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Review Article

Arbuscular Mycorrhizal (AM) Fungi Symbiosis in Sustainable Production of Sorghum (*Sorghum bicolor* L. Moench) Under Drought Stress: An Emerging Biofertilizer in Dryland Areas

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Sorghum (*Sorghum bicolor* L. Moench) is an important cereal crop grown in arid and semiarid regions where water and other resources are limited. Changes in temperature and rainfall patterns have resulted in frequent droughts, which caused significant yield loss in sorghum. In recent years, there has been an increasing interest in sorghum cultivation due to its resilience to climate change and potential source of food and income. The symbiotic interaction of sorghum with Arbuscular Mycorrhizal fungi (AMF) has been found to induce several physiological and molecular changes that improve the ability of sorghum to withstand drought stress. This symbiotic relationship enhances water and nutrient uptake, osmotic adjustment, activation of stress-responsive genes, stomatal regulation, and antioxidant defense, leading to improved drought tolerance in sorghum. Agricultural practices such as reduced tillage, cover cropping, intercropping, crop rotation, and the use of organic amendments promote the diversity and effectiveness of AM fungal symbiosis. Such agricultural practices create more favorable conditions for AM fungal establishment and growth while reducing dependence on synthetic fertilizers. In this review, we highlight AM fungal symbiosis on sorghum growth, physiology, and molecular mechanisms underlying the beneficial effects of AM fungal symbiosis under moisture deficit conditions. Overall, the present review elucidates sorghum production and breeding success in Ethiopia, the symbiotic mechanisms between plants and AM fungi, the prospects of biofertilizers in sustainable agriculture, the potential of AM fungal symbiosis as a sustainable approach to improve sorghum production and its synergistic effect with other crop management practices.

Keywords: Arbuscular Mycorrhizae; biofertilizer; drought tolerance; sorghum; sustainability; synergistic

1. Introduction

Climate change has a significant impact on agriculture worldwide. Increasing temperatures and decreased precipitation in combination with other improper anthropogenic activities lead to more frequent and severe droughts. This makes the agricultural sector more complex and uncertain worldwide in general [1] and in particular in East Africa [2]. Sorghum (*Sorghum bicolor* L. Moench, $2n=2x=20$) is a versatile plant that produces a four-carbon (C4) compound during the first step of photosynthesis in a bundle sheath. This characteristic enables the plant as a major food security

cereal crop cultivated in dry arid and semiarid parts of the world. It accounts for 43% of all major food staples available for consumption in sub-Saharan Africa [3]. It is an ideal crop for dryland areas due to its flexibility and tolerance to unfavorable conditions. Its ability to grow in adverse environmental conditions and its versatility make it a valuable resource for communities facing food insecurity. Sorghum production is the major livelihood strategy in arid and semi-arid agroecological zones, where subsistence small-scale and rainfed-based agricultural systems are dominant. Despite its multipurpose nature and yield potential, many sorghum-growing areas in Ethiopia are adversely affected by recurrent

drought due to the scarcity and/or uneven distribution of rainfall such as delay in onset of rains, dry spells after sowing, and drought stress during critical crop stages. Either late occurrence or early ending rainfall patterns cause the growing season to be very short, resulting in crop failure. A crop will completely fail if the dry spell is severe. Thus, in such circumstances, depending on the availability of improved seeds of early-maturing varieties, farmers replant plants with early-maturing genotypes [4]. Substituting sorghum with other crops such as teff (*Eragrostis tef*) has become a common trend in recent years when sorghum crops have failed.

Sustainable solutions are needed to improve the production and productivity of sorghum and address the challenges of food security and environmental sustainability in these regions. The potential for symbiotic interactions between plants and soil microbes has been widely recognized as a promising approach for enhancing plant growth and resilience, especially in drought-prone areas. The production and application of microbes as biofertilizers have gained popularity and contributed to sustainable agriculture and food security in different parts of the world, including southern, western, and central Africa [5, 6]. Arbuscular Mycorrhizal (AM) fungal interactions are among the most common symbiotic beneficial interactions between plants and microbes. It is the oldest (460 million years ago) and most ecologically important interaction, with more than 80% of land plants, including the agriculturally most important cereal and pulse crops [7]. These symbiotic relationships benefit both the plant and the microbe, as the plant provides nutrients to the microbe, while the microbe helps the plant obtain moisture and nutrients that enable the plant to withstand environmental stresses. Thus, Arbuscular Mycorrhizal fungi (AMF) play a key role in the maintenance of plant fitness and the development of agronomically feasible options under stress environments [8].

The role of AM fungi in improving the yield of sorghum in frequently drought-prone areas has been a major research area for the last few decades. Several research highlight the potential of AM fungi as a beneficial tool for improving sorghum plants' drought resilience and productivity. Therefore, this review summarizes the research achievements on AMF inoculation of sorghum under water deficit conditions. Recently published research articles are searched using words/phrases such as sorghum and food security, symbiotic interactions between AMF and plants, water deficit on sorghum, and the response of sorghum to AMF inoculation. Literature in English from scientific databases such as Google Scholar, Scopus, Web of Science, PubMed, Science Direct, Springer, and Wiley was obtained to prepare this review. The knowledge generated could be insightful for development agents, policymakers, and researchers to adopt and scale up affordable and sustainable management techniques for enhanced sorghum production in drought-prone regions of Ethiopia.

2. Sorghum in Ethiopia: Production, Utilization, and Breeding Effort

Sorghum is an important crop in Ethiopia and is grown for both subsistence and cash purposes. The crop is mainly grown in the

lowlands of Ethiopia, with major production areas including Tigray, Amhara, Oromia, and the Southern Nations, Nationalities, and Peoples' Region (SNNPR; Figure 1) [4]. Although there are several production systems for sorghum in Ethiopia, sorghum is grown in traditional systems using indigenous farming practices and low-input technologies. The production of sorghum is fourth after that of maize, teff, and wheat, covering an area of 1.35 million hectares of land under private peasant holdings during the middle season [9]. In terms of economic significance, sorghum is an essential crop for smallholder farmers in Ethiopia because it provides food security and generates income [10]. The crop also has various uses, including as a grain for human consumption, animal feed, and a raw material for local beer production. Sorghum beer, known as "tella," is a popular beverage in Ethiopia.

The difference between Ethiopia's national average sorghum productivity (2.6 tons ha⁻¹) [9] and the global average (3.2 tons ha⁻¹) highlights the potential for improvement in sorghum production. The low productivity of this crop is caused by several constraints, including drought, pests, diseases, poor soil fertility, low yields of local cultivars, and low access to inputs and credit services [11]. Among these factors, drought at the grain-filling stage strongly affects sorghum production by reducing yields and leading to crop failure. Pests and diseases, such as striga, shoot fly, and grain mold, also cause significant challenges in sorghum production. The use of local drought-tolerant but low-yielding landraces also limited the productivity of sorghum. Farmers depend on these landraces because frequent droughts make it challenging to grow high-yielding and late-maturing cultivars. However, these landraces usually produce lower yields than improved cultivars, which can affect the crop's overall productivity [11].

Climate change has significant impacts on sorghum production, as more than 95% of cultivated land in arid and semiarid regions of Ethiopia is rainfed. Increasing temperature, change in rainfall pattern, and less predictable rainfall contribute to lower yields and greater vulnerability to crop failure due to pests and disease. Traditionally, farmers practice sowing late-maturing landraces in April after 3–4 rain showers and expect to harvest their crops in November [4]. However, this approach is challenging, particularly when dry spells occur in May and June, when plants can be exposed to water limitations. To address this challenge, farmers need to consider alternative planting strategies, such as planting earlier in the season or using drought-resistant crop varieties. Additionally, irrigation systems or water management practices might help mitigate the effects of dry spells and water limitations on crops. Additionally, the changing climate has led to soil degradation and erosion, which can further reduce the productivity of sorghum crops. This has resulted in decreased yields and rising food insecurity in areas where sorghum is a staple crop for many communities. Unless some efforts are made to adapt and develop mitigation strategies, the future production of sorghum will be very risky due to climate change [12].

