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Using Beneficial Microorganisms to Promote Sustainable Crop Production and Resilience of Smallholder Agroecosystems to Changing Climate

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Abstract

Agriculture today faces a unique challenge of producing sufficient and nutritious food for the rising human population under finite natural resources, shrinking economies, and changing climate. Soil fertility is pertinent to sustainable agricultural production and mitigating the consequences of climate change drivers to crops. To promote healthy crop production practices, the search for alternative soil amelioration and plant disease management strategies is on the rise. Among the most feasible alternatives are beneficial soil microorganisms, which are central to many agroecological cycles and improvement of crop nutrient and water uptake and resistance to biotic and abiotic stresses. Since the majority of smallholder farmers in many parts of the world cannot afford inorganic fertilizers, there is a pressing need to develop sustainable and affordable soil fertility management strategies that focus on low-input cropping systems which is crucial for attaining agricultural sustainability and global food security. Therefore, this review explores the potential of beneficial microorganisms to promote sustainable crop production and resilience of smallholder agroecosystems to global climate change drivers.

Keywords

Beneficial microorganisms · Climate change · Food security · Microbial inoculants · Smallholder farmers

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11.1 Introduction

Meeting the increasing food demands of the rapidly growing population in the face of limited resources and changing climate presents an enormous challenge to several developing nations. Per capita agricultural production and food availability have decreased over time (Funk and Brown 2009), and many people, especially within the developing world, are in danger of widespread food insecurity. Smallholder farmers predominate in an environment of dwindling natural resources, especially arable land, rising population, changing climate, and environmental pollution (Aniah et al. 2019). Low soil fertility presents one among the main challenges to sustainable crop production since most smallholders cannot afford to invest in high-cost chemical fertilizers (Clair and Lynch 2010). Given that the majority of the populace in developing nations depends on smallholder agriculture, there is a pressing need to understand how soil fertility can be sustainably improved on a small scale and contribute to achieving the United Nations Sustainable Development Goals (UN SDG). This includes a strategic combination of the various alternative soil organic amendments and beneficial microorganisms with specifically adapted crop varieties under diverse agroclimatic conditions. Resource-saving strategies and landuse intensification require the development of more viable plant nutrition strategies in crop production as alternatives to the prevailing use of nonrenewable mineral fertilizers.

Beneficial soil biota provides essential agroecosystem services, especially in low-input agroecosystems, where the use of external inputs is usually limited. These include improving the nutritional status of their host plants and protecting them from deleterious effects of drought, high temperature, soilborne plant pathogens, and heavy metals (Goswami and Deka 2020; Jacoby et al. 2017). Beneficial microorganisms that support plant growth and development include plant growth-promoting rhizobacteria (PGPR), symbiotic fungi such as arbuscular mycorrhizal fungi (AMF), *Trichoderma* spp., and endophytic microorganisms. These promote plant growth and impart plant resilience to global climate change through a plethora of mechanisms including enhancing nutritional and water uptake, rhizoremediation, production of phytohormones, siderophores, secondary growth metabolites, and suppression of pathogenic microorganisms (Fig. 11.1).

11.2 Characteristics of Smallholder Agroecosystems, Opportunities, and Challenges

Agricultural ecosystems in the sub-Saharan African region are inherently diverse, indigenous, and resilient multifunctional complex systems that are sustainably managed to meet the farmers' subsistence needs (Mburu et al. 2016). They thrive without relying much on chemical fertilizers, mechanization, or other sophisticated modern technologies (Awazi and Tchamba 2019). The smallholder systems are the key drivers of the rural economies. Agroecologists acknowledge that they can provide resilient solutions to food security amidst several uncertainties challenging



Fig. 11.1 Different ways of plant growth promotion by beneficial microorganisms under changing climate. BRM beneficial rhizospheric microorganisms; PGPR plant growth-promoting rhizobacteria; PGPF plant growth-promoting fungi human existence such as climate change and economic and energy crisis (Altieri et al. 2012). Despite the characteristically highly fragmented small pieces of land, farmers engage not only in producing food (crops, animals, and their derived products) but also producing fiber-based products (cotton, sisal, and silk), fuel (wood and related biomass), and biochemicals (natural medicinal products). The dominantly practiced farming systems include crop rotation, intercropping, and agroforestry, which are often associated with conferring beneficial effects on the soil by stimulating soil microbiota such as AMF and PGPRs (Raimi et al. 2017). Smallholder farming systems have a high degree of plant and animal species diversity, which is a good strategy in promoting diet diversity and reducing unpredicted risk losses while maximizing farm returns. Such traditional ecosystems that are rich in wild populations of landraces well adapted to the local conditions could harbor a wide variety of pollinators, insect predators, beneficial microbes, and nutrient-enriching plants (Oruru et al. 2018).

Genetic diversity richness could be exploited by the breeders to heighten the stability of the local cropping systems against biotic and abiotic stresses and to promote genetic variations arising from the crossing of traditional landraces with the high-yielding modern cultivars (Govindaraj et al. 2015). Farmers are the key decision-makers supporting their agroecosystems through water and soil conservation, on-farm biodiversity, landscape aesthetic management, and engaging in off-farm activities that bring social cohesion and cultural exchange among different communities with diversified farming experiences. However, farmers' management decisions are highly limited and predetermined by a plethora of external factors such as resource availability, market access, knowledge and exposure, social and cultural needs, and environmental conditions (Mungai et al. 2016). The mismatch between farm size and the availability, access or economies of scale of machines remains a challenge that impedes the utilization of appropriate mechanization in smallholder farms. Besides, farmers mostly own or co-own separate and dispersed agricultural fields in areas that may not be easily accessible, and this leapfrogs any technocratic attempts to revolutionize and modernize agriculture in such setups (Van Loon et al. 2020). Farmer's knowledge capacity and educational needs still undermine the scaling up of innovations and the introduction of any new technology to such a constricted type of farming system which calls for farmers' active participation and approval (Muoni et al. 2019). It is, therefore, imperative to involve farmers in any technological importation if substantial positive changes are to be achieved in smallholder farming systems.

