Chapter 6
Arbuscular Mycorrhizal Fungi: A Next-Generation Biofertilizer for Sustainable Agriculture

Arti Sharma, Neelam P. Negi, Parul Narwal, Punam Kumari, and Deepak Kumar

Abstract Climate change has a significant impact on environmental conditions, which affects the growth and productivity of plants. As a result, sustainable crop production continues to be a major global challenge, attracting increasing attention from the scientific community in order to feed the world's growing population while reducing the use of conventional chemical fertilizers and pesticides. Arbuscular mycorrhizal fungi (AMF) are widely used to build symbiotic relationships with over 80% of the species of the land, including most of the cultivated plants. These fungi are of great interest because of their biofertilizer potential (microbial inoculants) in low-input and organic agriculture, which represents an adequate alternative tool for chemical fertilizers. Using AMF as biofertilizer enables plants to use mineral elements such as nitrogen and phosphorous effectively. In addition to an improvement in plant nutrition, AMF plays an important role in improving soil structure, fertility and heavy metal remediation. In conclusion, AMF can be used as a potential biofertilizer for control of environmental stress and may open new strategies to support agriculture and increase global food safety.

A. Sharma
University Institute of Biotechnology, Chandigarh University, Mohali, India

Department of Biotechnology, Guru Nanak College, Muktsar, India

N. P. Negi · P. Narwal
University Institute of Biotechnology, Chandigarh University, Mohali, India

P. Kumari
Department of Biosciences and Biotechnology, Fakir Mohan University, Balasore, Odisha, India

D. Kumar (✉)
Department of Botany, Institute of Science, Banaras Hindu University, Varanasi, Uttar Pradesh, India
e-mail: deepakkumar@bhu.ac.in

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6.1 Introduction

Food production needs to be doubled by 2050 in order to meet the demands of a growing population. The rising costs and adverse effects of chemical fertilizers on the environment and human health have pushed the agrarian community to look for substitutes for these chemical fertilizers (Srivastava et al. 2018). Biofertilizers are suitable alternatives to artificially synthesized fertilizers as they are less harmful to the environment, improve soil health and promote the quality and quantity of crop yield (Suhag 2016). Biofertilizers are "microbial inoculants" that allow effective intake of mineral elements such as nitrogen and phosphorus and enhance drought tolerance, salt tolerance and improve plant health (Alori et al. 2017; Igiehon and Olubukola 2017). Most farmers in the world widely use living organisms like bacteria, fungi and cyanobacteria etc. as biofertilizers that are inoculated with seed or in soil to colonize the rhizosphere to increase the availability of nutrients (Sadhana 2014). The use of symbiotic mycorrhizal fungi, particularly arbuscular mycorrhizal fungi (AMF), as biofertilizer has been adopted in agriculture systems because of their potential for improving soil quality, water stress tolerance, altering root architecture and pathogen resistance (Abbot and Robson 1991). The mycorrhiza is an obligatory symbiotic association between fungi and the roots of higher plants (Sieverding 1995). The German Forest pathologist Frank invented the name mycorrhiza in 1885, which comes from two terms, the Greek word "mycos" meaning fungus, and the Latin word "rhiza" referring to fungal roots (Frank 1885). The AMF are ubiquitous endomycorrhiza that can inhabit a variety of ecosystems and form symbiotic association with roots of angiosperms and other plants (Gerdemann 1968) with more than 80% of land plant species including crops (Wang and Qiu 2006). AMF also gives protection against abiotic stress (Auge 2001; Javaid 2007) and biotic stress to their host plants (Khaosaad et al. 2007). Mycorrhiza also increase the fixation of nitrogen in nodule plants. Plants which receive good nutrition can withstand infections, and this is one strategy to combat diseases that are transmitted to the soil (Linderman and Davis 2004). The barrier created by Ectomycorrhizae when they cover the exterior surface of the root is the most obvious mechanism for protecting against illnesses (Castellano and Molina 1989). The current chapter focuses on the significance of AMF as biofertilizers for sustainable agriculture, highlighting the importance of AMF and achievements in research related to their agricultural applications.