Therefore, improved production and management practices for sorghum are suggested to enhance food security and

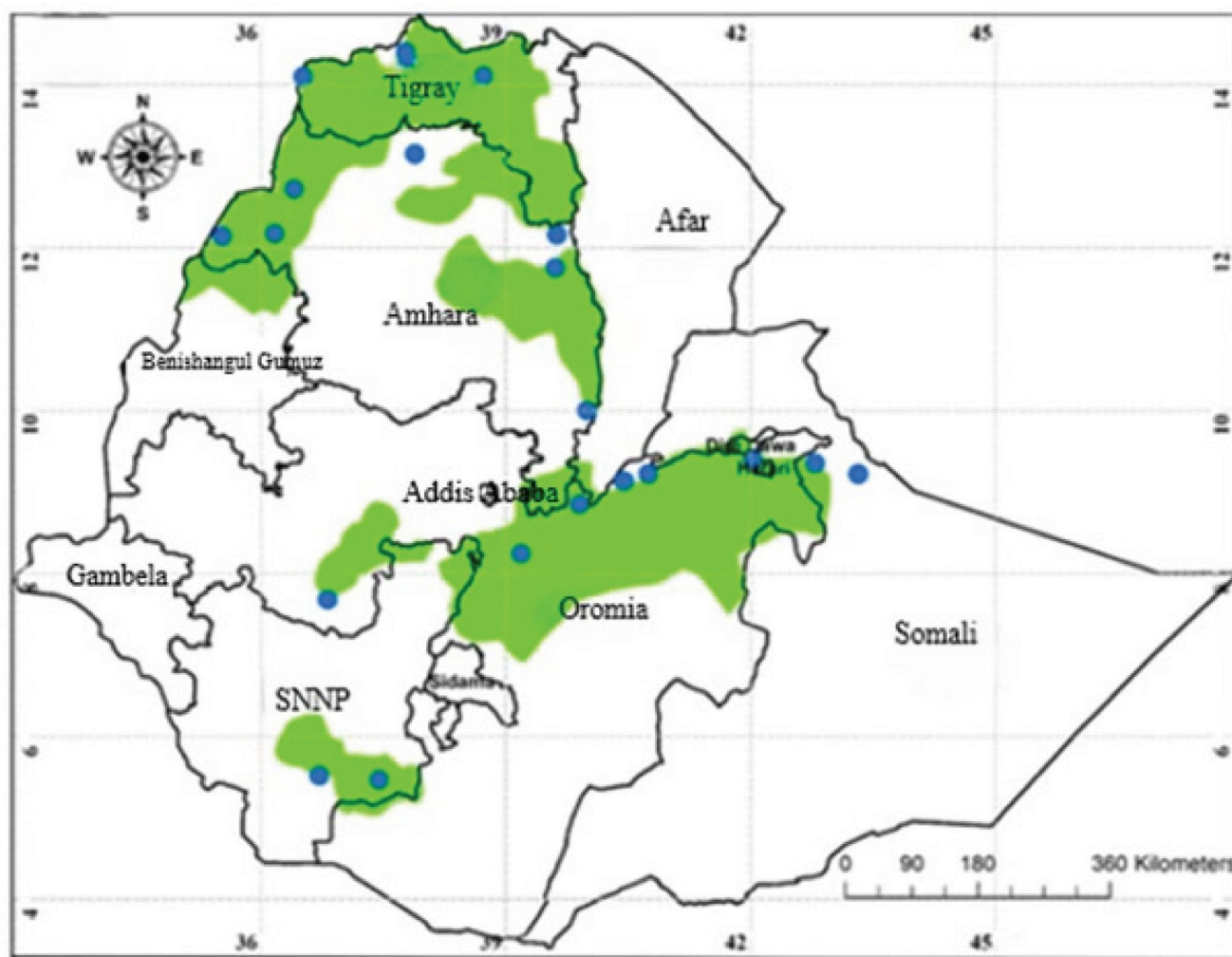


FIGURE 1: Dry lowland sorghum growing areas (shaded green) in four major administrative regions (Tigray, Amhara, Oromia, and SNNP) of Ethiopia. Source: [4].

water productivity in arid and semiarid regions [13]. In this regard, the farmers themselves have adopted several coping strategies. These include the use of drought-tolerant sorghum varieties, intercropping with legumes, conservation agriculture, and organic and inorganic fertilizers. Farmers have also adopted water harvesting techniques such as building small-scale water dams, shallow wells, and water ponds to save rainwater for irrigation during dry spells. Additionally, efforts to improve water management practices could help increase sorghum yields in these regions [11]. Irrigation and shifting planting dates (early planting) could be effective adaptation strategies for sorghum in the face of climate change [14]. Nonetheless, each method presents its challenges and may not be suitable or practical in every situation. Therefore, farmers should carefully evaluate the costs and benefits of each option before determining the best strategy to implement. A recent study suggested that the Agricultural Production Systems Simulator (APSIM), which includes major traits (G), the environment (E), management (M), and their interaction ($G \times E \times M$), is a well-established crop model used to simulate the adaptation of sorghum [4]. The model involves

simulating the growth and yield of sorghum cultivars under different environmental conditions (e.g., temperature, rainfall, and soil fertility) and management practices (e.g., planting date and fertilizer application). The simulation results might be used to identify the most promising cultivars and management practices for specific regions and climates in Ethiopia.

Furthermore, to improve sorghum productivity in drought-prone areas, there is a need for continued research and development of improved cultivars with better drought tolerance and higher yields. Significant progress has been made in sorghum breeding in Ethiopia. The country is considered one of the major centers of diversity for sorghum and contributes to global genetic improvement [15]. The germplasms are primarily composed of landraces, which are locally adapted and important sources of genetic diversity for sorghum breeding programs. One of the major achievements in sorghum breeding in Ethiopia has been the development of high-yielding and drought-tolerant cultivars. To date, more than 50 improved sorghum varieties have been released by both national and regional agricultural research

institutions and universities (Table 1) [10, 16]. These improved cultivars have played a vital role in increasing sorghum production and improving food security in the country.

Studies on phenotypic and genetic characterization of sorghum germplasms are still ongoing to exploit the available genetic resources in the country. A study on the genetic diversity of Ethiopian sorghum landraces under water-limited environment revealed significant genetic variability among genotypes and genotype-environment interactions. Among 315 sorghum accessions, 29 had higher yields than the check variety under drought stress. Furthermore, greater yield and drought tolerance of accessions from lowland areas suggest a potential for sorghum improvement programs targeting drought-prone regions [17]. The genetic mapping of agronomic and yield-related traits in multiple sorghum mapping populations under moisture stress conditions identified a total of 105 quantitative trait loci (QTLs). All the QTLs identified from individual populations were projected onto a combined consensus map, resulting in the identification of 25 meta QTLs for the seven traits [18]. The identified QTLs and meta-QTLs provide valuable information for understanding the genetic basis of drought tolerance in sorghum and offer potential targets for marker-assisted breeding (MAS). Similarly, genetic characterization of sorghum germplasms for drought adaptation using a high throughput root phenotyping identified QTL associated with root and shoot traits and tightly linked simple sequence repeat (SSR) markers [19]. Such genetic diversity studies provided valuable information for the advancement of MAS programs in sorghum, with potential implications for developing improved germplasm with enhanced drought tolerance.

