Chapter

Mycorrhizal Symbiosis for Sustainable Optimization of Tropical Agriculture: A Review of Research

*Ricardos M. Aguégué, Corentin Akpode, Tomabu Adjobimey,
Haziz Sina, Sylvestre A. Assogba, Abdel D. Koda,
Nadège A. Agbodjato, Nestor R. Ahoyo Adjovi,
Adolphe Adjanohoun, Olubukola O. Babalola
and Lamine Baba-Moussa*

Abstract

Excessive application of chemical fertilizers and other agrochemicals can cause significant imbalances in soils and agricultural ecosystems. To minimize these impacts, biofertilizers and organic fertilizers are needed to maintain a sustainable production system. The use of subterranean microorganisms in agriculture to stimulate plant growth and improve yields has recently received increasing interest. In this context, mycorrhizae represent a viable solution to mitigate these adverse effects. Mycorrhizal fungi are able to form a symbiotic relationship with the roots of plants in the environment. Mycorrhizal fungus helps the plant to absorb nutrients and water. In addition, mycorrhizal fungi play a crucial role in storing carbon (C) in the soil. Most previous studies have just considered the effects of AMF species on a specific crop in one particular area but have not assessed the balance of AMF in production systems in tropical agriculture. This consideration should allow for the optimization of cropping practices through a review of the work on the use of AMF in tropical agriculture production systems. In this paper, we will discuss, through different examples of experiments carried out in the tropics, the performance of different strategies for managing the potential of AMF to maintain a sustainable production system.

Keywords: bioinoculation, SDG#2, sustainable agriculture, symbiosis, tropical environment

1. Introduction

In Sub-Saharan Africa, the population increase is estimated at 2 billion in 2050. This is more than double what it was in 2010 (800 million inhabitants) [1, 2]. Food needs will evolve considerably, even four times those of 2010 [1, 3]. Indeed, the technical performance of African agriculture, particularly crop yields, which are generally low, would not be sufficient to cover such changes in needs [1] without an effective alternative in new agricultural technologies. It is, therefore, necessary to expand the cultivated land in Africa on a large scale by more than 122 million ha, that is, a growth of more than 47% compared to the initial situation in 2010.

In this context, it is essential to have a better yield of corn grains for the self-sufficiency of the population. Thus, in most cases, producers use chemical agricultural inputs (pesticides and mineral fertilizers), which, in the long run, degrade the soil and pollute waterways and the environment. Indeed, the contribution of organic fertilizer is necessary for these soils on which chemical fertilizers are used to avoid their rapid degradation by water and wind currents [4]. Establishing a reliable and sustainable agricultural technology without adverse effects on soil health and the environment to meet food needs remains the major concern of researchers in the agricultural field. Indeed, the organic farming system remains the best option because it obliges farmers to use organic amendment resources of the remains from livestock, green organic matter, and other organic manures [5, 6]. Nevertheless, these inputs are costly, and their forms remain relatively insoluble. Also, their effects on phosphorus availability in soils in organic agriculture are often limited [5, 7].

Techniques for regenerating the health of cultivated soils that incorporate a judicious combination of organic matter of different C/N ratios, on the one hand, and the use of the soil microflora and soil fauna, on the other, are needed to reduce the rate of mineralization of organic matter supplied to soils, thereby maintaining microbial life in these soils for long periods.

Beneficial microorganisms include arbuscular mycorrhizal fungi (AMF) that are associated with at least 90% of terrestrial plants [8, 9]. A majority of terrestrial plants, especially grapevine [10], are colonized by about 400 arbuscular mycohizal fungi that allow them better nutrient uptake and stress tolerance [11]. The interactions between plant, soil, and mycorrhizal fungi are ecologically and agriculturally beneficial systems. In nature, most plants are in association with mycorrhizae. Thanks to this association, the plant increases its water and nutrient-absorption surface. Also, they have better accessibility to the elements available in the soil but not accessible. In addition, mycorrhizae contribute to the mobilization of carbon (C) in the soil.

In this review, we will synthesize research on the performance of different AMF potential management strategies to maintain a sustainable production system.