11.3 Microbial Inoculants in Delivery of Multiple Agroecosystem Services

The application of microbial inoculants selected based on functional trait approach and that are adapted to the highly intensified smallholder agroecosystems is highly advocated in agroecology. Besides, the adoption of diversified farm management practices that complement microbial inoculation could optimize the provision and delivery of the essential agroecosystem services. For instance, the cultivation of legumes as relay intercrops with cereals and the inclusion of rhizobia inoculation enhance N acquisition through BNF and N transfer to non-legumes. Other microbialderived agroecosystem services important in smallholder farming systems include P and K acquisition, secretion of stimulatory phytohormones, and siderophores that help in phytopathogen control, biotic and abiotic stress management.

11.3.1 Biological Nitrogen Fixation

Nitrogen (N) is one of the essential nutritional components of plants that makes up a large portion of plant proteins and nucleic acids regulating the primary productivity of the soil ecosystem (Ahemad and Kibret 2014). Naturally, N exists in various chemical forms and oxidation states, and microorganisms play a key role in catalyzing the different N transformations into forms readily utilizable by plants (Pajares and Bohannan 2016). Biological nitrogen fixation (BNF) is a microbiologically driven process where microorganisms transform atmospheric nitrogen into forms that can be assimilated by the plants. The mechanism of BNF is a complex process that is majorly catalyzed by the nitrogenase enzyme complex and regulated by the *nif* genes produced by diazotrophic N-fixing microorganisms (Wang et al. 2013; Choudhary and Varma 2017).

Major groups of diazotrophs known for N-fixing abilities are the Cyanobacteria, green sulfur bacteria, *Azorhizobium, Sinorhizobium, Rhizobium, Azospirillum, Thiobacillus, Herbaspirillum, Bradyrhizobium, Frankia* sp., and *Clostridium pasteurianum* (Yeager et al. 2005; Mus et al. 2018). Legumes are the biggest beneficiaries of the BNF process as they are able to form a symbiotic association with most of the diazotrophs to meet their N demands. However, the efficiency of the symbiotic partnership in delivering the much-needed N to the plants varies highly and depends on the host genotype, soil conditions, microbial strain, and climatic conditions (Maingi et al. 2001; Mabrouk et al. 2018). In smallholder farming systems, the legume cultivation substantially reduces the overall amount of external N inputs required to sustain the present and subsequent crop production (Nyoki and Ndakidemi 2018). This could be ameliorated further by inoculating legumes with effective N-fixing microorganisms.

Inoculating legumes using a combination of rhizospheric nitrogen-fixing bacterial strains improves soil health, quality, and fertility. It enhances plant-microbe interactions through improved root exudation and signaling leading to better root development, nodulation, phytopathogen suppression, and water and nutrient acquisition (Ouma et al. 2016; Koskey et al. 2017; Mabrouk et al. 2018). Various stakeholders have initiated research-based projects aimed at empowering farmers with technologies that would contribute to improvement in their household income through the introduction of N-fixing inoculants that are effective in soil fertility restoration and crop productivity. N2Africa has actively researched on African indigenous rhizobia strains associated with chickpea, soybean, faba bean, common bean, and groundnut legumes since 2009 in more than ten sub-Saharan African

(SSA) countries (Giller et al. 2019). The Microbial Resources Centre Network (MIRCEN), in collaboration with the University of Nairobi in Kenya and other commercial private stakeholders, developed rhizobia inoculants known as Biofix[®] that is more cost-effective compared to chemical N fertilizers available in the Kenyan market (Odame 1997). In Nigeria, the International Institute of Tropical Agriculture (IITA) introduced promiscuous soybean (*Glycine max* L. Merrill) cultivars that nodulate with a wide diversity of the African *Bradyrhizobium* bacteria (Santos et al. 2019). Other recent researches on N-fixing rhizobia have been carried out across the SSA, and more effective indigenous rhizobia inoculants that could be used by farmers as single or a consortium of different strains are available (Koskey et al. 2018; Grönemeyer and Reinhold-Hurek 2018; Musyoka et al. 2020). However, large-scale production, commercialization, continuous adoption, and accessibility remain the most prominent challenges impeding the use of these elite inoculants by the SSA smallholder farmers (Oruru and Njeru 2016).

11.3.2 Phosphate Solubilization

Phosphorus (P) in the soil exists largely in the form of insoluble compounded deposits. It is one of the main essential macronutrients required by plants for growth and development (Walpola and Yoon 2012). Despite the presence of substantial P deposits in the soil layers, P content available for plant use in many smallholder farms is critically limited. Essential plant physiological, molecular, and biochemical processes such as metabolism, signal transduction, genetic, structural formations, energy storage and transfer, cell and tissue formation require the presence of the P element for optimal functioning (Dissanayaka et al. 2018). The uptake of P from the soil by plants is mainly in the form of orthophosphate anions, which are formed through a bacteria-mediated mechanism of acidic solubilization of inorganic phosphates (Lobo et al. 2019). Alternatively, P mobilization occurs via organic phosphatase enzymes such as phosphoesterases, phytases, phosphodiesterases, and phospholipases that catalyze the breakdown of phosphoric esters (Walpola and Yoon 2012; Novo et al. 2018).

Smallholder farmers often rely on phosphatic chemical fertilizers, which are expensive and unavailable and prone to precipitation by metal-cation complexes such as Ca²⁺, Al³⁺, and Fe³⁺ found in the soil leading to soil fertility depletion (Dissanayaka et al. 2018). Thus, there is a need for low-priced sustainable techniques that are environmentally friendly and efficient enough to supply adequate P to the plants. Microorganisms such as phosphate-solubilizing microbes (PSMs) form an integral part of the natural P cycle. Research on PGPR and plant growth-promoting fungi (PGPF) with the capability to solubilize and mobilize the insoluble organic and inorganic soil phosphates from the soil rocks to the plants has been done (Sharma et al. 2013; Alori et al. 2017; Selvi et al. 2017; Giovannini et al. 2020). This has led to the upsurge development of various commercial microbial inoculants containing

effective PGPRs and PGPFs for use by smallholder farmers to increase their crop production (Tabassum et al. 2017).