A large-scale genome wide association analysis of the Ethiopian sorghum landrace collection revealed loci associated with important traits such as awns, panicle compactness and shape, panicle exertion, pericarp color, glume cover, plant height, and smut resistance under diverse environmental conditions. A genome wide association study (GWAS) identified loci and single nucleotide polymorphisms (SNPs) associated with these traits, with a percentage of total phenotypic variation explained with significant SNPs across traits ranging from 2% to 43%. Candidate genes showing significant association with different traits were identified, including the sorghum basic helix-loop-helix (bHLH) transcription factor, ABORTED MICROSPORES, sorghum CLAVATA1 receptor-like kinase, and the ethylene responsive transcription factor gene (RAP2-7) [20]. Similarly, GWAS using high-quality SNP markers identified quantitative trait nucleotides (QTNs) associated with nine agronomic traits in sorghum landraces collected from diverse environments across Ethiopia [15]. The study used multilocus genome wide association studies (ML-GWASs) to identify 121 QTNs, including those for flowering time, plant height, tiller number, panicle weight, and grain yield per panicle. Ethylene responsive transcription factor gene (AP2/ERF) and Sorghum Terminal flower1 (TF1) gene were identified as strong candidate genes associated with plant height and 100 seed weight traits, respectively.

3. Symbiosis Mechanisms Between AMF and Plants

3.1. Root Colonization. The symbiotic relationship of AMF with terrestrial plants has a significant impact on almost all plant species [21]. The association is mutually beneficial, with the plant providing fixed photosynthates to the fungus, and the fungus aiding the plant in nutrient uptake and enhancing resistance to root pathogens and drought stress. Fungal growth initiates with the germination of hyphae from dormant spores. In the absence of a host plant, AMF exhibit minimal hyphal expansion, but with the presence of root exudates, hyphal growth, and branching are significantly enhanced [22]. Following the initial physical contact between hyphae and plant roots, the fungus develops appressoria and then proceeds to invade the root surface, establishing itself in the intercellular space of the root cortex. Upon penetrating the innermost cortical layers, arbuscular structures (arbuscules) are produced within individual root cortical cells through the repeated dichotomous branching of fungal hyphae. The AMF develop lipid-rich vesicles as intra- or intercellular storage organs to varying extents during the later stages of the symbiotic relationship. The arbuscules play a crucial role in AM to facilitate nutrient exchange.

3.2. Molecular and Biochemical Crosstalk Between AMF and Plants. The underlying molecular mechanism of the symbiotic association between AMF and plants remains largely unclear due to the obligate biotrophic nature of the fungi [21]. However, the successful establishment of mycorrhizal (Myc) fungi in plant roots, along with its impact on plant functions, relies on the recognition mechanisms governed by synchronized genetic programs in both organisms [23]. These processes are guided by mutual signaling events at every phase of the interaction. As plants are exposed to adverse conditions, various compounds such as sugars, polysaccharides, amino acids, and other metabolites are released to the rhizosphere, which influence root-microbe interactions around the root zone [24]. Here, strigolactones, function as germination stimulants of parasitic plants, have great impact on AMF development [25]. Under stress conditions, plants produce and exude hyphal branching factor (BF) to establish symbiotic interactions with AMF [26]. Hence, the release of these BFs stimulates the growth and hyphal branching of AMF during spore germination. AM also release the Myc factor, which activates the molecular and cellular responses of host plants [27]. After penetrating and colonizing host roots, AMF form branched structures (i.e., arbuscules), which serve as exchange sites for phosphate and/or nitrogen between the AM fungus and the host plant (Figure 2).

3.3. Physiomorphological Regulation in Host Plants and Productivity. The symbiotic interaction of AMF has significant positive effects on growth and physiological performance of several plants including sorghum, vegetable, and fruit crops [29–32]. To this end, genes related to osmotic adjustment, anti-oxidant defense, abscisic acid (ABA) signaling, and mitogen-activated protein kinase (MAPK) pathway are upregulated

TABLE 1: Released sorghum varieties and yield potential (on-farm and station) in Ethiopia.

S/N	Variety name	Year released	Adaptation area	Released by	Days to flowering	Height (cm)	Yield (qu/ha) station	Yield (qu/ha) farm	Seed color	Improved trait
1	Gambell 1107	1976	Dry low land	MARC/EIAR	80–90	150–200	30–50	25	White	High yield and grain quality
2	76T1#23	1976	Dry low land	MARC/EIAR	60–70	120–140	25–45	17	White	Earliness
3	Seredo	1986	Dry low land	MARC/EIAR	65–75	110–140	20–40	17	White	Bird tolerance
4	Meko-1	1998	Dry low land	MARC/EIAR	61–92	157–177	22–33	17	White	Earliness and grain quality
5	Abshir	2000	Dry low land	MARC/EIAR	83	110–140	15–25	—	White	Striga resistance
6	Gobiye	2000	Dry low land	MARC/EIAR	80	110–140	19–27	—	White	Striga resistance
7	Teshale	2002	Dry low land	MARC/EIAR	65–76	170–210	26–52	—	White	High yield
8	Macia	2007	Dry low land	MARC/EIAR	55–60	135–150	42–44	23–30	White	Malt
9	Redswazi	2007	Dry low land	MARC/EIAR	55–60	120–153	30–33	20–21	Red	Malt
10	Melkam	2009	Dry low land	MARC/EIAR	76–82	126–163	37–58	35–43	White	High yield
11	ESH-1	2009	Dry low land	MARC/EIAR	71–78	160–243	50–55	35–45	White	High yielding hybrid
12	ESH-2	2009	Dry low land	MARC/EIAR	61–75	150–192	42–60	35–43	White	High yielding hybrid
13	Dekeba	2012	Dry low land	MARC/EIAR	75	136	37–45	26–37	White	High yielding, earliness and stay green
14	Pac 537	2013	Dry low land	GCT/MARC	75	136	37–45	26–37	White	—
15	ESH-3	2014	Dry low land	MARC/EIAR	62–78	132–170	43–53	—	White	—
16	ESH-4	2016	Dry low land	MARC/EIAR	67	120	42	—	Red	—
17	IS 9302	1983	Intermediate	MARC/EIAR	87–120	100–180	30–60	25	Red	High yield
18	Dinkimash	1986	Intermediate	MARC/EIAR	—	103–150	—	—	—	—
19	Birmash	1989	Intermediate	MARC/EIAR	147–181	129–178	35–69	20	Red	High yield
20	Baji	1995	Intermediate	MARC/EIAR	147–181	139–164	35–56	20	Red	High yield
21	Geremew	2007	Intermediate	MARC/EIAR	103	170	49	40	Red	High yield
22	Dagem	2011	Intermediate	MARC/EIAR	87	156	27–54	42	Brown	—
23	Al-70	1970	High land	MARC/EIAR	120–130	250–384	30–55	33	White	—
24	ETS 2752	1978	High land	MARC/EIAR	130–140	243–285	30–56	36	White	—
25	Chiro	1998	High land	MARC/EIAR	130–140	234–315	42–58	38	Red	—
26	Chelenko	2005	High land	MARC/EIAR	124–131	250–410	29–64	—	Red	—
27	Dibaba	2015	High land	MARC/EIAR	120–140	290–320	37–50	30–40	Brown	—
28	Jiru	2016	High land	MARC/EIAR	117–144	239–389	33–86	32–44	Brown	—
29	Adelle	2016	High land	MARC/EIAR	123–149	255–356	37–72	30–40	White	—
30	Bonsa	2017	Intermediate	MARC/EIAR	111.7	168.1	50	43	Brown	—
31	Argiti	2017	Lowland	MARC/EIAR	79.4	200	37.82	21	White	—
32	Yeju	2002	Dry low land	SARC/ARARI	68	172	50.9	—	White	Disease resistance
33	Birhan	2002	Dry low land	SARC/ARARI	63	106–167	40	—	Brown	Striga resistance
34	Abuare	2003	Dry low land	SARC/ARARI	67–80	134–156	26–57	26	White	High yield and disease resistance
35	Hornat	2005	Dry low land	SARC/ARARI	71	161–171	23.3	16–22	White	Striga resistance
36	Mesay	2011	Dry low land	SARC/ARARI	65–79	137–231	38–62	—	White	Disease and pest resistance
37	Raya	2007	Dry low land	SARC/ARARI	82	185.7	37.68	22.77	White	Disease and pest resistance
38	Misikir	2007	Dry low land	SARC/ARARI	76	123–191	40.73	37	White	High yield
39	Girana-1	2007	Dry low land	SARC/ARARI	75	135–305	40.86	38.7	White	High yield and good <i>injera</i> making
40	Dano	2006	Intermediate	BARC/OARI	132	350	40–50	30–48	Orange	High yield
41	Lalo	2006	Intermediate	BARC/OARI	129	300	40–52	35–48	Red	High yield and stay green

TABLE 1: Continued.