2. Functional diversity of arbuscular mycorrhizal fungi in the rhizosphere

The first classification was established by Taxter [12] and later modified by many mycorrhizologists [13, 14]. The classical identification of arbuscular mycorrhizal fungi is based on the structural morphology of the spore. Those that have similar morphology and form a single type of spore wall are phylogenetically related. However, populations of spores isolated and identified from rhizophytic soils do not always constitute communities of arbuscular mycorrhizal fungal species that infect roots [15]. Nevertheless, the low morphological variation among spores often makes their identification difficult.

Schwarzott et al. [16] describe the molecular classification based on in vitro DNA amplification of variable regions of the fungal genome from spores or from mycorrhized roots [17]. Indeed, multigene analysis has been used to identify arbuscular mycorrhizal fungi [18] to confirm the phylogenetic structure proposed by Schüßler

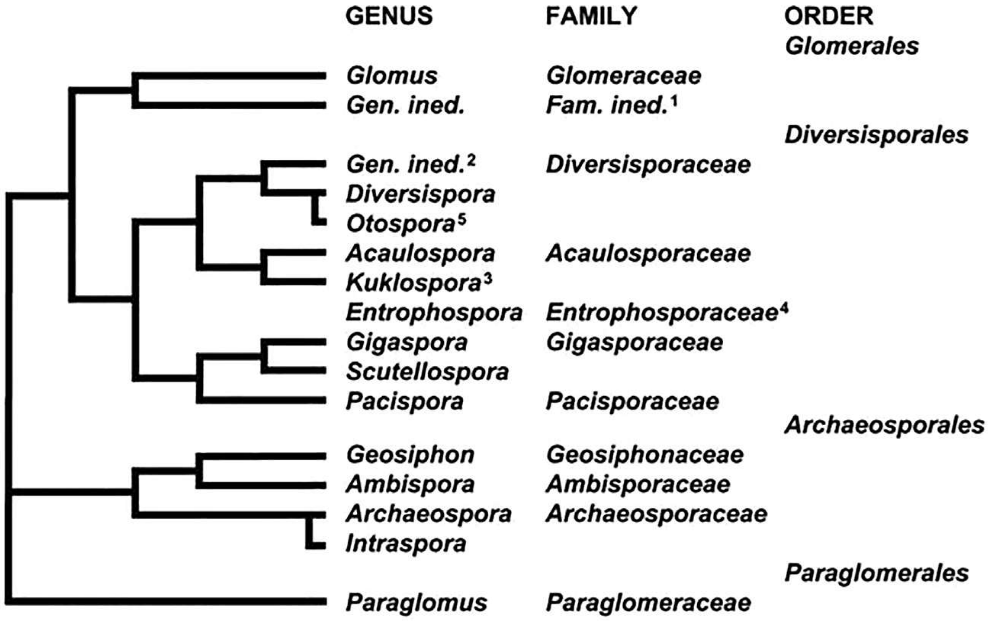

Figure 1.
Phylogenetic relationships of Glomeromycetes taxa [13, 24].

et al. [13]. Furthermore, biochemical approaches based on the use of specific antibodies [19] and lipid profiles [20] are also used for the identification of arbuscular mycorrhizal fungi.

Morton and Benny [21], who classified arbuscular mycorrhizal fungi in the order Glomales, subdivided them into two suborders, Glominae (vesicles forming) and Gigasporinae. The Glominae include two large families, the Glomaceae represented by the genera Glomus and Sclerocystys, a genus eliminated by Redecker et al. [22], and the Acaulosporaceae by Acaulospora and Entrophospora. The Gigasporinae include three families, the Gigasporaceae represented by Gigaspora and Scutellospora, the Archaeosporaceae represented by the genus Archaeospora, and the Paraglomaceae by Paraglomus [23].

Figure 1 shows the phylogenetic classification of the kingdom Mycota (Fungi) based on the analysis of 18S rRNA nucleotide sequences [13]. [1]Species currently named *Glomus* [2]contains *Glomus fulvum, Gl. megalocarpum, Gl. pulvinatum*; [3]contains *Kuklospora colombiana* and *Ku. kentinensis* (formerly *Entrophospora*) [25]; [4]contains one genus with *Entrophospora infrequent* and *A. baltica* [25], neither of which are phylogenetically characterized; [5]*Otospora* [26] contains *Otospora bareai* [27].