The potential PSMs from the bacteria genera include Pseudomonas putida, Pseudomonas calcis, Pseudomonas fluorescens, Pseudomonas striata (Mohammadi 2012; Thakur et al. 2014), *Pseudomonas canescens* (Alam and Rashid 2002), Rhizobium leguminosarum (Walpola and Yoon 2012; Hajjam and Cherkaoui 2017), Rhizobium meliloti, Thiobacillus ferrooxidans (Sharma et al. 2013), Mesorhizobium mediterraneum (Peix et al. 2001), Bacillus subtilis, Bacillus polymyxa, Bacillus megaterium, Bacillus circulans, Bacillus fusiformis, Bacillus coagulans, and Bacillus chitinolyticus (Chen et al. 2006; Thakur et al. 2014; Satyaprakash et al. 2017). The members from the fungal genera include Aspergillus niger, Aspergillus fumigatus, Aspergillus parasiticus, Aspergillus terreus, Aspergillus candidus, Penicillium simplicissimum, Penicillium rubrum, nematophagous fungus Arthrobotrys oligospora, Trichoderma viride, and Trichoderma spp. (Reddy et al. 2002; Aseri and Jain 2009; Selvi et al. 2017). Other important microorganisms include arbuscular mycorrhizal fungi (Giovannini et al. 2020) and Streptomyces actinomycetes such as Streptomyces albus, cyaneus, and Streptoverticillium album (Kumar et al. 2018). Mixed cultures of bio-inoculants and multiple crop-stage inoculations are known to increase the potential effectiveness of PSMs in enhancing plant growth, shoot development, and yield productivity (Muthukumar and Udaiyan 2018).

AMF have a greater inter- and intraspecific biodiversity due to its ability to colonize the roots of 80–90% of plants (Oruru and Njeru 2016). They thus can be fully exploited as a resource in smallholder farming systems by selecting AMF isolates, species, and strains with the highest colonization efficiency, P solubilization, and siderophore production, among other indirect beneficial traits (Giovannini et al. 2020). Many studies have reported significant contributions of AMF bio-enhancers based on their use either as individual or a consortium of AMF inoculants in improving the yield productivity and nutrient quality of cereals, legumes, vegetables, fruits, and agroforestry trees (Njeru et al. 2017; Avio et al. 2018; Musyoka et al. 2020). Among the AMF communities, the most commonly available commercial inoculants are derived from the species *Funneliformis mosseae* and *Rhizophagus irregularis*. These AMF species coincidentally are broad symbionts widely spread throughout the sub-Saharan African soils and other tropical zones of the world predominated by smallholder farmers (Oruru and Njeru 2016; Giovannini et al. 2020).

11.3.3 Potassium (K)-Solubilizing Microorganism (KSMs)

Potassium (K) is available in the soil in various forms such as exchangeable and non-exchangeable K, mineral, and soluble K. However, depending on the soil type, most of the K^+ ions are bounded and are unavailable for direct uptake by the plants (Etesami et al. 2017). Apart from growth and developmental roles, K promotes plant resistance against pest and disease and takes part in the activation of over

80 physiological processes, including starch synthesis, energy metabolism, sugar degradation, photosynthesis, and nitrate reduction (Gallegos-Cedillo et al. 2016; Hussain et al. 2016). A group of microorganisms, K-solubilizing bacteria (KSBs), have the potential to solubilize the fixed forms of K through various mechanisms such as acidolysis, complexolysis, chelation, exchange reactions, and production of low-molecular-weight organic and inorganic acids (Meena et al. 2014; Etesami et al. 2017). Inoculation of KSBs on to K-deficient soil has been shown to boost seed germination, growth vigor, and yield effect of various crops (Bakhshandeh et al. 2017; Meena et al. 2014; Xiao et al. 2017). Some of the potential KSBs reported solubilizing K include *Enterobacter hormaechei, Burkholderia sp., Aminobacter sp., Acidithiobacillus ferrooxidans, Pseudomonas sp., Bacillus circulans, Bacillus mucilaginosus*, and *Paenibacillus glucanolyticus* (Singh et al. 2010; Sangeeth et al. 2012; Liu et al. 2012).

Arbuscular mycorrhizal fungi (AMF) have also been reported to indirectly play a key role in K solubilization by releasing H⁺ protons and organic acid anions that increased K absorption and accumulation on the plant shoot and fruits (Dominguez-Nuñez et al. 2016). In maize (Zea mays L.), Glomus mosseae and Rhizophagus intraradices inoculation increased K uptake significantly compared to non-inoculated plants (Wu et al. 2005). Other fungi with K solubilization traits include Aspergillus niger, Aspergillus terreus, and Penicillium sp. (Sangeeth et al. 2012). In addition to K solubilization, they play a key role also in the secretion of low-molecular-weight organic acids that dissolves other nutrients bounded to the soil cations such as phosphates (Meena et al. 2014). The application of microbial K solubilization in smallholder settings should, however, be taken keenly as the process is profoundly affected by soil factors such as pH, clay percentage, oxygen concentration, the type of K-bearing minerals, and the microbial strains used (Sheng 2005; Etesami et al. 2017). Optimal conditions for KSB should be determined before inoculation for farmers to achieve good yields.

11.3.4 Siderophore Production

Siderophores are relatively low-molecular-weight complexes, iron-specific chelating molecules whose presence is highly dependent on the amount of iron (Fe) concentration in the soil (Mohammadi 2012). Siderophores are produced by specific strategy II plants and soil microorganisms, which play a key role in transporting iron molecules (Novo et al. 2018). Rhizospheric iron deficiency in smallholder production systems presents a great challenge, especially in parts of SSA with the calcareous type of soils. Its limitation causes leaf chlorosis, reduced photosynthesis, and stunted plant growth leading to reduced crop yields (Lewis et al. 2019). In most of the cases, under aerobic soil conditions, iron is compounded in the form of Fe³⁺ ions and oxy-hydroxides, making them unavailable for plants and microbes that readily utilize the Fe²⁺ forms (Pahari and Mishra 2017). Iron starvation in the soil triggers a specific group of bacteria, fungi, actinomycetes, and algae to synthesize and secrete ferric ion-specific chelating biomolecules.

biomolecules not only improve the colonization of the microbes on the plant rhizosphere but also stimulate antagonistic reactions against phytopathogens and the acquisition of iron nutrients by the plant (Novo et al. 2018). Siderophores such as salicylate, hydroxamate, carboxylate, and catecholate are produced by bacteria, including Salmonella sp., Vibrio anguillarum, Aerobacter aerogenes, Yersinia sp., Aeromonas sp., Enterobacter sp., and Escherichia coli. Fungal species with siderophore-producing traits include Penicillium citrinum. Penicillium chrysogenum, Ustilago sphaerogina, Ustilago maydis, Rhizopus sp., Rhodotorula minuta, Mucor sp., Trametes versicolor, Aspergillus versicolor, Aspergillus fumigatus, and Aspergillus nidulans, while actinomycetes include Streptomyces griseus, Nocardia asteroides, and Actinomadura madurae (Ahmed and Holmström 2014; Kannahi and Senbagam 2014). Precaution has to be taken while selecting siderophore-based microbial inoculants as some of the human pathogenic microbes have this capacity, which may lead to hazardous effects.