S/N	Variety name	Year released	Adaptation area	Released by	Days to flowering	Height (cm)	Yield (qu/ha) station	Yield (qu/ha) farm	Seed color	Improved trait
42	Chemeda	2013	Intermediate	BARC/OARI	120	290	32	25	Creamy	—
43	Gemedi	2013	Intermediate	BARC/OARI	115	287	33	28	Yellow	—
44	Muyra-1	2000	High land	HU	100–140	—	30–65	—	Red	Earliness
45	Muyra-2	2000	High land	HU	100–140	—	30–65	—	White	Earliness
46	Fendisha-1	2015	High land	HU	147	332	63	—	Red	—
47	Adukara	2015	Humid low land	AARC/EIAR	148–154	161	35.6–41.6	30–30.6	Red	—
48	Assosa 1	2015	Humid low land	AARC/EIAR	138–144	260	35.3–41.3	27.6–33.3	White	—
49	Abamelko	2001	Intermediate	JARC/EIAR	91–100	250	75	50	Brown	Stalk borer and grain disease resistant
50	Emahoy	2007	Humid low land	PARC/EIAR	73–78	220–300	40–45	—	Red	High yield and bird resistance
51	Chare	2011	Dry low land	DBARC/ARARI	73	192	42	33	White	—
52	GEDO	2007	Dry low land	EIAR	75	116–138	34	27–36	White	High yielding and earliness

Note: Source: [10, 16].

Abbreviations: AARC, Assosa Agricultural Research Center; ARARI, Amhara Regional Agricultural Research Institute; BARC, Bako Agricultural Research Center; DBARC, Debre Birhan Agricultural Research Center; EIAR, Ethiopian Institute of Agricultural Research; HU, Haramaya University; JARC, Jimma Agricultural Research Center; MARC, Melkassa Agricultural Research Center; OARI, Oromia Agricultural Research Institute; PARC, Pawe Agricultural Research Center; SARC, Sirinka Agricultural Research Center.

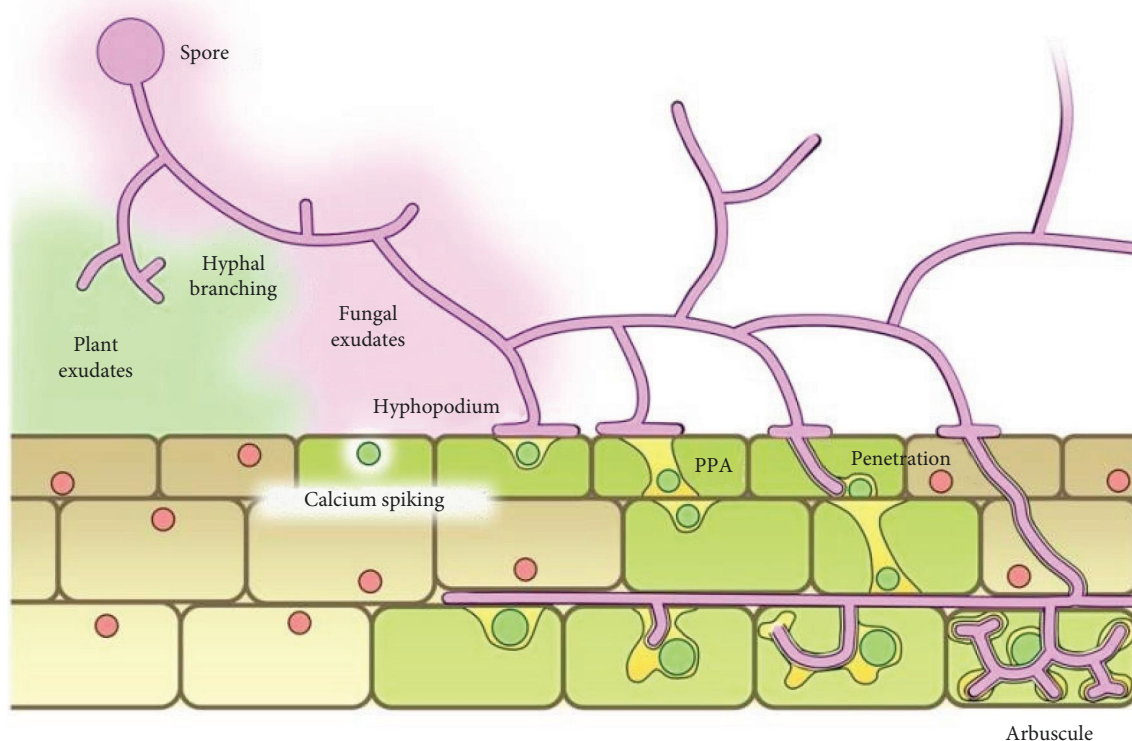


FIGURE 2: Schematic representations of AMF root colonization. Source: [28]. AMF, Arbuscular Mycorrhizal fungi; PPA, prepenetration apparatus.

which in turn enhances the tolerance level of plants under water deficit conditions [29].

The hyphae of AMF extend far from the root zone and form a network of hyphae (mycelium), which increases the availability of phosphate, ammonium, and water to host plants [33]. AMF, for instance, transfer the absorbed nitrogen (N) from the extraradical tract to the intraradical mycelium in the form of arginine and are subsequently delivered to the plant through the arbuscules in the form of ammonium [34]. Sorghum plants connected to the common Myc networks and formed AM symbiosis earlier survived better under severe moisture stress with longer life-spans, more and intact arbuscules [35]. The significant role of AMF on plant growth (shoot length and biomass) is correlated with an increase in enzymatic and biochemical activity [36]. AM fungal colonization and phosphorus fertilization both influenced the flowering time of sorghum [31]. Sorghum genotype with greatest AM colonization struggled to produce grain without AMF. This finding further demonstrated that AMF enhanced sorghum grain yield by improving the plant's resource allocation towards grain production over vegetative biomass. This process is often reflected in an increased harvest index in sorghum plants associated with AMF. Furthermore, the symbiotic interaction with AMF exhibits greater shoot-to-root biomass in other crop species (12.5% to 33.8%), as well as greater chlorophyll content and photosynthetic activity [37]. The activity of antioxidants (e.g., superoxide dismutase (SOD) and catalase (CAT)) enhances water uptake efficiency and photosynthetic capacity of plants thereby alleviating drought-induced oxidative stress and altering the phytohormone balance [38]. The AMF, *R. intraradices* produce glomalin, a protein that stabilizes soil aggregates and retains

moisture in the soil, which could further enhance plant growth and performance in stressful environments [38]. AM symbiosis also confers tolerance to stress in sorghum by modulating dehydrogenase and alkaline phosphatase enzymes under saline and sodic soils [8].

4. Prospects of Biofertilizers in Sustainable Agriculture

Biofertilizers are formulations containing microorganisms such as bacteria, fungi, and algae [39]. Currently, biofertilizers have gained global attention due to harmful environmental impacts, the inflation costs of synthetic commercial fertilizers, and the growing awareness of the relationships between soil microbes and plants [40]. These microorganisms enhance soil fertility by fixing nitrogen, solubilizing nutrients, and improving nutrient uptake by plants. Biofertilizers are becoming increasingly popular worldwide due to their numerous benefits (Figure 3), including their ability to improve soil health, reduce the need for chemical fertilizers, increase crop yields, and tolerate stress factors [41].