3. Role of arbuscular mycorrhizal fungi in promoting crop growth

The success of a production technique could depend on controlling the factors that influence the development of arbuscular mycorrhizal fungi (AMF). AMF are another group of symbiotic soil microbes capable of directly or indirectly influencing soil properties, affecting plant growth and community structure [28, 29]. Their multiple beneficial attributes allow them to be involved in many processes, such as biofertilization, biostimulation, and bioprotection [30]. Indeed, AMF confer many positive effects on host plants, including promoting plant growth, stabilizing soil aggregation, maintaining soil moisture, improving tolerance to abiotic and biotic

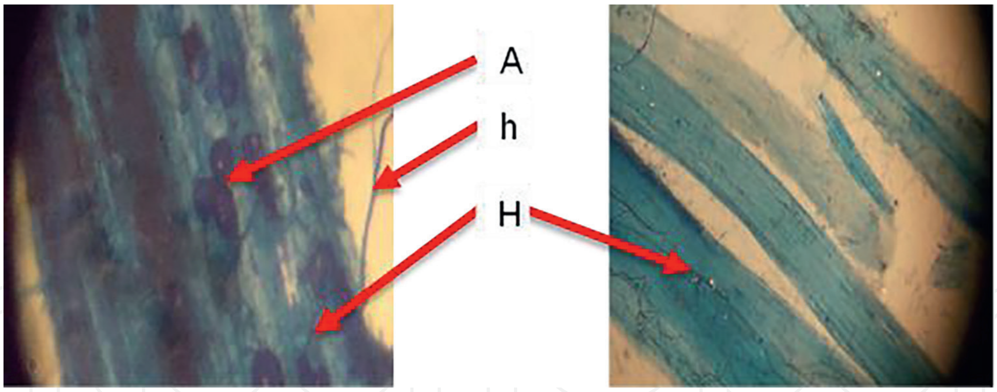

Figure 2.
Infected corn roots colonized by shrub-shaped mycorrhizal fungi structures. (A: vesicular; h: intra-root hyphae; H: extra-root hyphae (×180) [38].

stress, and increasing plant biodiversity [30–33]. In addition, these beneficial fungi have shown a potential ability to increase crop resilience and performance [34] and are known to affect their host plants differently. AMF are present in the soil in the form of spores and extra radicular hyphae, as well as in plant roots, with which they form a mutualistic association, and are considered an essential component of various ecosystems [35, 36]. The most important contribution of AMF fungi to plant growth is due to the uptake of phosphorus and other elements by the extra-radical hyphae and their transfer to root tissues. Indeed, intra-root hyphae, vesicles, and intra- and extra-root spores are structures capable of AMF propagation [37]. In addition to being a propagule, vesicles (**Figure 2**) are a reserve organ; their production is related to the stage of AMF development, and their presence can vary with carbon allocation by the host plant [39, 40]. However, factors such as low light intensity and defoliation, factors that limit photosynthesis and thus the carbon content of the plant, significantly reduce sporulation as well as colonization of new roots [37]. AMF provides nutrients, primarily phosphorus (P) and nitrogen (N), to host plants in exchange for carbon (C). The increase in available phosphorus and exchangeable potassium and magnesium levels in the soil of AMF-treated plants would certainly mean more leaves, branches, and biomass in AMF-treated plants than in control [41]. Mycorrhization of tissue-grown propagules can produce plants with increased levels of biologically active secondary metabolites [42]. The exploration of a larger volume of soil and the possibility of alteration of primary minerals by mycorrhizal fungi improve the phosphate nutrition of plants [43, 44]. This improved acquisition of inorganic nutrients by fungal symbionts also concerns other macro- (N, K, Mg, Na, S) and micro- (B, Br, Cl, Cu, Cr, Cs, Co, Fe, Mo, Mn, Ni, Si, Zn) soil nutrients [37, 44]. Mycorrhizal associations play a potential role in the decomposition and mineralization of plant organic matter and the mobilization of nutrients to the host plant [44, 45].