11.3.5 Microbial Secretion of Stimulatory Phytohormones

Crops are constantly exposed to environmental stresses such as salinity, drought, heavy metal contamination, floods, extreme temperature, and radiations that are detrimental to their growth, development, and productivity (Goswami and Deka 2020). Biotic stress caused by pathogenic soil microorganisms, toxic root exudates secreted by higher plants, and toxins released from animals will reduce plant productivity (Gouda et al. 2018). Smallholder farming systems, often faced with a wide range of challenges which include but not limited to financial constraints, are highly exposed to the adverse effects brought by these abiotic and biotic stresses. Thus, there is a need for self-sustaining exogenous biochemical techniques that not only mitigate stress responses but also regulate plant hormonal and nutritional balance and induce systemic tolerance (Egamberdieva et al. 2017). Soil harbors a diverse pool of beneficial hormone-producing microorganisms that colonizes the plant roots where signaling and exchange of nutrients occur. Microorganisms in the nutrient-rich rhizosphere synthesize active biomolecules such as auxins, gibberellins, cytokinin, abscisic acid, antifungal compounds, degrading enzymes, and other beneficial solute metabolites that promotes plant growth, nutrition, stress tolerance, and resistance (Ahemad and Kibret 2014).

Many free-living, endophytic, and symbiotic root-associated microorganisms have been identified or engineered to produce phytohormones that alleviate plants against specific stresses. For instance, Acinetobacter, Marinobacterium, Pseudomonas, Bacillus, Sinorhizobium, Pantoea, and Rhizobium isolated from halophytic weed *Psoralea corylifolia* L. were shown to produce IAA (indoleacetic acid) auxins that enhanced wheat seed germination (Sorty et al. 2016). A review by Gouda et al. (2018)noted that Pseudomonas aeruginosa, Pseudomonas putida, Stenotrophomonas maltophilia, Mesorhizobium cicero, Azotobacter chroococcum, Klebsiella oxytoca, Enterobacter asburiae, and Rhizobium leguminosarum secrete gibberellin, kinetin, auxin, and ethylene phytohormones linked to plant root

invigoration. Likewise, phytohormones promoting shoot invigoration have been associated with PGPRs, including *Pantoea agglomerans, Bacillus subtilis, Pseudo-monas fluorescens, Rhizobium leguminosarum, Paenibacillus polymyxa,* and *Rhodospirillum rubrum* (Prathap and Ranjitha 2015). Actinomycetes and fungi such as *Streptomyces, Nocardia, Spirillospora, Micromonospora, Microbispora, Nocardiopsis,* and *Aspergillus* have been isolated in mandarin and other medicinal plants and produce IAA phytohormones (Ruanpanun et al. 2010; Shutsrirung et al. 2013; Lin and Xu 2013). The introduction of microbial inoculants with the capability to regulate plant hormone production could be a critical step to revolutionize smallholder crop production systems and improve crop qualities. However, caution has to be taken when applying the phytohormone-inducing microbes as studies have shown that the biosynthesis of phytohormones differs depending on the microbial strain, environmental stress levels, and host genotype (Egamberdieva et al. 2017).

11.3.6 Use of Plant Growth-Promoting Rhizobacteria (PGPRs) in Stress Management

The most common stressful conditions affecting crops include drought (water stress), heat, salinity, floods, and metal toxicity (Egamberdieva et al. 2017). Under stress conditions, plants increase the production of reactive oxygen (ROs) species and OH^- radicals causing an oxidative stress condition that damages membrane lipids, proteins, nucleic acids, and photosynthetic pigments, leading to a progressive plant physiological system shutdown (Foyer et al. 2016). Beneficial microorganisms play an active role in stress management against biotic and abiotic agents to induce stress tolerance or resistance (Table 11.1). Extreme temperature, drought, floods, salinity, and wind can result in up to 70% yield losses and, therefore, could threaten smallholder farmers' food security status. Tolerance to these stresses could be induced by exogenous application of PGPRs that stimulates the accumulation of osmolytes critical in maintaining the plant cellular integrity such as proline, trehalose, glycine betaine, enzymatic and nonenzymatic antioxidants, abscisic acid, superoxide dismutase, glutathione, ascorbate peroxidase, and ascorbic acid (Agami et al. 2016; Gouda et al. 2018).

Heavy metal pollution is a common phenomenon in agricultural fields located close to the mining zones. In phytoremediation studies by Baharlouei et al. (2011) on canola and barley plants and Dourado et al. (2013) on tomatoes, it was reported that Cadmium (Cd) soil contamination can be alleviated by PGPRs such as *Pseudomonas fluorescens*, *Pseudomonas putida*, and *Burkholderia* sp. SCMS54 due to their ability to scavenge and translocate Cd²⁺ from the soil. Islam et al. (2016) similarly showed that chromium (Cr) toxicity that could significantly affect maize production could be stabilized using PGPR *Proteus mirabilis* isolates T2Cr and CrP450. There has also been a strong link reported between the presence of PGPRs and drought tolerance (Ngumbi and Kloepper 2016), PGPRs, and salinity stress (Cardinale et al. 2015; Habib et al. 2016). Some of the actively used PGPRs against salinity stress in wheat, maize, and barley include *Ensifer garamanticus* E110, *Curtobacterium*