4.1. Increased Crop Productivity. Biofertilizers improve soil structure, nutrient uptake, and root development, which result in increased crop yields [39]. A high-throughput phenotyping study demonstrated the effects of AMF on sorghum growth and phenology, as well as grain biomass, nutrition, and bioavailability of zinc (Zn) and iron (Fe) [31]. The findings reveal that sorghum plants colonized by AMF generally performed better than non-AM control plants exhibiting

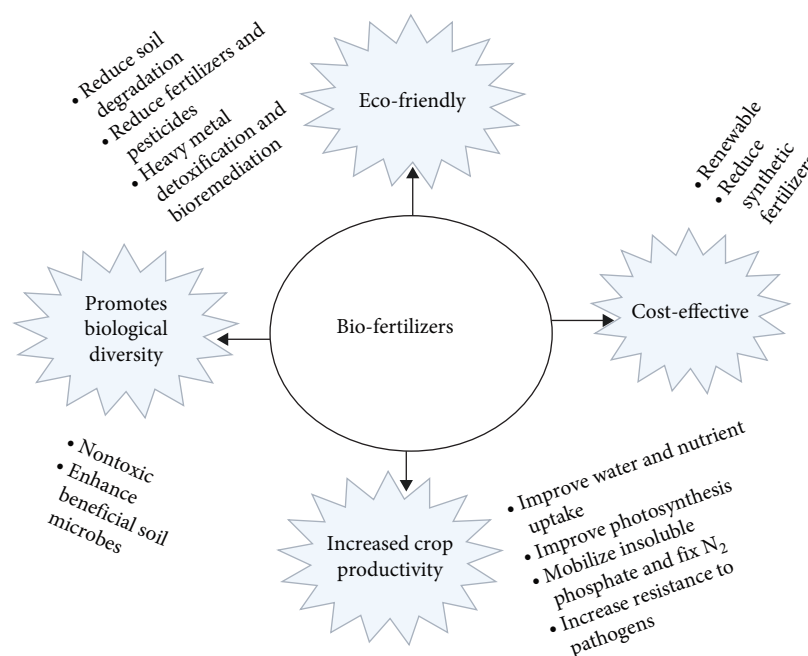


FIGURE 3: Potential role of biofertilizers in sustainable crop production. N₂, nitrogen.

greater yield, harvest indices, and grain phosphorus (P), Zn, and Fe contents. However, genotypic variations were observed in sorghum's response to AM colonization, with some genotypes showing a strong dependence on AM associations for grain production. Temporary growth depression was observed at the early growth stage due to AM colonization. Biofertilizers also improve soil health by increasing nutrient availability and promoting beneficial microbial activity [5]. Using biofertilizers allows farmers to reduce their dependence on synthetic fertilizers, which are costly and harmful to the environment. Therefore, AMF play a crucial role in enhancing sorghum grain yield and nutritive quality, particularly in low P soil conditions, and in improving consumer outcomes in sorghum production systems [31].

4.2. Environmentally Friendly. Biofertilizers are eco-friendly and reduce the negative impact of chemical fertilizers on the environment by increasing soil organic matter, which in turn reduces soil degradation, increases the soil–water holding capacity, and prevents desertification [42]. Biofertilizers are eco-friendly as they are made from natural sources and contain living microorganisms that improve soil fertility and plant growth. Unlike chemical fertilizers, which can harm the environment by polluting water sources and damaging soil health over time, biofertilizers are sustainable and do not have any adverse effects on the environment compared to chemical fertilizers [5]. Biofertilizers also have several other benefits, such as reducing the need for chemical pesticides and herbicides, promoting biodiversity, and improving soil structure [5]. Some biofertilizers are also used to remove heavy metals from soil and water through various detoxification mechanisms and are used for bioremediation [43]. AM inoculation increased molybdenum (Mo) concentrations and uptake without

exacerbating phytotoxicity, indicating a preference for Mo and higher tolerance in Myc plants. Arbuscular mycorrhiza enhanced the performance of sweet sorghum in Mo-contaminated soil by improving nutrient uptake (P, N, and S) and photosynthesis efficiency, aiding biomass production [44]. Similar results have been reported on cadmium (Cd) phytoremediation by sorghum inoculated with *Rhizophagus irregularis* [45]. Consequently, inoculating sorghum with AMF could serve as a phytoremediation and revegetation of heavy metal-contaminated soil. Furthermore, combined application of three AMF isolates (*R. neocaledonicus*, *P. simplex*, and *S. ovalis*) improved the biomass yield of forage sorghum in ultramafic environments suggesting the crucial role of AM fungal symbiosis in phytoremediation of contaminated soil [46].

4.3. Cost-Effective. Using biofertilizers involves a lower investment compared to chemical fertilizers and offers long-term advantages for soil health and crop productivity [39]. Compared with chemical fertilizers, biofertilizers could be more cost-effective in the long run due to several reasons such as crop yield enhancement, reduce the use of synthetic fertilizers, and minimize environmental pollution [43]. In addition, biofertilizers are renewable and eco-friendly. Although biofertilizers may have a higher upfront cost than chemical fertilizers, they can provide better returns on investment over time. This is because biofertilizers improve soil fertility, which leads to higher yields and reduced fertilizer costs in the long term. Furthermore, biofertilizers can also reduce soil erosion and promote biodiversity, which can lead to lower costs associated with soil degradation and loss of genetic diversity. Overall, the cost-effectiveness of biofertilizers depends on several factors, such as crop type, climate, and local market conditions [5].

Given the potential benefits and advantages of biofertilizers, they are considered cost-effective alternatives to synthetic fertilizers, particularly in the long term.

5. AM Fungal–Mediated Alleviation of Drought Stress in Sorghum

The mechanism underlying drought tolerance of sorghum involves complex physiomorphological, biochemical, and molecular modifications [47, 48]. The response mechanisms also differed with the intensity of drought stress and the period at which drought occurs [49]. Stomatal closure, change in enzymatic (i.e., glutathione reductase, SOD, CAT, ascorbate peroxidase (POD), etc.) and nonenzymatic antioxidants (ascorbate, glutathione, and carotenoids) are some of the adaptive mechanisms that could help to maintain the cellular function and integrity of sorghum during drought stress.

AMF colonization significantly improved the growth, kernel weight, and grain yield of sorghum under drought stress [50]. Moreover, the symbiotic interaction enabled sorghum to minimize water loss, enhance photosynthesis, and improve root development under drought stress [8]. These improvements are attributed to the substantial increase in enzyme activity, such as dehydrogenase and alkaline phosphatase, in saline and sodic soils of semiarid regions. In addition, AMF also enhance the accumulation of health-promoting phenolic compounds (flavonoids, carotenoids, and tannins) and antioxidants in sorghum grain, suggesting that AMF could enhance the grain quality of cereal crops [51]. Indeed, the variability in growth, physiological, and transcriptional responses of sorghum to AMF across different genotypes highlights the significance of genetic diversity in influencing plant–fungal interactions [47, 48, 52]. This diversity might lead to distinct outcomes in terms of plant performance and gene expression when exposed to AMF.

Myc colonization (*Funneliformis mosseae*) also enhances the tolerance of sorghum to water deficit conditions by maintaining proline level, enhancing nutrient uptake, regulating water balance, and detoxifying reactive oxygen species (ROS) by promoting enzymatic and nonenzymatic antioxidant activity [47, 53]. Specifically, mutualistic relationships promoted the synthesis and accumulation of glutathione (GSH) in the roots, while also increasing the ability of the roots to synthesize proline. Inoculation with *F. mosseae* improved the drought tolerance of sorghum plants by enhancing the levels of ROS scavengers such as SOD, POD, CAT, and polyphenol oxidase (PPO). Furthermore, genes coding for nonenzymatic antioxidants (*GST29*, *P5CS2*, *FD3*, *GST*, and *GAD*) were upregulated, which enabled sorghum to perform well under water deficit conditions [53]. It is important to note that the mechanism of *F. mosseae* in improving the drought tolerance of sorghum plants differs with the genotypes. For instance, the accession Konawe Selatan (KS) exhibited increased levels of nitrogen content, leaf number, above-ground biomass, chlorophyll, and relative water content (RWC). While, the Super 2 (S2) accession showed higher levels of below-ground biomass, root length, root colonization, and P content [47].