4. Arbuscular mycorrhizal fungi as biofertilizers to increase crop yield

The work of Xie et al. [46] and Battini et al. [47] on tomato showed that AMFs were responsible for P mobilization in inoculated tomato plants. In addition, Balliu et al. [48] on tomato plants inoculated with AMF observed a significant increase in N uptake. Campo et al. [49] showed the importance of mycorrhizal fungi on growth, productivity, and disease resistance in the rice crop. In addition, in the pasture, the dry season appears to favor AMF species diversity. It is possible that the lower humidity of this season influences the sporulation of more species [50, 51]. Studies conducted by Nekou et al. [52] and Ngakou et al. [53] in Cameroon in 5 agro-ecological zones showed that the use of commercial mycorrhizal fungi on cowpea plants improved their growth by 17–46%. In Togo, inoculation of soybean plants with mycorrhizae resulted in an improvement in plant height from 14 to 32 cm [54]. Also, the work of Ngakou et al. [55] on garlic plants inoculated with mycorrhizae under greenhouse conditions observed an improvement in plant growth from 4.85 cm to 6.28 cm. Ogou et al. [54] obtained in Togo an average mycorrhizae-induced pod gain on soybean of +126.83% compared to the control. Moussa et al. [56] reported an average mycorrhizal inoculation-induced improvement of 23.4% on *Vigna subterranea* plants. Hemissi et al. [57], in Tunisia, obtained a gain of 20 kg/ha more wheat in mycorrhized plants than in control plants. The role of AMF on *Drymaria cordata* is indicative of the apparent potential of this association to improving production [41]. Similar efficacy of G. fasciculatum on the growth and performance of normal and regenerated *Andrographis paniculata* plants has been studied [58]. Numerous works have shown the effectiveness of endomycorrhizal symbiosis in improving maize productivity [59–63].

These improvements in plant growth and yield by arbuscular fungi are explained by the fact that mycorrhizae degrade and mineralize soil organic matter and mobilize the resulting nutrients to the plant [64, 65]. In addition, mycorrhizae develop extra-radical mycelial hyphae that explore a larger volume of soil not accessible to plant roots [66]. *Solanum lycopersicum*, inoculated with *G. fasciculatu*m significantly improved morphological characteristics [67].

Another important point regarding plant health is the presence of toxic metals such as Cu, Cd, Zn, and Pb in the soil. It has been suggested that the most appropriate use for these elements is potentially toxic elements (PTEs) [68, 69]. AMF are capable of absorbing Cu, and 1 g of AMF hyphae has a Cu content of 3–14 mg [70].

5. Role of glomalin secreted by mycorrhizal fungi

The growth of mycorrhizal hyphae in the soil is accompanied by the production of glomalin (a glycoprotein), which improves the aggregation of soil particles [44, 71]. Glomalin is a hydrophobic protein. Glomalin, an N-linked glycoprotein [72], which is considered to be an AMF gene product, is defined as a protein secreted by AMF hyphae and spores [73]. It contains iron (2–5%), oxygen (4–6%), phosphorus (0:03–0.1%), carbon (36–59%), hydrogen (33–49%), and nitrogen (3–5%) [73–75]. The reddish-brown appearance of glomalin extracts is due to the iron content [71, 75]. According to Wright [76], the concentration of glomalin in soils is very high compared to humic acid, especially in the presence of insoluble humus or minerals in soils treated with sodium hydroxide. The glomalin secreted by the mycorrhizae in the soil allows the stabilization and optimization of the PTE. Moreover, in addition to its beneficial roles for the soil, in the rhizosphere of plants, it plays a protective role for the microorganism and the plant roots against toxins [73]. There is a strong relationship between glomalin concentration and soil aggregate stability [75, 77]. Because of this role, glomalin preserves unstable compounds in soil aggregates and thus reduces the degradation of soil organic matter [78]. N-linked glomalin [72], which is considered the gene product of AMF, is defined as a glycoprotein secreted by AMF hyphae and spores [73]. Glomalin, plays an excellent protective role for hyphae as well as promotes soil aggregation.