Microorganisms	Plant	Stress type	Plant changes	Reference
Bacillus methylotrophicus SMT38, Bacillus aryabhattai SMT48, Bacillus aryabhattai SMT50, and Bacillus licheniformis SMT51	Spartina maritima	Heavy metal pollution	Reduced respiration of the roots and oxidative stress	Mesa- Marín et al. (2018)
Bacillus cereus and Pseudomonas moraviensis	Wheat	Heavy metal pollution	Decreased biological accumulation coefficient and translocation factor	Hassan et al. (2017)
Funneliformis mosseae (Fm) and F. caledonium	Sunflower (Helianthus annuus L.)	Heavy metal pollution	Reduced heavy metal concentration in the shoots	Zhang et al. (2018)
Mixed culture of AMF was used which mainly comprised of <i>Funneliformis</i> species	Maize (Zea mays L.)	High temperature	Regulation of photosystem II heterogeneity	Mathur and Jajoo (2020)
Bacillus safensis and Ochrobactrum pseudogrignonense	Wheat (<i>Triticum</i> <i>aestivum</i> L.)	High temperature	Antioxidant signaling and reducing chloroplast and membrane injury	Sarkar et al. (2018)
Funneliformis mosseae and Paraburkholderia graminis C4D1M	Tomato (<i>Solanum</i> <i>lycopersicum</i> L.)	Chilling stress	Increasing the efficiency of photosystem II, reduced cell membrane injuries	Caradonia et al. (2019)
Funneliformis mosseae and Rhizophagus intraradices	Tomato (Solanum lycopersicum)	Water stress	Enhanced water use efficiency, net photosynthetic rate	Chitarra et al. (2016)
<i>Bacillus megaterium</i> and <i>Enterobacter</i> sp.	Okra (Abelmoschus esculentus L.)	Salinity	Reactive oxygen species scavenging enzymes	Habib et al. (2016)
Rhizophagus irregularis and Funneliformis mosseae	Durum wheat (<i>Triticum</i> <i>durum</i> Desf.)	Salinity	Greater stability of plasma membranes	Fileccia et al. (2017)
Pseudomonas fluorescens, Enterobacter hormaechei, and pseudomonas migulae	Foxtail millet (<i>Setaria</i> <i>italica</i> L.)	Drought	Stimulated seed germination and seedling growth	Niu et al. (2018)
Indigenous arbuscular mycorrhizal fungi	Leymus chinensis and Hemarthria altissima grasses	Drought	Altering antioxidant enzyme activities and photosynthesis	Li et al. (2019)

Table 11.1 Overview of ways through which beneficial microorganisms promote plant growth of various plants under stress conditions

flaccumfaciens E108 (Cardinale et al. 2015), *Bacillus licheniformis, Bacillus subtilis, Arthrobacter* sp. (Upadhyay et al. 2012), *Enterobacter* sp. (Sorty et al. 2016), and *Pseudomonas* sp. (Mishra et al. 2017).

11.3.7 Biological Control

The use of microorganisms antagonistic to plant pathogens has revolutionized agriculture and could be considered as a modern substitute for the environment-insensitive chemical pesticides (Raimi et al. 2017). This remains one of the innovative ways of the twenty-first century in which smallholder farmers can sustainably control plant pathogens. For example, inoculation of crops with formulations containing PGPRs that colonize the rhizosphere and act against phytopathogens through competition for resources, niche exclusion, and induction of plant systemic resistance has been demonstrated (Fukami et al. 2018). Among the PGPRs, Bacillus sp. and Pseudomonas sp. are the most studied and mainly effective biocontrol agents that have been commercially produced over the past decades. They produce antagonistic secondary metabolites (antibiotics) that act against a wide range of pathogens and, most importantly, the biomolecules which are biodegradable, unlike the case of many agrochemicals (Wang et al. 2015).

Pseudomonas sp., for instance, produces antimycotics (pyrrolnitrin, 2.4-diacetylphloroglucinol, ecomycins B and C, oomycin A, visconamide, phenazine-1-carboxamide, phenazines, rhamnolipids, sulfonamides, pyocyanin, and butyrolactones), antitumor agents such as cepafungins, and antiviral agents such as Karalicine (Ramadan et al. 2016). Similarly, Bacillus sp. produces antimycotics and active antibacterial molecules that are mainly derived from non-ribosomal and ribosomal sources. These include subtilosin A, mycobacillin, difficidin, bacillaene, chlorotetain, and rhizocticin, surfactin, bacillomycin, and iturin molecules (Wang et al. 2015; Gouda et al. 2018). Trichoderma sp., a fungal biocontrol agent, has been of great importance in the crop protection industry. Trichoderma viride and Trichoderma harzianum species have been demonstrated to effectively control Fusarium graminearum pathogen that causes Fusarium head blight in wheat (Triticum aestivum L.) (Panwar et al. 2014). Spraying of non-aflatoxigenic Aspergillus flavus on the reproductive structures of Zea mays L. cobs could reduce the levels of aflatoxin contamination (Lyn et al. 2009). Entomopathogenic fungi, Beauveria bassiana GHA, and Metarhizium brunneum strains have been effectively used to control soybean aphids (Clifton et al. 2018). Despite the success, up to date, a broadspectrum biocontrol agent that is more efficient and persistent remains a challenge. In addition, the efficacy of antifungal agents greatly varies and is determined mainly by the moisture content, number of applications, and target stage of the pest.

Rhizobium etli, a nitrogen-fixing symbiotic bacteria, have been shown to have antagonistic properties against soil nematodes by activating ethylene and jasmonic acid biochemical pathways that induce resistance against root-knot nematode in tomatoes (Martinuz et al. 2012). Enzyme-secreting bacteria that hydrolyze proteins, cellulose, chitin, and hemicellulose of phytopathogens could be used as biocontrol

agents to suppress plant diseases. Bacteria bearing such important traits should be able to colonize the target niche of the plant for an effective pathogen suppression to be achieved. A lot of bacteria, including *Lysobacter* sp. and *Myxobacteria* sp., produce chitinases, glucanases, proteases, cellulases, and lytic enzymes that effectively hydrolyze the fungal cell wall components. These bacteria can be utilized by farmers to suppress the incidence of diseases caused by *Rhizoctonia*, *Pythium*, and *Sclerotium* species (Saraf et al. 2014).

11.3.8 Microbial Inoculants, Yield Quality, and Human Health

In the developed world, microbes have been used extensively by farmers to boost soil health, plant growth, and productivity and to strengthen the plant's resilience and adaptability to the constantly changing climatic conditions. Indeed, especially in organic and low-input agricultural setups, microbial inoculants have positively impacted on agriculture and well-being of the farmers (Alori and Babalola 2018). The African continent is known for its biodiversity, and her soil harbors a wide range of soil microorganisms (bacteria and fungi) that are beneficial. Proper utilization of its rich biodiversity could revolutionize the deteriorating African agriculture, which is mainly characterized by resource-constrained smallholder farming systems (Grönemeyer and Reinhold-Hurek 2018).