6.2 Development of Mycorrhizal Network

The AM fungi are classed as a separate phylum termed glomeromycota, which has roughly 150 species with considerable genetic and functional diversity (Smith and Read 2008; Bucking et al. 2012). A study by Hosny et al. (1998) indicates that asexually reproducing fungi have coenocytic hyphae and spores. The mycorrhizal fungi is not strictly a biofertilizer as it does not add mineral nutrition to soil like nitrogen-fixing bacteria but it improves the uptake of soil nutrients through arbuscules and improves plant development and soil health (Garg and Manchanda 2007; Solaiman 2014). An arbuscular is a tiny tree-shaped fungal structure that grows in the intercellular and intracellular regions of roots and is a key site for the exchange of nutrients between the two symbiotic partners (He and Nara 2007). A variety of genes and hormones initiate the symbiotic interaction between plant roots and the fungi. Strigolactones and lipochito-oligosaccharides generated by fungi are important in the development of the association (Mohanta and Bae 2015; Sharma et al. 2021).

The symbiosis is established through a series of morphological and physiological interactions between the two hosts (Amalero et al. 2003). The various developmental stages of the AM colony in the plant roots are as follows.

6.2.1 Pre-symbiotic Stage

AM fungi are obligatory biotrophs; they rely on their autotrophic host to complete their life cycle in a symbiotic association and generate the next generation of spores (Fig. 6.1). Germination of fungal spores in a soil is the only plant-independent phase in the life cycle of mycorrhizal fungi (Bonfante and Bianciotto 1995). The spores germinate and grow into an extended mycelium for 2–3 weeks into extended mycelium, displaying apical dominance. The mycelium growth ceases after 2–4 weeks in the absence of an appropriate host. The presence of host root exudate stimulates intense hyphal growth and branching to increase the probability of contact with host roots (Paszkowski 2006).

6.2.2 Early Symbiotic Phase

Between the fungus and plant root epidermis AMF forms a cell-to-cell contact called appressorium (hypophodium). The formation of appressorium is the first morphological sign of symbiosis. The AM fungi penetrate into the roots of the host plant by penetrating the hyphae emerging from the appressorium. The hyphae successfully penetrates the cell wall using both mechanical and enzymatic catalysed mechanisms (Garcia-Garrido and Ocampo 2002).

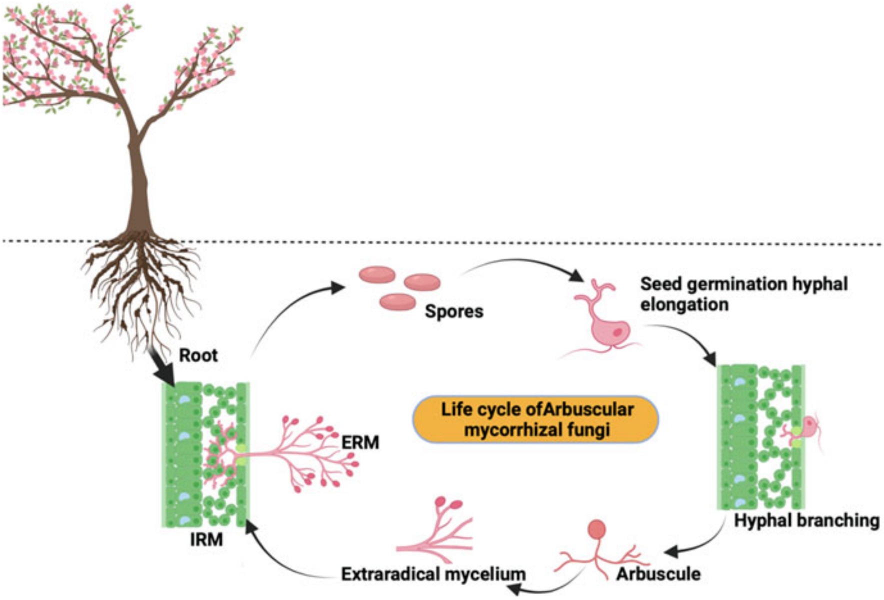

Fig. 6.1 Life cycle of arbuscular mycorrhizal fungi

6.2.3 *Mature Symbiotic Phase*

The mycorrhiza colonizes roots by arbuscule, the tree-like fungal structures formed intracellularly subtended by intercellular hyphae in the cortical region. The structures are key sites for exchange of nutrients between two hosts (Dickson et al. 2007). The periarbuscular membrane (PAM), a key interface for symbiotic interaction, keeps the fungus excluded from host cytoplasm. The exchange of nutrients between the two partners is mediated by membrane transport proteins such as P-type H^+ ATPase and phosphate transport (Bucher 2007).