Glomalin is measured from the soil as Glomalin-Related Soil Protein (GRSP) [78–80]. Among soil microorganisms, AMF have the ability to stabilize soil structure, which reduces stress at the plant level [81, 82]. Indeed, glomalin produced by arbuscular mycorrhizal fungi is one of the key factors of soil quality. It is essential for the formation of soil aggregates because it is one of the components of soil organic matter [75, 83]. Also, it contributes to the nutrient storage capacity and water holding capacity [83]. Land use change can alter the abundance and diversity of arbuscular mycorrhizal fungi species and the content of glomalin-related soil protein (GRSP) in the soil [84–86]. Glomalin from the decomposition of hyphae wall and spores of mycorrhizal fungi even after their death is quantified in soil as GRSP [87, 88]. GRSP is considered an essential component of the soil organic carbon (SOC) pool in terrestrial ecosystems [80, 89]. Indeed, GRSP is a key link in appreciating soil fertility, its water holding capacity, and aeration and nutrient content for better plant productivity [90].

GRSP is composed of two soil proteins: the easily extractable protein (EE-GRSP) and the total protein (T-GRSP). Assuming the C content of glomalin to be 32% [91], concerning equivalent dry mass of soil. The contribution of TG to SOC varies from season to season in agroforestry and forest [92]. Indeed, it is higher during the dry season compared to the rainy season, when it is 5.69% in soils under pasture, followed by AS3 (4.5%) and AS2 (4.31%). The work of Driver et al. [93] on *Rhizophagus intraradices* (N.C. Schenck & G.S. Sm). C. Walker & A. Schüßler showed that 80% of the glomalin secretion came from the wall of hyphae and spores.

The glomalin secreted by the mycorrhizae in the soil allows the stabilization and optimization of the PTE. In addition, glomalin plays a protective role for microorganisms and plant roots against toxins [73].

6. Mechanisms employed by arbuscular mycorrhizal fungi for salt stress amelioration

Soil salinity is a global problem because it negatively affects plant productivity and yield, especially in arid and semi-arid regions of the world. Under salt stress, plant growth and biomass have suffered a setback. The reasons may be the unavailability of nutrients and the expenditure of energy to counteract the toxic effects of NaCl. This is because excess salt decreases the availability of soil water to plants, inhibits plant metabolism and nutrient uptake, and is also responsible for osmotic imbalance [94]. Among the various biotechnological techniques used to combat the harmful effects of salt stress, the use of arbuscular mycorrhizal fungi (AMF) is considered an effective approach for bioenhancement of salt stress [95]. Possible mechanisms for salinity stress mitigation by AMF include: (1) enhancing plant nutrient uptake, particularly P; (2) elevating the K/Na ratio; (3) providing higher osmosolute accumulation; and (4) maintaining higher antioxidant enzyme activities [94]. AMF adjust all physiological and biochemical properties of the host plant (**Figure 3**) [96–98]. The mycorrhizal symbiosis with the roots of plants includes several stages, namely, (i) the formation of the appessoriun (ap), (ii) the penetration and development of hyphae into the root cortex (a), and (iii) the formation of vesicles in the root cortex (v). The salinity has a very negative impact on the productivity of the plant. Indeed, it inhibits the fundamental needs of the plant in water and nutrients, which leads to its physiological dryness and the decrease of the osmotic potential. Nevertheless, with the symbiosis of arbuscular mycorrhizal fungi, the plant resists saline stresses by a better absorption of water and nutrients. The action of mycorrhizae can be summarized as: (i) increased accumulation