Unlike in other regions with developing economies such as Asia, the issue of adopting green energy sources to address low soil fertility, malnutrition, and food insecurity remains underutilized in sub-Saharan Africa. Various initiatives, which have been undertaken to address this challenge, including the establishment of projects like N2Africa, AgBiome, and UNESCO-MIRCEN, among others, that incorporate different groups of stakeholders. To ensure the success in adopting technologies developed from soil microorganisms, participatory field-based experiments for demonstrations should be conducted in strategic locations where farmers can access as this will benefit and empower the local communities. In most cases, experienced researchers, universities, funding agencies, private commercial companies, and African farmers collectively steer the exploration, identification, field testing, evaluation, and adoption of microbial inoculants and ensure their sustainability for farmers' use.

Previous studies have also shown that adaptation of the microbes to the local soil and environmental conditions is a huge factor to consider when exploring beneficial microbial inoculants because they are better adapted to the ecological conditions (Ouma et al. 2016; Koskey et al. 2017). Grönemeyer and Reinhold-Hurek (2018) reported a hidden high diversity of *Bradyrhizobium* species, with exceptionally heattolerant traits, that form a symbiotic partnership with legume pulses such as soybean (*Glycine max* L. Merrill), peanut (*Arachis hypogaea* L.), cowpea (*Vigna unguiculata* L.), and bambara groundnut (*Vigna subterranean* L.) commonly grown by smallholder farmers in SSA. These types of microbes can be utilized in most parts of the SSA, where heat is the primary ecological stress for the crops. Modern breeding methods have greatly affected scaling up food production in the SSA



Fig. 11.2 A smallholder farm in Embu County, Kenya, showing healthy and high-yielding cowpea crop following inoculation with effective indigenous rhizobia isolates. Indigenous rhizobia isolates are cheaper and more adapted to the local agroclimatic conditions and develop positive microbial interactions with existing soil microflora compared to exotic commercial isolates

region. In Nigeria, the development and introduction of promiscuous soybeans, by the IITA, that form symbiotic association with diverse *Bradyrhizobium* strains has been an eye-opener to many smallholder farmers (Gabasawa 2020). In addition, Oruru et al. (2018) have shown the benefits of using modern cowpea (*Vigna unguiculata* L.) cultivars in Kenya in enhancing AMF root colonization, NPK uptake, and growth compared to the wild-type cultivars (Fig. 11.2).

Other co-inoculation studies have also shown the importance of soil biodiversity in managing the depleted soil nutrients. N'cho et al. (2013) demonstrated that co-inoculation of *Bradyrhizobium* spp. (RACA6), *Trichoderma harzianum* (Eco-T), and AMF (Rhizatech) with the commercial Agrolyser and Agroleaf foliar fertilizers increased soybean nodulation, shoot P, and grain yields significantly. Under intense water stress, Musyoka et al. (2020) demonstrated through a greenhouse experiment that a consortium of AMF isolates *Glomus etunicatum*, *Rhizophagus irregularis, Glomus aggregatum*, and *Funneliformis mosseae* could increase green grams' (*Vigna radiata* L. Wildzek) shoot and root biomass and P uptake compared to the *Bradyrhizobium* inoculants and uninoculated controls. However, some studies suggest that functional identity could be more important under specific situations, mainly when using selective microbial inoculants that colonize specific crop genotypes. For instance, a study by Njeru et al. (2017) clearly demonstrated that functional identity of individual AMF isolates *Funneliformis mosseae* IMA1 and *Rhizoglomus intraradices* IMA6 could play a more significant role than their compounded diversity in enhancing AMF root colonization and fresh weight of marketable tomato fruits in specific tomato genotypes.

It wasn't until the mid-1990s that AMF was discovered to harbor mycorrhizospheric helper (MH) endobacteria that synergistically interact with the AMF and are reportedly known to associate with the spores, plant roots, and hyphae, thus extending the hyphae-absorbing network (Bianciotto et al. 1996). The MH bacteria are affiliated with Pseudomonales, Burkholderiales, Bacillales, Rhizobiales, and Actinomycetales, which are known for their beneficial plant growth-promoting traits. Further, these MH bacteria were discovered to take part in the establishment of plant-AMF symbiosis and promote spore germination, hyphal growth, and root colonization (Agnolucci et al. 2015; Giovannini et al. 2020). The multiple beneficial traits of AMF and their associated endo-bacteria could be efficiently exploited in smallholder food production through further research on the best effective combinations that can work well in the context of ecological conditions of the SSA. However, their cost of production has to be drastically reduced for the farmers to access cheap, high-quality, and well-packaged microbial products for their farm use.

11.4 Enhancing Healthy Plant-Microbe Interactions in Smallholder Agroecosystems

To achieve a sustainable food production for the growing population, amid the rising cases of climatic instability in SSA, more attention should be given to the innovations that promote self-sustainability of the natural ecosystems and those that advocate for agricultural biodiversity at genetic, species, and habitat management levels (Costanzo and Bàrberi 2014). Soil fertility restoration through mycorrhiza, BNF, and PGPRs aided symbiosis processes that is a complex phenomenon and does not always result in significant improvement in soil quality. This is true in the context of SSA where the soils are exposed continuously to various mechanisms that minimize the benefits that could be gained via the interactions (Raimi et al. 2017). Indigenous AMF, which are beneficial to plants and soil in increasing P solubilization, nutrient availability, carbon sequestration, soil aggregation, and plant stress resistance, do require appropriate agronomic management practices for their maximum contribution to be realized (Giovannetti et al. 2004; Avio et al. 2006). Some of the commonly used agricultural practices that support plant-soil-microbial tripartite interactions include reduced physical soil disturbance (minimum or no-tillage), continuous and rotational cropping, organic amendments, intercropping, cover cropping, use of microbial inoculants, and balanced nutrient management (Njeru 2013). The idea of promoting the presence of high microbial diversity in agricultural soil is to ensure that critical soil functions are carried out by different groups of soil microorganisms at a particular time when other redundant groups are unable or unavailable due to the drastic change in climatic or physical conditions (Mburu et al. 2016). In this way, a highly diverse microbial community offers the much-needed insurance to the farmers that the soil processes that maintain and support plant growth under changing environmental conditions are performed. Long-term experiments on frequent tillage against minimum or no-tillage have been carried out, and results indicated that reduced tillage leads to increased bacterial and fungal biomass, which are the main drivers of natural ecosystems (Frey et al. 1999; Marzaioli et al. 2010). Intensive cultivation, which is often practiced by smallholder farmers in the SSA region, has been shown to lead to soil organic matter depletion progressively, higher CN ratio, reduced biodiversity, and microbial functionality, which consequently lead to reduced crop performance (Ventorino et al. 2012).