The AM fungi can make a network of mycelia in plant roots and in the soil. Extraradical mycelium (ERM) grows in the soil (Fig. 6.2). They draw nutrients from the soil and deliver them to the plant's roots. The mycelium formed within the roots is called intraradical mycelium (IRM). The IRM releases nutrients at the interface and absorbs carbon from the plant roots in exchange. The absorbed carbon is utilized for expansion and spore formation by ERM. The spores can initiate colonization of nearby plants (Bucking et al. 2012).

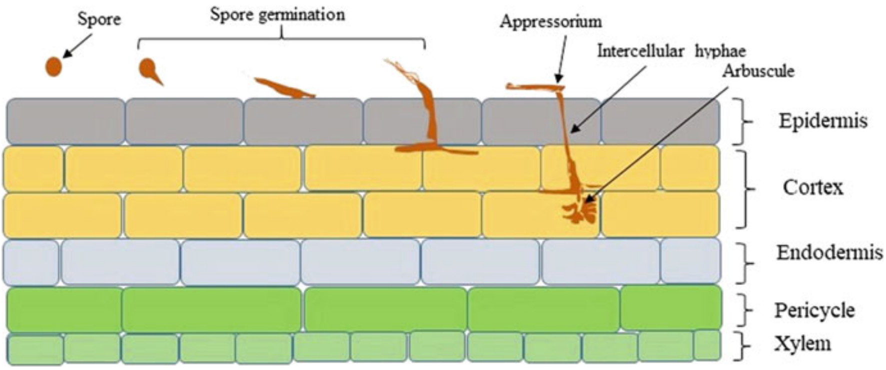

Fig. 6.2 Development of mycorrhizal network

6.3 Arbuscular Fungi as a Potential Biofertilizer

The AM fungi act as an important link between plants and the soil to achieve the goal of sustainable agriculture. They mediate nutrient transfer and therefore contribute to the maintenance of soil structure, soil nutrition and plant nutrition (Gentili and Jumpponen 2006). The high metabolic rate and efficient translocation of micronutrients and macronutrients from soil to plant mediated by fungi improve plant growth and yield in chick pea, custard apple and olive plantlets (Kumar et al. 2002; Briccoli et al. 2015). Fungi can mobilize important nutrients like phosphorus (P), nitrogen (N) and act as a carbon sink in the soil (Bonfante and Genre 2010). As a result, the fungi have the potential to act as biofertilizer for sustainable agriculture (Giri et al. 2019).

6.4 The Role of AMF in Improving Soil Health and Fertility

By enhancing soil nitrogen intake by the plant, fungal hyphae stabilize soil aggregates. Extracellular polysaccharide and glomalin exudates aid in the formation of network hyphae in the soil. The polysaccharide glomalin is the main contributor to soil formation because it promotes the development of organic matter and attachment of the hyphae to the soil (Adetunji et al. 2019). Soil aggregation improves soil health and quality by improving soil porosity, water-holding capacity, gaseous exchange, protecting organic carbon and promoting the growth of beneficial micro-fauna (Srivastava et al. 2018). Several studies show that AMF reduces the harmful impact of heavy metal contamination in soil caused by anthropogenic activities and the usage of agrochemical products (Schützendübel and Polle 2002; Dong et al. 2008). The fungi can absorb calcium, aluminium, cadmium, selenium and arsenic acid (Khan et al. 2000; Al-Agel et al. 2005). It mitigates the effects of these heavy metals by immobilization, adsorption on the hyphal wall. The AMF also causes metal resistance in plants by altering metabolic processes such as phenylpropanoid pathway (Janeeshma and Puthur 2020).

6.4.1 Role of AMF in Plant Nutrition

Many studies have shown that AMF colonizes plant roots containing essential plant nutrients such as nitrogen (N), phosphorus (P), sulphur (S), potassium (K), calcium (Ca), copper (Cu), iron (Fe), and magnesium (Mg), among others. (Marschner and Dell 1994). AMF facilitates dissolution, transportation of immobile nutrients bound to rocks and mineralization of organic matter (Parihar et al. 2019).