Several studies have reported that AMF increase the expression of genes that regulate stress responses and water

regulation mechanisms in sorghum (Table 2) [47, 48, 52, 54–56]. A study was conducted to investigate the effect of AMF species on major intrinsic protein (MIP) genes in sorghum roots under water deficit conditions compared to those under noninoculated and well-watered conditions [54]. The results revealed variability in the adaptive response of AMF species to *Rhizophagus arabicus*, which is highly adaptable to severe water stress (in arid desert areas), while *R. irregularis* was not influenced by the water regime. In addition, expression analysis of several selected MIP genes known to be involved in drought or symbiosis regulation indicated that inoculation with *R. irregularis* resulted in the upregulation of two plasma membrane intrinsic proteins (*SbPIP2.2* and *sbPIP2.5*) both under stress and under well-watered control conditions, whereas inoculation with *R. arabicus* caused the downregulation of tonoplast intrinsic proteins (*SbTIP2.1*), and NOD26-like intrinsic proteins (*SbNIP1.2* and *SbNIP2.2*) under water deficit conditions, indicating the differential modulatory effect of AM fungal species on MIP genes. Furthermore, Watts-Williams et al. [52] reported that mycorrhiza-induced gene expression varies across sorghum genotypes (accessions) indicating substantial diversity in their interactions with AMF. Furthermore, the study identified 278 genes with mycorrhiza-inducible expression independent of genotype and 55 genes showing genotype-dependent expression, suggesting variation in phosphate transport and defense mechanisms across different accessions.

AMF modify the expression of various transporter genes [55]. The expression of ammonium transporter genes (AMTs) is induced by the symbiosis of AMF in sorghum. Automated annotation of the sorghum whole genome assembly resulted in eight genes coding for putative AMTs. Among these, two AMTs (*SbAMT1*; 1 and *SbAMT1*; 2) were identified as members of the AMT1 family. The remaining other AMTs (*SbAMT2*; 1, *SbAMT2*; 2, *SbAMT3*; 1, *SbAMT3*; 2, *SbAMT3*; 3, and *SbAMT4*) belong to another clade containing three clusters. The two AMTs of sorghum (*SbAMT3*; 1 and *SbAMT4*) are locally rather than systematically expressed highly in the root cortex, which contains arbuscules, and in adjacent cells, whereas the AM-inducible phosphate transporter gene (*SbPt11*) is encoded both locally and systematically in response to AM fungal symbiosis [55]. However, contrasting results were reported by Varoquaux et al. [48] in which the expression of AM symbiosis-induced genes related to phosphorous transporter and senescence-associated genes (*SAG*), were downregulated under drought conditions.

The dynamic adaptive strategies employed by AMF communities and host plants (sorghum) under drought stress conditions suggest a correlation between the successional shift from ruderal to competitive AMF and changes in the expression of both AM fungal and sorghum genes encoding strigolactone signals, Myc-lipochitinoligosaccharide (LCO) signals, and transporters (sugars, lipids, minerals, and water) [56]. The abundance of ruderal species was positively correlated with the expression of AMF Myc-LCO (*DMI2*), whereas the abundance of competitive AMF was strongly correlated with the transcription of genes involved in strigolactone signaling pathways (*D27*, *CCD7*, *CCD8*, *P450* and *PDR1*) and a sorghum phosphate transporter (*Sobic.001G234800*). Furthermore, the

TABLE 2: AM fungal inoculations regulate the expression of genes involved in the drought stress response in sorghum (*sorghum bicolor* L.)

Gene family/code	AMF species	Gene action	Possible tolerance mechanism to drought stress in sorghum	Reference
MIPs (SbPIP2.2, SbPIP2.5, SbTIP2.1, SbNIP1.2, and SbNIP2.2)	<i>Rhizophagus irregularis</i> , <i>Rhizophagus arabicus</i>	Upregulated	Increased water transport capacity and cellular water conservation	[54]
MIP (SbPIP2.8)	<i>Rhizophagus arabicus</i>	Downregulated	Mediate water permeability	[54]
AM symbiosis-induced genes (Sobic.003G243400, Sobic.006G026800, Sobic.001G502000 and Sobic.006G026900)	—	Downregulated	P transportation	[48]
SAG12	—	Downregulated	SAG	[48]
Phosphate transporters (SbPht1, Sobic.001G234800)	<i>G. versiforme</i> , <i>Rhizophagus irregularis</i>	Upregulated	Phosphate uptake from the soil	[52, 55]
Ammonium transporters (SbAMT3; 1 and SbAMT4)	<i>Rhizophagus irregularis</i>	Upregulated	N transfer during symbiosis	[55]
Strigolactones signaling genes (D27, CCD7, CCD8, P450 and PDR1)	—	Upregulated	Increase P uptake	[56]
Enzymatic (SOD, POD, CAT) and non enzymatic genes (GST29, P5CS2, FD3, GST and GAD)	<i>Funnelformis mosseae</i>	Upregulated	Reduce the damage caused by oxidative stress	[53]

Abbreviations: AM, Arbuscular Mycorrhizal; AMF, Arbuscular Mycorrhizal fungi; CAT, catalase; CCD7, carotenoid cleavage dioxygenase7; CCD8, carotenoid cleavage dioxygenases 8; D27, DWARF27; MIPs, major intrinsic proteins; N, nitrogen; P, phosphorous; P450, cytochrome P450; PDR1, pleiotrophic drug resistance 1; POD, peroxidase; SAG12, senescence-associated gene 12; SbAMT3, sorghum bicolor ammonium transporter3; SbAMT4, sorghum bicolor ammonium transporter4; SbNIP, NOD26-like intrinsic protein; SbPIP, sorghum bicolor plasma membrane intrinsic protein; SbPIP2.8, sorghum bicolor plasma membrane intrinsic proteins2.8; SbPht1, sorghum bicolor phosphate transporter 1; SbTIP2.1, tonoplast intrinsic protein; SOD, superoxide dismutase.

change in the abundance of AMF from ruderal to competitive species correlated with a shift in transcription.

6. Agricultural Intensification and AM Fungal Symbiosis

Agricultural management practices such as fertilization, cropping systems, tillage and land use forms, and irrigation influenced AMF symbiosis in several crop species [57–62]. Furthermore, AMF root colonization was also influenced by host plant and soil properties including texture, pH, phosphorus availability, and organic matter [63].

6.1. Fertilization. Myc root colonization and microbial diversity were higher in sorghum plants amended with compost compared to commercial fertilizers [64]. Moreover, the nutritional quality of sorghum grain was higher in intercropping and/or soil amended with compost as compared to sole cropping and/or commercial fertilizer amendment in a genotype-dependent manner. Applying nitrogen, phosphorous, and potassium (NPK) fertilizer decreased the colonization percentage of AMF in sorghum [65]. This could be the fact that fertilizer application may have increased the concentration of these elements in sorghum plant tissue which could have reduced the secretion and release of root exudates (strigolactones) to the rhizosphere and reduced hyphal branching of AMF [26]. However, sorghum response to AMF and P fertilization varied among sorghum genotypes [66]. The addition of phosphorus decreased the dependency on AM fungi for shoot dry weight and shoot P concentrations. AMF and P fertilization significantly influenced sorghum time-of-flowering across different sorghum genotypes [31]. Besides, strigolactone profiles of sorghum cultivars also influenced AM colonization and response to phosphorus acquisition efficiency (PAE) [57]. The results indicated that orobanchol, a specific type of strigolactone, promoted AMF colonization, specific P uptake (SPU), and PAE in a cultivar-specific manner.