Continuous cropping has been shown to add more organic carbon to the soil and maintains obligate beneficial soil microorganisms such as AMF that would not survive without a living host (Hontoria et al. 2019). Crop rotation, on the other hand, has been studied, and results indicate that it plays a critical role in maintaining higher biodiversity. However, it does not always hold that the higher the aboveground plant diversity, the better the soil microbial diversity. It depends on other factors like the plant genotype used during the rotation. The inclusion of legume cover crops, cultivar mixtures, and other mycotrophic crops highly encourages the colonization of symbiotic N-fixing bacteria and P-solubilizing AMF fungi (Njeru et al. 2015; Lazzaro et al. 2018). Therefore, farmers should have some knowledge of the crop types they choose to have a better structured and functional microbial diversity that will aid crop production. The addition of organic amendments helps to sustain high energy demanding soil processes like microbial degradation and nutrient recycling, maintains nutrient and water retention, stabilizes soil structure, and creates a favorable resource-rich microhabitat for plants and other microbial dependents (García-Orenes et al. 2013; Nyamwange et al. 2018). None of the opportunities, as mentioned above, would succeed without the farmers' knowledge. The local knowledge of the farmer is essential for the adoption of modern innovations and agricultural practices. Therefore, unlocking the power of the smallholder farmers' understanding of modern agronomic management practices that promote microbial functions, improves soil fertility and crop productivity and could revolutionize the agricultural sector in many parts of the world.

11.5 Towards the Development of Effective Microbial Inocula

Microbial inoculants carrying beneficial microorganisms have been widely adopted in organic and low-input agricultural systems because of their ability to deliver target microorganisms into the root rhizosphere. For instance, after AMF inoculation, AMF interacts with the plant host-symbiont and develops extra-radical mycelia that colonizes the rhizosphere, solubilizes nutrients, and interacts with other rhizospheric microorganisms and plants (Avio et al. 2006). Ideally, the generation of microbial inoculants starts with the identification of microorganisms with the target trait-effect, which are then grown as lab cultures, followed by lab or greenhouse testing on target plants for their efficacy. The promising microbial candidates are then tried under natural field conditions (Ouma et al. 2016). For effective inoculation and plant growth to be achieved, several factors need to be considered, including mode of delivery, colonization ability, and efficacy. Colonization ability refers to the strength of the microorganism to rapidly and extensively colonize the root and its surroundings. At the same time, efficacy is determined by the symbiotic performance of the microbe on the plant host in enhancing plant growth, development, and nutrition (Giovannini et al. 2020).

A right microbial culture for use in agricultural inoculation should depict a high colonization ability and should compete with other existing native microbial populations in the soil. There are external factors that could affect the colonization ability of the inoculant, which include soil pH, salinity, and environmental conditions such as water stress, heat, and radiations. Inoculants should, therefore, be prepared from the native microbial strains that have adapted to the local climatic and soil conditions over a long time. It is also vital for commercial companies to prepare formulations with known shelf lives as this could critically determine the number of viable microbial cells after inoculation. Some microbial products are incompatible with other commonly used agricultural inputs, hence the need for proper labeling and declaration by the manufacturers.

For maximum efficacy to be achieved, microorganisms must overcome the soil barriers and competition from the resident microbiota and establish large, active, and functional populations that would confer an observable effect on soil health and crop productivity (Lewis et al. 2019). Thus, understanding the physiology and growth requirements of a specific microbial inoculant strain is essential to enhance the growth efficiency, functionality, and stability of the inoculant strain. Nowadays, formulations are available either in liquid or solid form depending on the manufacturer's choice, market demands, and storage. Overcoming desiccation and temperature stresses is mostly considered while choosing the type of microbial formulations to be used in preparing inoculants targeting seed dressing.

Seed companies have introduced "custom inoculation" where seeds are inoculated with specific microbial inoculant strains only on farmers' demands after sale and "pre-inoculation" where seeds are inoculated prior to sale (Deaker et al. 2012). These two approaches relieve the farmer from the hustle of inoculation of seeds on-farm however; there is some extra cost that the farmer needs to incur. Remarkably, the need to bioprospect for better and effective microbial inoculants has led to the production of broad-spectrum combinations of elite strains unlike in the past where first companies produced inoculants with only one or two specific microbial strains (Santos et al. 2019). The idea is supported by targeting a combination of different strains that can carry out different microbial processes efficiently and ultimately produce higher yields. Co-inoculation of seeds with BNF-associated microbes phytohormone (Rhizobium sp.), producers (Pseudomonas sp., Azospirillum sp.), P solubilizers (Bacillus sp.), and biocontrol agents (Trichoderma sp., Bacillus sp.) is commonly used by the SSA farmers (Trabelsi and Mhamdi 2013). With the increasing concerns about the changing climates evident by prolonged droughts, frequent heat waves, flooding, and extreme temperatures, the

performance of the currently available microbial inoculants may not be guaranteed. It is, therefore, mandatory to do further research on inoculants that are well adapted to the current and incoming stressful conditions.

11.6 The Role of Microorganisms in Supporting the Resilience of Smallholder Agriculture Systems

The agricultural productivity of the African smallholder systems is gradually declining owing to soil impoverishment instigated by the changing climatic conditions and insufficient adoption of modern sustainable farming technologies (Ngetich et al. 2012). The decreasing soil fertility is further exacerbated by the high decomposition rates of organic matter, rapid soil weathering conditions, high soil acidity, excessive leaching, and intensive cultivation practices (Mukhongo et al. 2016). The appropriate and consistent use of bio-inoculants could offer farmers various biological and agronomic benefits, including nutrient solubilization and uptake, growth stimulation, yield increase, cost reduction, soil health, and fertility restoration (Masso et al. 2015). Therefore, the role played by microbial inoculants is critical in revolutionizing smallholder agricultural systems, maintaining the soil nutrient balance, and crop productivity.