6.4.1.1 Phosphorus (P) Absorption

Phosphorus is an essential nutrient for plants but difficult to absorb from soil due to low diffusion rate. Mycorrhizal fungi release an enzyme phosphatase that mobilizes organic P and increases its absorption by plants (Shen et al. 2011; Malla et al. 2004; Nath et al. 2018). Phosphorus deficiency in plants inhibits photosynthesis, respiration and cell division, which subsequently reduces the yield (Baas and Kuiper 1989). A study by Walder et al. (2015) indicates that the symbiotic interaction between the two hosts induces the expression of the Pi transporter in sorghum and flex plants. The fungal hyphae also reduce phosphorus leaching by different mechanisms involving extensive adsorption on the hyphae surface, storage of orthophosphate and polyphosphate in the hyphae and chelation of P with fungi exuded glycoprotein (Parihar et al. 2019).

6.4.1.2 Nitrogen (N) Absorption

The AMF can absorb N in both organic forms as amino acids (Whiteside et al. 2012) and inorganic form as nitrate and ammonium (Govindarajulu et al. 2005). The extraradical mycelium of the fungi absorbs the inorganic forms. In the soil, the hyphae can take ammonium at a lower quantity than the roots (Johansen et al. 1994). Ammonium transporters are found in arbuscules which provide nutrients to the host plant. The AM fungi-inducible nitrate and ammonium transporters have been identified in tomato and soyabean plants that facilitate the absorption of nutrients by the plants (Kobae et al. 2010). Several amino acids such as glycine, cysteine, serine, arginine, aspartic acid, glutamine acids and cysteine etc. are absorbed by the fungi and then converted to ammonium for translocation at the symbiotic interface with the plant (Smith and Smith 2011).

6.4.1.3 Sulphur Absorption

Because of its redox characteristics and capacity to form disulphide bonds between cysteine amino acids, sulphur plays an important role in the biological function of many substances. Although plants absorb inorganic sulphate as their primary source of sulphur, 95% of soil sulphur is bonded in organic molecules. The form is not directly available to plants. The mycorrhizal fungi have sulphur transporters that make the element available to the plants (Giovannetti et al. 2014). The mycorrhizal plants can obtain sulphur from organic sources. Allen and Shachar-Hill (2009) observed 25% more sulphur content in plant roots with mycorrhizal association at moderate sulphur concentration as compared to nonmycorrhizal plant roots.

6.4.1.4 Potassium Absorption

Potassium is considered an important macronutrient for plants responsible for enzyme activation, regulation of stomatal opening and serving as an osmolyte in plant cells (Morgan and Connolly 2013; Kumar et al. 2020). Although potassium is abundant in soil, it is not readily available to plants. The role of AMF in potassium uptake by host plants has received less attention. A study by Jianjian et al. (2019) observed the overexpression of potassium transporter protein in the roots of *Lotus japonicas* plants infected with AMF. Furthermore, AM symbiosis associated with potassium nutrition is correlated to alleviating abiotic stresses including salinity, drought, heavy metals and temperature stress (Berruti et al. 2016).

6.4.2 Role of AMF in Plant Biotic Stress Tolerance

More than 90% of total mycorrhizal roots colonize the fungus in intercellular and intracellular tissues. It is proposed that plants can tolerate the intense mycorrhizal network by suppression of plant defence mechanisms against the AMF (Chen et al. 2018). However, the general disease resistance of the plant is not attenuated. Indeed, plants show increased disease resistance against rhizospheric pathogens, pests and parasitic plants either by secreting repulsive exudates from mycorrhizal roots (Kwak et al. 2018). The AMF provides an effective way to control the biotic stress by improved nutrition and induction of plant defence process called as systemic acquired resistance (SAR). Additionally, plants exhibit fast and strong reactions against pathogens by a phenomenon called priming or induced systemic resistance (IRS) (Conrath et al. 2006). The AMF can directly interfere with plant pathogens either by release of antimicrobial substances or by competing with the pathogens for space and resources (Jacott et al. 2017). AMF-induced alleviated plant defence response against various biotic stress is as follows.