6.2. Cropping System. The use of different cover crops in combination with N fertilizer influenced the population and establishment of Myc fungi [67]. Though the colonization rate was almost similar among the cover crops, species *A. scrobiculata*, *A. tuberculata*, *G. tortuosum*, *S. persica*, and *S. pellucida* were identified in the sorghum rhizosphere, regardless of the application of N fertilizer. Whereas species *G. macrocarpum* was identified only in the sorghum rhizosphere without N application [67]. The role of cover crops in AMF establishment and stability of soil aggregates was also investigated in other crop species such as barley (*Hordeum vulgare* L.) and vetch (*Vicia villosa* L.) in maize and sunflower cropping systems [68]. Compared to the bare fallow, the hyphal length and enzyme activity (β -glucosidase) increased by 80% in sunflower, while the AMF spores and hyphal length increased by 60%–70% with a twofold increment of enzyme activity. This suggests the paramount role of replacing fallow conditions with cover crops to increase AMF abundance in the subsequent main cropping season. Cultivation of cover crops during the fallow period in a crop-fallow-based rotation system is an effective approach to

increase the microbial community, abundance, and enzyme activities related to carbon and nutrient cycling [69]. Microbial community analysis using ester-linked fatty acid methyl ester (EL-FAME) indicated that oat cover cropping increased AMF abundance (84%) as compared to fallow cropping.

Cultivating sorghum with agroforestry tree (*Faidherbia albida*) improved spore abundance and colonization of AMF under and close to the canopy of *F. albida* [70]. These AM fungal root colonization and spore abundances significantly reduced striga infestation which could be attributed to the high grain yield of sorghum. Crop diversity in intensive agricultural systems influences AM fungal community. The polyculture field contained a greater number of AM fungal taxa than the monoculture site although affected by soil properties [61]. Similarly, the diversity of AMF at the polyculture sites was nearly 50% greater than at the monoculture site. Here, the richness and diversity of AMF increased with increasing duration of polyculture cropping. Sorghum–legume (groundnut, cowpea, dry bean, and soybean) intercropping influenced the establishment and core abundance of fungal community [71]. The abundance of core mycobiomes varied with the crop type, plant and soil substrate, and across years. The diversity of such fungal communities could improve the productivity and disease resistance of sorghum and legume crops. Besides, intercropping (configuration) ratio in sorghum–soybean intercropping system improved the rhizosphere soil property and productivity of waxy sorghum [72].

6.3. Tillage and Land Use Types. Soil management practices influence the composition and functional structure of rhizosphere microbes in sorghum [73]. Particularly, AMF species composition and diversity have been influenced by location and land use forms [74, 75]. The number of spores, species richness, and AMF diversity increased in undisturbed land, such as forest lands, suggesting the negative impact of soil disturbance on the colonization and diversity of AMF [75, 76]. This could be the fact that soil disturbance affects soil attributes, plant species composition, and hyphal development, which in turn affect AMF diversity and colonization. In contrast, Wipf et al. [73] reported that standard tillage enhanced bacterial and AMF diversity in sorghum compared to no-tillage practices. The possible justification was the impact of tillage on creating open niche space for broad colonization. On the other hand, conservation tillage increased AMF spore density, community composition, and species richness compared to conventional tillage systems [58]. Significantly higher percentage of AM colonization was recorded in bean and sorghum plants under no-tillage practices compared to other management practices. Whereas the lowest AM fungal colonization was recorded under the moldboard tillage system for all the tested crop species (sorghum, bean, and maize). Moreover, AMF diversity was greater in sorghum as measured by the Shannon–Weiner diversity index (H'), at 0.8, 0.6, and 0.4 in sorghum, maize, and bean, respectively. Similarly, Egboka et al. [60] also clearly assessed the influence of land use types on AMF spore abundance in the humid tropical rainforest of Nigeria. His study revealed that the highest AMF spore abundance was recorded in cassava-based land use types compared to fallow land, yam fields, and vegetable

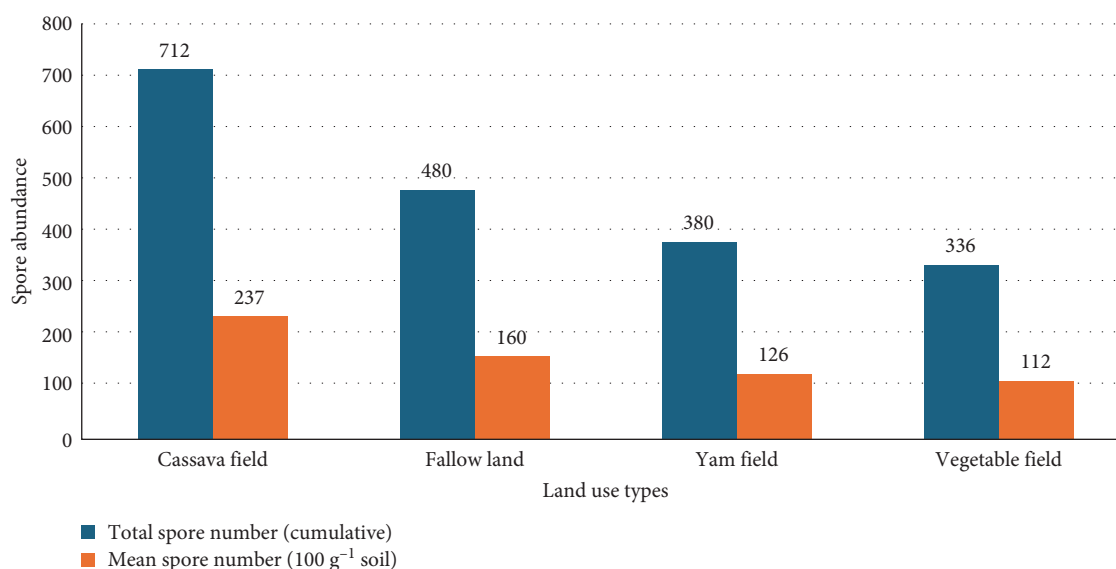


FIGURE 4: AMF spore abundance in different land use types. Source: [60]. AMF, Arbuscular Mycorrhizal fungi.

farms (Figure 4), suggesting that cassava is a potential source of soil-borne propagules of AMF.

6.4. Availability of Moisture. Root colonization by AMF increased (~86%) with increasing water stress [77]. However, contrasting results have been reported by Varoquaux et al. [48], who noted that drought reduces AMF abundance and the symbiotic interaction at different growth stages in sorghum genotypes. Similarly, the role of AMF on growth (biomass) enhancement on forage sorghum decreased at severe moisture deficit conditions with reduced levels of root colonization. [35]. Moreover, drought stress reduced the effectiveness of AMF and collapsed the arbuscules, which resulted in growth reduction and mortality of sorghum. The effectiveness of root colonization and the AMF community composition varied with the species of AMF, the genotype of sorghum [52, 78], and the time point at which drought occurs [56]. Very few generalists from *Rhizoglossum* species were found to adapt and colonize sorghum in a semiarid region characterized by drought and alkaline soil [79].

In a field experiment undertaken to evaluate the effects of different sorghum cultivars and species of AMF, *F. mosseae* effectively promoted root colonization and improved growth and yield performance of sorghum among the studied species under high moisture stress [78]. Variability in symbiosis among sorghum accessions also suggested the potential to develop AMF-responsive cultivars [52]. Some of the tested sorghum accessions showed a negative growth response to Myc inoculation, while other sorghum accessions exhibited significantly greater shoot biomass and high concentrations of minerals, both macro and micro, during uptake. In addition to exhibiting variability in responsiveness to AMF, the accessions also exhibited differential putative symbiotic-related gene expression. In contrast, targeting AMF-related root colonization in the breeding program was not promising for West African sorghum genotypes due to the polygenic nature and low heritability of the trait despite genotypic

variability existing under different P fertilizers at various growth stages of the crop [80].