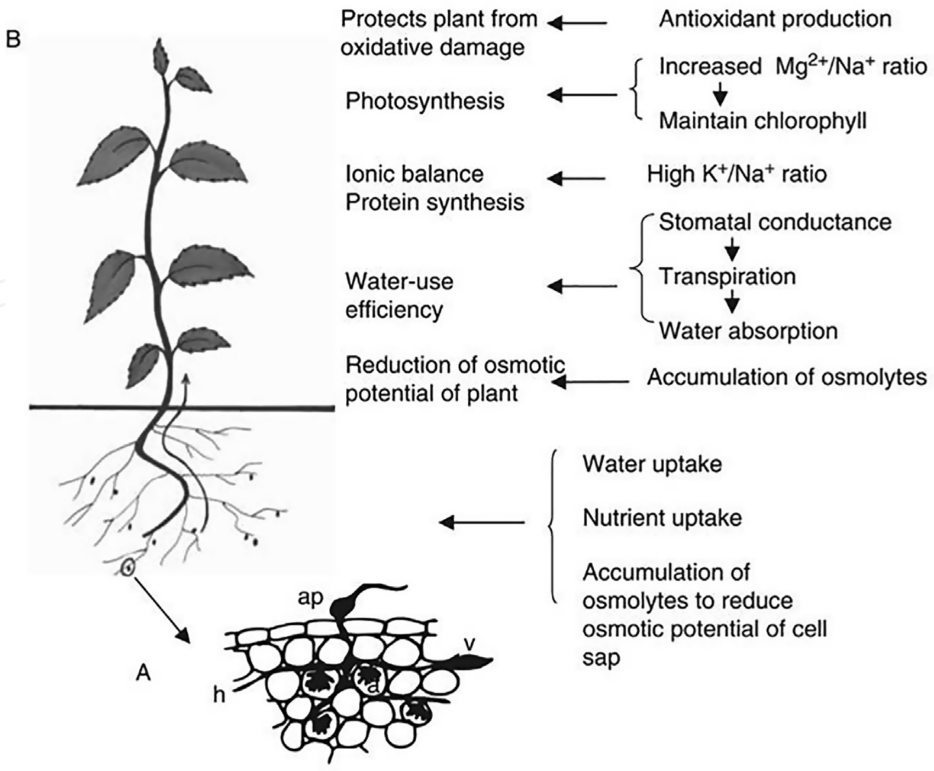

Figure 3.
The intricate functioning of arbuscular mycorrhizal fungi in ameliorating salt stress in plants [96].

of osmolytes, which allows a decrease in osmotic potential; (ii) efficient management of water and photosynthesis; and (iii) production of antioxidants to scavenge ROS [96].

AMF can protect cucumber growth from salt stress [99]. However, AMF inoculation ameliorated the negative effects by increasing biomass; pigment synthesis; antioxidant enzyme activity, including superoxide dismutase, catalase, ascorbate peroxidase, and glutathione reductase; and ascorbic acid content, which might be the result of lower levels of lipid peroxidation and electrolyte leakage. Mycorrhization has been found to increase the capacity of the host plant by improving its growth and biomass [96]. Colla et al. [100] reported improved growth, yield, water status, nutrient content, and fruit quality of *Cucurbita pepo* plants colonized by Glomus intraradices when exposed to salinity stress. Under NaCl stress, the combination of mycorrhizal fungi with compost significantly improved plant growth; P, K+, N, and Ca^{2+} uptake; leaf water potential; stomatal conductance; all antioxidant enzyme activities; and proline and soluble sugar content [101]. The application of anti-salinity increased the yield of green bean pods under all levels of salinity stress, especially with AMF followed by B. Megatherium, compared to non-inoculated plants [102].

The positive action of AMF under salt stress may be due to higher concentration of osmolytes (glycine-betaine, sugars) and polyamines and more and larger plastoglobules (higher concentration of α-tocopherol) in AMF-inoculated plants compared to in non-AMF-inoculated plants. While lower Na + and Cl—ions provide less ion toxicity, higher osmolytes and tocopherols provide osmotic adjustment and better ability to scavenge free radicals generated by salt stress, respectively [103]. Landwehr et al. [43] reported abundant AMF spores in extremely alkaline soils with a pH as high as 11, independent of soil types and NaCl, Na_2CO_3, Na_2SO_4, or $CaSO_4$ salt types, although the degree of colonization varied among individuals. Saint-Etienne et al. [104] reported significant negative correlations between salt levels and soil mycorrhizal infection (measured as most probable number values); that is, as soil salinity increased from 5 to 22%, the level of infection decreased from 301 to 20 most probable numbers per 100 g of soil. Under salt stress conditions, a beneficial effect of AMF symbiosis has been observed on water status, osmolyte accumulation, and plant growth of *Phragmites australis* [105].