6.4.2.1 AMF and Parasite Tolerance

Plants colonized with AMF increase tolerance against parasitic *Meloidogyne* species of nematode. The AMF competes directly with the nematode for root space and reduces the process of reproduction (Dar and Reshi 2017). A study by López-Ráez et al. (2009) indicates that the AMF inhibit the growth of parasitic plants like *Striga hermonthica* in maize and *Striga* and *Orobanche* in sorghum. Thus, the presence of fungi in plant roots can act as biocontrol agents for sustainable agriculture.

6.4.2.2 AMF and Soil-Borne Pathogens

A number of reports have explained the positive effect of AMF-induced plant tolerance to biotic stress triggered by soil-borne pathogens. The symbiosis suppresses growth of fungi *Fusarium, Macrophomina, Rhizoctonia*, *Verticillum*, and oomycetes like *Pythium* and *Phytophthora* responsible for wilting and root rot disease (Hao et al. 2009; Harrier and Watson 2004; Whipps 2004).

6.4.2.3 AMF and Insects

Rhizophagous insects are a common biotic stress for many plants. Hartley and Gange (2009) explained that the mycorrhiza can strongly influence the insect's growth by enhancing insect resistance of plant, but the effects may vary with the feeding mechanisms and lifestyle of the insects. Additionally, AMF-associated plant defence against insects is closely associated with levels of flavonoids and phenolic compounds in host plants (Wang et al. 2020).

6.4.3 Role in Plant Abiotic Stress Tolerance

The plants confront abiotic stress like drought, salinity, extreme temperature, and heavy metals which show harmful effects on their growth and yield (Kumar et al. 2017; Nath et al. 2017). Abiotic stress can negatively affect plant survival and productivity. Therefore, it can act as a foremost threat to global food security (Kumar and Verma 2018). The AMF improves plants' tolerance to these abiotic stresses by various metabolic and physiological changes in plants (Malhi et al. 2021). The role of AMF to combat various abiotic stresses is as discussed below:

6.4.3.1 AMF and Drought Stress Tolerance

Drought is a condition when water is unavailable to plants for its physiological functions. The environmental condition is also known as water stress (Subramanian and Charest 1998). The fluctuated transpiration rate generates reactive oxygen species (ROS), and consequently accelerates oxidative stress in plants (Auge 2001; Barzana et al. 2012). Mycorrhiza can progress plant development and growth by enhancing root network and thickness, plant biomass and nutrient absorption and transport during drought conditions (Davies et al. 2002). The mycorrhizal inoculation facilitates synthesis of more dense hyphal networks and excretes glumalin which augment more water and nutrients absorption, which in turn improves soil quality (Gholamhoseini et al. 2013).

The AMF symbiosis influences numerous biochemical and physiological processes such as (1) augmented osmotic regulation, (2) enhanced gas exchange, (3) absorption and transport of water and nutrients, and (4) better defence against oxidative stress (Marulanda et al. 2007). A study on *Zea mays* plants colonized with mycorrhiza *Glomus intraradices* reported expression of two aquaporin genes (Gint AQPF1 and Gint AQPF2) in root cortical cells holding arbuscules under drought stress (Moussa and Abdel-Aziz 2008; Li et al. 2013). AMF-mediated enhancement in drought resistance has been demonstrated by (Li et al. 2019) in C3 plant (*Leymus chinensis*) and C4 plant (*Hemarthria altissima*) observed because of alteration in expression of antioxidants enzyme.

6.4.3.2 AMF and Salt Stress Tolerance

Salinity in soil is a prime problem for many plants growing in arid and semiarid regions (Giri et al. 2003; Al-Karaki 2006). The high accumulation of salt in soil decreases aeration and porosity of soil and therefore affects water translocation, which results in drought-like stress (Mahajan and Tuteja 2005). Plants under salt stress show decrease in rate of photosynthesis, reduction in activities of antioxidant enzyme, less stomatal conductance, decreased membrane stability, and low relative water content of the plants (Talaat and Shawky 2012). Salinity also causes oxidative stress in the plant by producing more reactive oxygen species (ROS) (Ahmad et al. 2010). AMF inoculated plants develop strategies to enhance the antioxidant system which protects the plant cells from oxidative damage (Rai et al. 2011). The defence system develops superoxide dismutase (SOD) antioxidant enzyme that converts superoxide molecules to oxygen and hydrogen peroxide (H_2O_2). Besides SOD, catalase (CAT) enzyme clears H_2O_2 by decomposing it to less reactive water and oxygen. These enzymes are continuously generated in the mitochondria, peroxisome and cytoplasm of the plant.