7. Synergistic Effect of AMF on Drought Tolerance of Sorghum

Inoculation of AMF with organic and inorganic soil amendments or with other soil microbes significantly enhances tolerance to drought stress in sorghum (Table 3) [57, 81, 82] and other several crop species [81, 86–89]. Combined inoculation of AMF with K fertilizer improved water stress tolerance, biomass, and sugar yield of sweet sorghum under moisture deficit conditions [57]. Besides, AM fungal colonization and P fertilization influenced the flowering time of sorghum [31]. The sorghum genotype with the greatest AM colonization struggled to produce grain without inoculation. Kamali, Meh-raban, and Gururani [81] investigated the combined effect of AMF (*F. mosseae*) and Nitroxin biofertilizer (containing the genera *Azotobacter* and *Azospirillum*) on the physiological and grain yield of sorghum under water stress conditions. Co-inoculation of sorghum seeds with *Rhizobium* bacteria and AMF enhanced the chlorophyll (a, b, and total) content, soluble protein content, water use efficiency (WUE), RWC, N content in plant tissue, electrolyte leakage, and pore content [78]. The application of the two microorganisms (*Azotobacter* and *Azospirillum*) increased the sorghum protein content (26.7%), proline content (25.4%), and N concentration (49%) under severe water stress conditions. Furthermore, co-inoculation of both Nitroxin and AMF under severe water stress conditions strongly reduced the membrane leakage of sorghum plants by up to 20.6% compared to that of noninoculated plants [81]. Sorghum plants inoculated with the two biofertilizers had higher WUE and maintained open stomata to produce more dry matter than the noninoculated plants, suggesting that the rhizobacteria and AMF had synergistic effects on the plants. These factors all resulted in up to a 27% increase in sorghum grain yield compared to that in

TABLE 3: Synergistic effect of co-inoculating AMF with other biofertilizers and organic or inorganic amendments on growth performance and stress tolerance of sorghum.

Co-inoculant	Synergistic effect to drought stress response	Reference
<i>Funneliformis mosseae</i> + Nitroxin biofertilizer	Enhanced chlorophyll content, soluble proteins, WUE, RWC, and proline content	[81]
AMF + P fertilizer	Improved uptake of P, N, and K	[57]
AMF + P fertilizer	Improved the yield and WUE of grain sorghum	[82]
AMF + <i>Pseudomonas fluorescens</i>	Improved P uptake and enhanced microbial population	[65]
AMF + K fertilizer	Improved uptake of N, P, and K	[57]
AMF (<i>Rhizophagus irregularis</i>) + <i>Streptomyces coelicolor</i>	Enhanced microbial population, phosphatase, and chitinase activities	[83]
AMF + PGPR	Increased in plant biomass, leaf area, and total chlorophyll content	[84]
AMF + PGPR	Increased photosynthetic pigment, biomass, and sugar content	[85]

Abbreviations: AMF, Arbuscular Mycorrhizal fungi; K, potassium; N, nitrogen; P, phosphorus; PGPR, plant growth promoting rhizobacteria; RWC, relative water content; WUE, water use efficiency.

the noninoculated treatment, indicating their synergistic effect and promising approach to improve growth and grain yield under drought conditions [81]. In line with this, the effectiveness of Myc symbiosis also depends on the species and the composition of the AM fungal taxa when applied together [46]. Mixture of different AM fungal species increased sorghum biomass, with a significant positive effect at the flowering stage. Furthermore, inoculation of AMF in combination with exogenous application of osmoprotectants significantly reduced the damage caused by oxidative stress and increased the antioxidant activities of sorghum plants under heavy metal stress conditions [81].

The combined effect of AM fungal and synthetic chemical fertilizers on sorghum has been reported previously [57, 82]. Myc inoculation and K fertilization had significant positive effects on the grain yield and nutrient uptake of sweet sorghum plants under water stress in calcareous soil [66]. The combined application of Myc fungi and K fertilizer increased the grain yield by up to 30% compared to that in the control treatment. Furthermore, Myc inoculation significantly increased the uptake of P, N, and K, while K fertilization increased the uptake of K and calcium (Ca). The results suggested that the combined application of Myc fungi and K fertilizer could improve the productivity and nutrient uptake of sweet sorghum in water-stressed and calcareous soils (Abdelhameid, 2020)[57]. Similarly, research conducted on the response of grain sorghum to AMF and P fertilizer under deficit irrigation revealed that the application of AM fungal combined with P fertilizer enhanced sorghum's ability to tolerate water stress [82]. Deficit irrigation is a common practice in arid and semiarid regions, where water resources are limited. Thus, the combined use of AMF and P fertilizer improved grain sorghum's yield and WUE. This combined fertilizer application was suggested as a promising management strategy for sustainable grain sorghum production and an alternative to chemical P fertilizer under deficit irrigation conditions. Furthermore, AM fungal inoculation in combination with P fertilization significantly increased the uptake and concentration of P in shoots and roots [77].

8. Challenges of AMF as Biofertilizers

Despite the potential role of AMF in mitigating drought stress in sorghum, various challenges hinder its effectiveness and widespread adoption in sustainable agriculture. Some of the major challenges include strain instability under field conditions, complexities in formulations, and large-scale production [90]. Such complexity of the symbiotic relationship makes difficult to predict the outcomes of AMF applications in different regions and under varying drought conditions. The other key challenge is that the interaction between AMF and other soil microbiota such as bacteria and non-Myc fungi under drought stress is poorly understood [91]. Potential competition with native soil microbes for resources may reduce the effectiveness of AMF in enhancing sorghum drought stress tolerance.

Thus, researchers need to select and develop AMF strains that are effective for different crops and climatic conditions. Addressing all these challenges could lead to AMF's greater potential as a biofertilizer, particularly in the tropics, where the cost of chemical fertilizers, environmental and health consequences, and climate change pose significant challenges.

9. Gaps and Future Prospects

In recent years, considerable achievements have been made globally in studying the symbiosis of AMF in sorghum under drought stress. However, there are still some research gaps that need to be addressed. While AMF are known to enhance drought tolerance in sorghum, the underlying molecular pathways that govern the symbiotic relationship are complex and not fully understood. These gaps pertain to fully understand the symbiosis's mechanisms, benefits, and practical applications. Research activities are also required to determine the optimal application rates and timing of AM fungal inoculation (especially under prolonged drought periods) and organic amendments on the productivity of sorghum under drought conditions. Moreover, advancements in technology (biotechnology) are lacking to facilitate mass production of AM fungal biofertilizers at a lower cost and make

accessible to the farmers. To our knowledge, research on the impact of AMF inoculation on morphological, physiological, and/or molecular responses of sorghum in drought-prone regions of Ethiopia remains very limited. Thus, future research should focus on identifying the most effective AMF strains for different sorghum genotypes and integrating into sorghum breeding programs could enhance the development of drought-tolerant varieties. Furthermore, identifying genetic markers associated with beneficial AMF symbiosis could speed up breeding programs. The diverse sorghum germplasms available in the country could be a valuable opportunity for such research interventions to enhance the productivity and resilience of this staple crop.

10. Summary and Conclusion

Biofertilizers are environmentally friendly and safer than synthetic chemical fertilizers, making them a more viable option for sustainable crop production. AM fungal symbiosis regulates diverse physiomorphological, biochemical, and molecular responses of sorghum under drought stress. The symbiotic interaction regulates key physiological processes such as maintaining water balance, improving nutrient and water uptake, minimizing oxidative damage, and modulating hormonal responses of sorghum under drought stress. Hence, AM fungal has a significant economic benefit in terms of increasing sorghum yield while reducing the risk of crop failure and providing food security to smallholder farmers in arid and semiarid regions. The integration of AMF in sorghum cultivation is a promising strategy for sustainable agriculture. It aligns with the principles of low-input farming, reduces dependency on chemical fertilizers, and enhances crop resilience to climate variability. This could be attributed to the different modes of action of AMF and their synergistic effect on improving soil health, nutrient availability, and growth enhancement of sorghum under stress conditions. Furthermore, the use of AMF can be combined with other sustainable practices like crop rotation, organic amendments, and reduced tillage to further improve soil health and crop productivity.

In conclusion, AMF symbiosis plays a vital role in enhancing sorghum production under drought stress. Its role in improving water and nutrient uptake of sorghum, along with promoting sustainable agricultural practices, is a key component in addressing food security challenges in drought-prone regions.

Data Availability Statement

The data used to write this review are from previously reported studies, which have been cited appropriately in the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

M.W.B. wrote the original draft and prepared the figures and tables. Z.T.N. edited the manuscript. All the authors have read and agreed on the final version of the manuscript.

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