However, it should be noted that in the presence of NaCl, colonization of plant roots by some AMF is reduced [106], probably due to the suppression of arbuscular mycorrhizae formation due to the effect of NaCl on its fungi [95, 106, 107]. In addition, in the presence of NaCl, spore germination is delayed [107].

7. Interactions between mycorrhizae and beneficial rhizobacteria

Plant growth and development can be promoted or inhibited by microorganisms in the rhizosphere [108]. The synergistic action between plant growth promoting rhizobacteria (PGPR) and mycorrhizae (AMF) is of great importance for the improvement of productivity and sustainability of agricultural and natural ecosystems [109–111]. The beneficial effect of the interaction between RMPs and MFAs is demonstrated by several authors [108, 112, 113]. Indeed, the phytohormones produced by PGPRs allow a good development of the plant roots, which favors the colonization of the latter by AMF [112, 114]. According to Hodge [113], the accumulation of photosynthetic products is affected by the activities of AMF on PGPR in the mycorrhizosphere. As a result of increasing mycorrhizal colonization by PGPR, glomalin production increases [115].

The latest studies have shown various abiotic factors that have had marked effects on plant growth and development. Among these, N soil, pH, temperature, erosion, waterlog, salinity, heavy metals, fungicides, and drought are the major factors that affect plant growth [116, 117]. Hence, plant growth and yield will be affected [118]. However, diverse research [119, 120] have explored the significance of beneficial rhizobacteria and mycorrhizae in the growth and development of several plants in stress environments (**Figure 4**).

This positive interaction mainly occurs among PGP rhizobacteria, mycorrhizae, and plants [122]. The addition of a single bacterial inoculum might have core effects on the rhizosphere structure. Still, it will depend on whether the fresh inoculum is already a part of that bacterial population or not [123]. Similarly, it can be more effective when a combination of PGPR is used [124]. The inoculum composed of the mixture of PGPR and AMF, due to the synergistic effect of its two microorganisms, allows for better colonization and nutrient uptake by plant roots [122]. In the same way, the rise in root exudates by the microbes triggers the fungus growth and hence increases the rate of root colonization BN [108]. After the inoculation of 20 different *Medicago truncatula* assents with Funneliformis mosseae strains, several interesting results on physiology and gene expression at the level of individual plants were observed [125]. Studying the *P. fluorescens* C7R12, it was shown as an operative biocontrol mediator in comparison to the Fusarium species [126]. Antifungal metabolites produced by Pseudomonas, instead of inhibiting the action of the G. mosseae strain, allowed the colonization of the roots by the hyphae of the latter [127]. In addition, the synthesis of Rhizobia exopolysaccharides (EPSs) improved the synergy between bacterial strains and mycorrhizal structure [128]. Thus, the combination of the rhizobacteria can raise the activity of arbuscular mycorrhizae in the symbiotic association [129]. The occurrence of PGP rhizobacteria, as well as mycorrhizae in the rhizosphere, can encourage the growth of fungus hyphae by enhancing cell permeability and help the roots in penetration to fungus [130], and fungus hyphae can raise the activities of bacterial strains, which solubilize the phosphorus [62, 131–134].