Several research investigations have reported on AMF's efficiency to promote growth, yield and development in plants subjected to salinity stress. AMF is effective for plants' response under different salt concentrations. *Allium sativum* plant inoculated with AMF showed expanded leaf area, more fresh and dry weights under high NaCl concentration (100 mM) as compared to the plant without mycorrhizal association (Borde et al. 2010). A study of Ghazi and Al-Karaki (2001) on tomato plant inoculated with fungi *Glomus mosseae* observed increase in biomass under moderate saline conditions. Under salt stress, AMF-inoculated rice plants preferably absorb more K^+ ion and avoid intake of Na^+ ions compared with control rice plants. The crop showed AMF induced more salt tolerance and crop yield (Mohsin et al. 2020). El-Nashar (2017) observed that the *Antirrhinum majus* plants improved their growth rate, their feed-water potential and their water efficiency. The favourable benefits of AMF association on biological parameters like photosynthetic rate, stomatal conductivity, and leaf water relationships under salt stress have been described by Ait-El-Mokhtar et al. (2019).

6.4.3.3 Heavy Metal Tolerance

Heavy metals like Cu, Co, Fe, Mn, and Zn are essential for plant growth. However, increased concentrations of these metals are hazardous to the plants due to the production of reactive oxygen species (ROS) by the plants (Palmer and Guerinot 2009; Puig and Penarrubia 2009). The AMF shows positive effects on plant growth under cadmium stress by lowering the levels of hydrogen peroxide and malonaldehyde (Hashem et al. 2016). A study by Yong et al. (2014) reported effective removal of heavy metals from polluted environments in clone of *Schizosaccharomyces pombe*. Metal dilution in plant tissues is also thought to be caused by increased growth or chelation in the rhizospheric soil (Kapoor et al. 2013; Audet 2014). AMF would have reportedly bind Cd and Zn in the cortical cells and mental hyphae to restrict their intake by plant and increase growth, yield and nutrient status of plants (Andrade and Silveira 2008; Garg and Chandel 2012).

6.4.3.4 Thermal Stress Tolerance

Thermal fluctuations lead to reduced germination, low rate of photosynthesis, retarded plant growth, yield and biomass production (Wahid et al. 2007; Hasanuzzaman et al. 2013). A study by Maya and Matsubara (2013) reported the beneficial effects of AMF on plant growth and yield under thermal stress in *Glomus fasciculatum*. A number of reports suggest AMF improves growth rates in plants grown under low temperatures when compared to plants without mycorrhizal association (Zhu et al. 2010a, 2010b). The AMF symbiosis supports the plants' survival under low temperature along with improved plant growth and development (Gamalero et al. 2009; Birhane et al. 2012). AMF strengthens the plant defence system, leading to more synthesis of various secondary metabolites and proteins (Abdel Latef and Chaoxing 2011b). It also facilitates the plant in efficient moisture retention, improved chlorophyll production and better osmotic adjustment capacity (Abdel Latef and Chaoxing 2011a; Zhu et al. 2010a, 2010b). In addition, the AMF can maintain host plant moisture (Zhu et al. 2010a), boost secondary plant metabolites leading towards strengthening plant immune systems and enhance plant protein in support of cold stress conditions (Abdel Latef and Chaoxing 2011b).

6.5 Conclusion and Future Challenges

There are many factors, such as compatibility with the environment, competition with other soil organisms, and timing of the inoculation, that can affect the success of establishment of symbiosis. The use of AM fungi in agriculture requires the knowledge of its adaption in the target ecosystem and the establishment of a functional symbiosis in different types of soils.

The use of AM fungi as a biofertilizer is an economical, effective and eco-friendly approach toward the attainment of low-input farming. The symbiotic fungi develop an intensive network of mycelium that improves soil structure, fertility and plant health by efficient absorption of micro- and macronutrients from the soil. Fungi have a number of genes and molecular pathways that facilitate more effective nutrient uptake and transport to the plant roots as compared to plants without a mycorrhizal association. AMF association in plant roots is an effective tool to combat biotic and abiotic stresses responsible for loss of crop productivity and yield. Therefore, the AM fungi have potential biofertilizer to act as sustainable agriculture.

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