Recently, the use and adoption of effective microbial bio-inoculants such as AMF, rhizobial, and phosphatic inoculants in SSA have slightly increased among smallholder farmers, although the increase is much lower compared to that of other regions of the world (Raimi et al. 2017). Commercial companies such as Dudutech Ltd. in Kenya and Mycoroot Pty Ltd. in South Africa have increased their AMF production due to the increasing demand by the smallholder farmers in their respective regions (Mukhongo et al. 2016). It is estimated that the global market for bio-inoculants could increase progressively at a rate of 12.5% per annum, and by the year 2025, its global value would have reached the US \$4092 million, up from the US \$1254 million in 2016 (Transparency Market Research 2017). The cost of peat-based rhizobia fertilizers for white clover and faba beans ranges from US \$0.25 to 6.5 ha^{-1} , and this could fit the constrained budget of the smallholder farmers. Comparably, these prices are far much below the cost of mineral N fertilizers that could be needed to supply the same quantity of nutrients (Raimi et al. 2017).

The profitability benefits of using bio-inoculants are primarily based on the amount of nutrient fixed/solubilized and/or yields. For instance, in Ghana, Masso et al. (2016) used Legumefix, a rhizobia-based bio-inoculant, to grow soybean and common beans and found that farmers could profit from the inoculation with a net value-cost ratio of >3 when compared to uninoculated control. Nitrogen-fixing rhizobia bio-inoculants increase legume yield, a factor considered by the majority of smallholder farmers. According to a review by Ngetich et al. (2012), legumes through the BNF process can naturally contribute about 48–300 kg of N/ha in a season, and this amount could significantly increase if legumes are inoculated with effective bio-inoculants. Soybean *Bradyrhizobium* inoculants increased soil organic matter and yield and fixed about 80% of the total soybean N requirements in

smallholder farm settings in Southern Africa (Kasasa et al. 1999). In West Africa, Osunde et al. (2003) demonstrated that about 54% (the equivalent of 78 kg N/ha) of the total N requirement is fixed by inoculated soybean, and farmers could minimize the supply of external inputs required for subsequent cereal cropping systems. Similarly, in the rice experiment conducted by Rose et al. (2014) using a farmer participatory approach, bio-inoculants were reported to ease the chemical N fertilizer supply by about 52% without significant yield loss. As an alternative source of inorganic N fertilizer, Gebre and Lelago (2017) showed that cyanobacteria bio-fertilizer could be used to reclaim the nutrient-poor alkaline soils, improve soil resilience, and increase yields of kales in Eastern Africa. Bio-inoculants with specific strains of *Bacillus* and *Pseudomonas*, which produce hydrolytic phosphatase enzymes that mineralize organic P, can save African smallholder farmers by adding up to 30-50 kg/ha of P₂O₅ fertilizers (Richardson and Simpson 2011).

Most parts of the SSA are arid and semiarid areas, characterized by long drought seasons that expose plants to frequent water and salinity stresses (Falkenmark and Rockström 2008). Smallholder farmers would benefit from using bio-fertilizers that contain microorganisms that would increase plant tolerance to salinity and water stress. Inoculation of plants with auxin-, cytokinin-, and gibberellin-producing microbes has been reported to improve plant tolerance to water stress and reduce the risk of yield losses significantly (Goswami and Deka 2020). Gururani et al. (2013) observed an increased tolerance to salt and water stress in potatoes inoculated with *Bacillus* spp. That stimulates the production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase. Likewise, plant-mycorrhizal symbiotic relationships can be exploited to enhance root development, moisture, and P uptake, thus ensuring agricultural resilience and productivity under water stress and low soil P conditions (Oruru and Njeru 2016; Musyoka et al. 2020). According to Masso et al. (2016) and Raimi et al. (2017), smallholder farmers in drought-prone areas of the SSA could get more yield benefits by inoculating sweet potato, maize, and rice with effective AMF strains. The extensive hyphal network of AMF reduces localized competition for limited water and nutrients, thus supporting plant biodiversity and maintaining the sustainability of the agricultural ecosystems (Mukhongo et al. 2016).

Bacterial and fungal diseases often cause substantial yield losses in African smallholder production systems, and using low-cost bio-inoculants that produce antimycotic and antibacterial substances could assist in suppressing the associated crop losses (Strange and Scott 2005). In Kenya, Masso et al. (2016) demonstrated that *Trichoderma* inoculants could control late blight disease in tomatoes much better (p < 0.05) than the commercial pesticide Ridomil that is commonly used by the farmers. Similarly, other cost-effective inoculants containing *Bacillus* spp., *Pseudomonas fluorescens*, and *Sinorhizobium* spp. can be used in controlling *Fusarium* wilt in pigeon pea, bacterial soft rot in potato, and *Rhizoctonia solani* infections in pepper (Kumar et al. 2010). Co-inoculation of AMF and rhizobia not only increases NPK availability and uptake (Tairo and Ndakidemi 2014) but also enriches the soil with trace minerals such as calcium (Ca), iron (Fe), sulfur (S), zinc (Zn), copper (Cu), and manganese (Mn) that are not often externally supplied by the smallholder farmers (Bambara and Ndakidemi 2010). Furthermore, AMF are known

to suppress soilborne pathogens, and this offers crop protection services to the farmers and reduces the overdependence of nonselective pesticides that are harmful to other beneficial soil microbiota (Mukhongo et al. 2016).

11.7 Conclusion

Notwithstanding the plausible contribution of beneficial microbial communities in smallholder agriculture, their adoption and conservation have remained significantly low across many developing nations. Among the various reasons for this is inadequate training and research on beneficial microorganisms in smallholder farms. Therefore, there is a need for the formulation of policies and subsidy programs on bio-fertilizers and biopesticides, besides investment in research and development. Furthermore, a more holistic approach including laboratory, greenhouse, and field experiments established through participatory research and used for on-farm assessment of low-cost microbial inocula is imperative, since some promising microorganisms may not necessarily harbor favorable survival characteristics in the field (Parnell et al. 2016). It is envisaged that the effective, low-cost inocula would be widely adopted by farmers and used to promote sustainable food production, cash generation, and resilience of smallholder agroecosystems to changing climate.

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