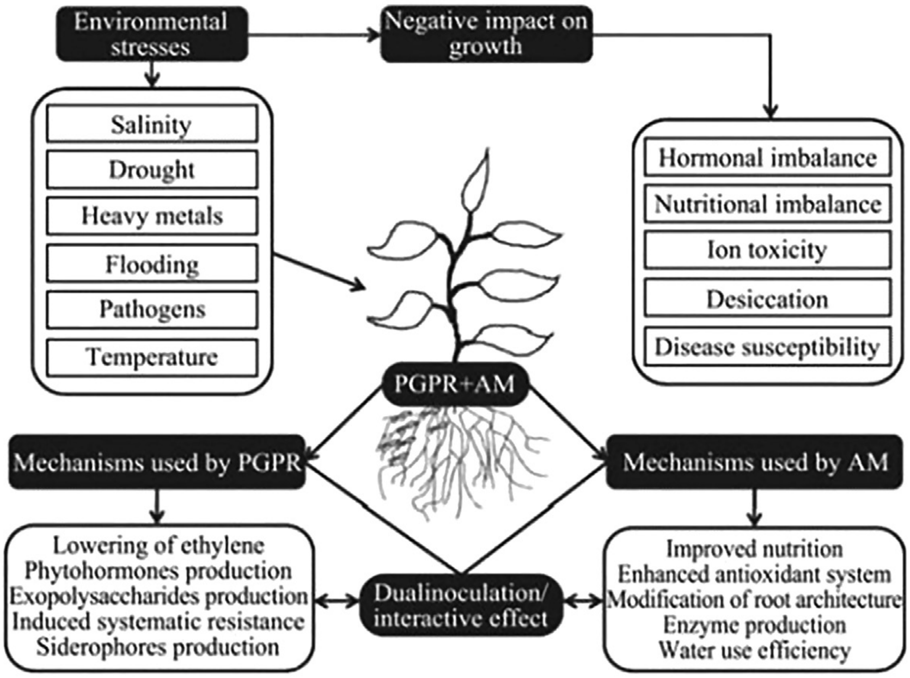

Figure 4.
Potential mechanisms used by PGP Rhizobacteria and mycorrhizae for improving plant growth under stress circumstances [121].

In addition, AMF increase plant uptake of water and mineral elements, especially phosphorus, to the plant [135]. This is because the elongation of the extra-radical mycelium increases the exchange surface between soil minerals and plant roots. Thus, areas inaccessible to the plant are explored by the extra-root mycelia to collect water and nutrients and transfer them to the host plant, allowing for improved growth, yield, and quality of plant production [134]. Moreover, Raklami et al. noted that the field inoculation with PGPR-Rhizobia-mycorrhizae improved growth, nutrition, and productivity of bean and wheat plants compared to the uninoculated control and other treatments based on PGP rhizobacteria as well as mycorrhizae. All the treatments were beneficent for *Vicia faba* L. and *Triticum durum* L. plants. The best treatment was the inoculation with PGPR- Rhizobia-mycorrhizae. Plant growth under normal or stressful situations could be improved by the use of PGP rhizobacteria and mycorrhizal strains, alone or in combination [118].

Authors' contributions

RMA, CA, TA: Conceptualization, methodology, writing—original draft; RMA, CA, TA; HS, SAA, ADK and NAA: Writing—Revision; NRAA, AA, OOB, and LB-M: Acquisition of financing; OOB and LB-M: Writing and editing. All authors have read and approved the published version of the manuscript. All authors participated equally in the work and approved the final submission.

Declaration of competing interest

The authors declare that they have no financial interests or personal relationships that might have appeared to influence the work reported in this article.

Author details

Ricardos M. Aguégué[1], Corentin Akpode[1], Tomabu Adjobimey[2], Haziz Sina[1], Sylvestre A. Assogba[1], Abdel D. Koda[1], Nadège A. Agbodjato[1,3], Nestor R. Ahoyo Adjovi[4], Adolphe Adjanohoun[4], Olubukola O. Babalola[3]* and Lamine Baba-Moussa[1]*

1 Laboratoire de Biologie et de Typage Moléculaire en Microbiologie, Département de Biochimie et de Biologie Cellulaire, Faculté des Sciences et Techniques, Université d'Abomey-Calavi, Cotonou, Bénin

2 Unité de Biochimie et de Biologie Moléculaire, Faculté des Sciences et Techniques, Université d'Abomey-Calavi, Bénin

3 Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Mmabatho, South Africa

4 Institut National des Recherches Agricoles du Bénin, Cotonou, Bénin

*Address all correspondence to: olubukola.babalola@nwu.ac.za and laminesaid@yahoo.fr

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