed improved growth after inoculation with *Rhizophagus irregularis*, *R. fasciculatum*, and *Funneliformus mosseae*. In one example, 45% better growth was achieved when inoculated with *R. manihotis*. However, the response varied with soil origin and environmental conditions (Ndoye et al., 2013). The authors concluded that similar to rhizobia, mycorrhiza, especially native AM fungi, accelerated the recovery of degraded soil, which then enabled the planting of crops. Prior work also studied the effects of singly inoculated *S. senegal* with either rhizobia or AMF alone versus co-inoculating with both symbionts. Ndoye et al. (2015) found that single inoculation with either AMF or rhizobia improved *S. senegal* seedling growth in non-sterilized soil. However, more studies need to be performed to develop optimal combinations of microsymbionts, which consist of compatible strains that reliably enhance plant growth in nutrient-deficient soils.

Inoculation of *S. senegal* trees with selected symbiotic microorganisms was shown to increase gum arabic production per tree (Table 1). Except for the 2010–2011 field trial of Dahra plantation 2 (inoculated with rhizobial strains ORS 3574, ORS 3593, ORS 3607, and CiradF 300), the annual production of gum arabic was higher in treatments inoculated with both rhizobia and mycorrhizal fungi in all plantations and field trials, and for both sites (Table 1). Also, the percentage of trees producing gum arabic was proportional to gum production per tree and was generally higher in inoculated treatments.

7. Effect of *S. senegal* on soil fertility

Soil fertility has been in decline in many arid and semi-arid zones of Africa (Turenne et al., 1991). African drylands suffer from severe land degradation brought about by several factors: deforestation, overgrazing, unsustainable agriculture, and climate change. These soils can be transformed by planting nitrogen-fixing trees. In Africa, low and irregular rainfall (<100–600 mm per annum), poor soil water and nutrient availability, and also elevated temperatures limit crop productivity (Wickens et al., 1995). This combination of factors has severe negative effects on perennial multi-purpose tree species that normally maximize their agricultural potential when grown under less stressful conditions (Fagg and Allison, 2004). Besides promoting soil stability and fixing N_2, another advantage of these trees is that they transfer fixed N to other crops (Kang et al., 1985), and in addition, acacias play an especially important role in rehabilitating sandy or clay soils. By fixing N_2, *S. senegal* improves the soil, which permits crop growth in restored gum arabic agroforestry systems of sub-Saharan Africa (Raddad and Luukkanen, 2006). Moreover, *S. senegal* has also been used for enhancing soil fertility in sorghum fields in Sudan (Blue Nile region) and in rotational bush-fallow systems (El Houri, 1986). Thus, these trees have significant potential for restoring soil fertility in several African countries.

In African drylands, *S. senegal* is recognized as being critical for increasing and diversifying agricultural production systems and also for stabilizing and restoring damaged agroecosystems. Njiti and Galiana (1996) concluded that *S. senegal* has an important role in restoring these eroded fields because of the tree's ability to associate with N_2-fixing bacteria that improve the nutrient-depleted soil. *Senegalia senegal* trees are responsible for the accumulation of large amounts of N, especially in the first few years after their establishment. Much of that N, which is generated from turnover of underground plant tissues, is taken up by the roots of nearby non-N_2-fixing trees or crops (Khanna, 1998). At a density of 400 trees ha^{-1}, *S. senegal* biomass accumulates to a total of 18.0, 1.21, 7.8, and 972 kg ha^{-1} of N, P, K, and organic carbon, respectively (Raddad and Luukkanen 2006). Dean (1999) reported an increase in both N and K (24 and 4 kg ha^{-1} year^{-1}, respectively) under 3 to 18 year-old *S. senegal* trees. However, P was not shown to increase in the topsoil. Interestingly, Ndoye et al. (1995) reported that a significant unevenness exists among acacia species for their ability to fix N_2 and the total amount of N fixed. In their study, *Vachelia seyal* (previously *Acacia seyal*) was identified as having a higher N_2-fixing ability than *S. senegal, Acacia raddiana*, and *Faidherbia albida* acacia species.

The carbon (C) stocks of African drylands also have declined because of land degradation and loss of soil fertility/water retention. Planting acacia trees in these areas could increase soil organic carbon (SOC) stocks considerably. The SOC in drylands was estimated to be 16–25% of global terrestrial SOC storage (MEA, 2005; Lal, 2004) with a surface cover of 41–47% of the Earth's land (Wessels, 2006). Abaker et al. (2016) showed that *S. senegal* trees planted in drylands increased SOC stocks, especially in the upper soil. Plantation SOC stocks varied from 846 to 1250 g m^{-2}, and those values rose with age and reached 867–950 g m^{-2} in open grassland. The optimum of SOC stock piling occurs within one to two decades after planting acacia trees. These authors also reported that SOC stock accumulation originated not only from acacia trees, but also from ground level vegetation. Thus, planting N_2-fixing trees not only promotes ground vegetation growth in semi-arid

Table 1
Annual gum arabic production per tree and percentage of trees producing in 2009–2010 and 2010–2011 in Senegalese (Dahra and Goudiry) plantations.

Site	Plantation	Years	Results	Control	R	M	R + M
Dahra*	1	2009–2010	Gum arabic (g tree^{-1})	42.44^{a}	70.65^{ab}	99.40^{ab}	112.58^{b}
			% producing trees	14.06	20.48	25.64	33.8
Dahra**	2	2010–2011	Gum arabic (g tree^{-1})	48.72^{a}	46.97^{a}	65.22^{a}	52.16^{a}
			% producing trees	75.62	70.89	81.54	79.95
Goudiry*	1	2009–2010	Gum arabic (g tree^{-1})	ND	ND	ND	ND
			% producing trees	ND	ND	ND	ND
Goudiry***	2	2010–2011	Gum arabic (g tree^{-1})	34.07^{a}	57.99^{ab}	51.96^{ab}	72.03^{b}
			% producing trees	62.82	61.11	68.33	80.15

In each site, two different plantations were inoculated. For each year, values followed by the same letters are not significantly different according to *Student–Newman–Keuls* ($P < .0.05$) test; ND: not determined data. R: rhizobia, M: mycorrhiza.

* Rhizobial inoculum, Sarret al. (2005b) (genus *Ensifer*: CiradF 300, CiradF 301, CiradF 302 and CiradF 303), mycorrhizal inoculum (*Funneliformis intraradices* (Fi), *F. faciculatum* (Ff), *F. mosseae* (Fm) et *F. vericulosum* (Fv)).

** Rhizobial inoculum, Bakhoum et al. (2012) (genus *Mesorhizobium*: ORS 3574, ORS 3593, ORS 3607 and CiradF 300), mycorrhizal inoculum (*Funneliformis intraradices* (Fi), *F. faciculatum* (Ff), *F. mosseae* (Fm) et *F. vericulosum* (Fv)).

*** Rhizobial inoculum, Bakhoum *et al.* (2012) (genus *Mesorhizobium*: ORS 3588, ORS 3593, ORS 3604 and ORS 3607), mycorrhizal (*Funneliformis intraradices* (Fi), *F. faciculatum* (Ff), *F. mosseae* (Fm) et *F. vericulosum* (Fv)).

areas, but these trees also support much of the plant growth in these areas.

The *S. senegal* rhizosphere has a positive effect on soil microbial biomass as reported previously (Fall et al., 2012). Recently, these authors showed that rhizobial inoculation also enhanced total microbial and acid phosphatase activities significantly, but no meaningful effect was observed with regard to C mineralization and mineral N content (Fall et al., 2016a). The establishment of *S. senegal* in degraded lands could positively impact soil enzymatic processes and vegetation establishment. In so doing, *S. senegal* benefits crops in agroforestry systems in N-limited soils of the Sahelian zone.

8. Use of *S. senegal* to address soil affected by salinity

Accumulation of salts in soil, often from the overuse of fertilizers, is an emerging environmental problem worldwide. Salinity is a major limiting factor for plant growth especially in drylands (Zahran, 1999). Natural environments are also threatened by salt-affected soils. A large portion of the world's surface (8%) has become saline (estimated to be over 953 million ha) (Singh, 2009). Arable areas are threatened, and one solution for reclaiming saline soils is the planting of halophytic plants, which absorb or tolerate salt (De Lacerda et al., 2005; Singh, 2009). In the salt-affected soils of Senegal, legume species (species of acacia, *Prosopis*, and *Sesbania*) with moderate salt tolerance are able to grow. These species persist in nutrient-poor and degraded soils most likely because of their associations with N_2-fixing rhizobia and AMF, both of which occur naturally in the rhizosphere (Dommergues, 1995). Symbioses with microorganisms are known to be critical for plant adaptation to adverse environmental conditions, such as drought and salinity stress (Zahran, 1999). Inoculation with rhizobia that tolerate salinity helps acacia trees grow in saline soils (Diouf et al., 2005; Lal and Khanna, 1994).

AMF are also major contributors to plant growth promotion in stressful environments worldwide (Aliasgharzadeh et al., 2001; Becerra et al., 2014; Ho, 1987). Mycorrhization facilitates the adaptation to saline conditions by helping plants procure soil nutrients, particularly magnesium, during the growth cycle (Giri and Mukerji, 2004). Nevertheless, the ability of an AMF strain to enhance plant growth and development is not directly correlated to whether or not it originates from a saline area (Cantrell and Linderman, 2001; Manga et al., 2017). Thus, the fact that plant growth promotion occurs suggests that this trait is a characteristic of the individual isolate's ecotype, and is not directly related to salt. Moreover, different AMF have varied responses to NaCl levels. These authors suggested that the variability of responses that occur in response to abiotic stress should be more carefully considered in plant–fungus interactions research.

Earlier studies also did not consider *S. senegal* to be a salt-tolerant acacia, but recently Fall et al. (2016b) showed that *S. senegal* maintains a good germination rate and a high level of growth in 257 mM NaCl. In summary, *S. senegal* is similar to *Vachellia seyal* and *Prosopis juliflora* in being able to grow in salty soils. Thus, *S. senegal*, in addition to *P. juliflora*, which was previously described as a salt-tolerant acacia, should also be employed for restoring saline soils.

9. Conclusion

The relationship of *S. senegal* with soil microorganism is positively associated with this tree species' ability to survive in harsh conditions. Moreover, inoculation with rhizobial strains increases plant growth, microbial biomass and diversity, and soil health in the plant rhizosphere. Under natural conditions, inoculation of even mature trees of *S. senegal* with selected rhizobia significantly increased total microbial activities, acid phosphatase activity, and also gum arabic production, but it had no effect on soil microbial CO_2 respiration and N content. This deficiency might be overcome by selecting effective combinations of microorganisms × provenances relative to the soil and the overall environment and climate where the trees are to be planted.

Because of their tolerance to adverse soil and climate conditions, *S. senegal* trees are an excellent biological means for rehabilitating degraded soils. In drylands overall, *S. senegal* trees increase SOC stocks, especially in the upper soil, and thus may help restore soil fertility specifically in arid environments. Moreover, like *P. juliflora*, *S. senegal* should be considered as a salt-tolerant species.

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