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Interaction of Arbuscular Mycorrhizal fungi with biotic and abiotic factors and its ecological role and significance

Mariyam Khan, Praveen Kumar Maddheshiya and Kapil Gupta

Department of Biotechnology, Siddharth University, Uttar Pradesh, India

ABSTRACT

Arbuscular mycorrhizal (AM) symbiosis is one of the most ancient and extensive mutualistic relationships seen in nature. It is formed between terrestrial plants and fungus belonging to the phylum Glomeromycota. Plant nutrient uptake, stress tolerance, and ecosystem stability all depend on these interactions, which have existed for more than 400 million years. After colonizing plant roots, AM fungus creates complex structures called arbuscules inside cortical cells that enable two-way nutrition exchange. In exchange for carbohydrates produced by the plant, fungi help plants obtain essential minerals including potassium, nitrogen, and phosphorus. We now have a better knowledge of the mechanisms underlying the beginning and maintenance of this symbiosis because to recent research that has identified important genetic and molecular pathways controlling it. AM fungi have an impact on soil microbial populations and structure in addition to nutrient exchange, which greatly aids in ecological preservation and sustainable land usage. Their use as biofertilizers promotes ecologically friendly agriculture by providing promising substitutes for artificial fertilizers. Even though AM fungi are obligatory biotrophs and difficult to cultivate on their own, these obstacles are being overcome by developments in genomes, imaging, and molecular tools. In light of the growing environmental difficulties facing the world, a better understanding of AM symbiosis holds considerable promise for raising crop yield, promoting sustainable agricultural methods, and improving soil health.

KEY WORDS

Arbuscular mycorrhizal fungi; Plant-fungi symbiosis; Nutrient exchange; Sustainable agriculture; Soil microbial ecology

ARTICLE HISTORY

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Introduction

Most terrestrial plant species have a mutualistic relationship with arbuscular mycorrhizal fungus (AMF), which are members of the phylum Glomeromycota. This symbiosis is an essential part of the plant microbiome and is crucial to soil ecology and plant growth. These fungi enter the cortical cells of their host roots and develop into highly branching structures known as arbuscules, which are specialized for exchanging nutrients.

The fungi gain from the carbon-rich photosynthates that their plant hosts give, and plants can obtain otherwise immobile nutrients, including phosphorus (P), nitrogen (N), and certain micronutrients, thanks to this reciprocal exchange [1]. Although A.B. Frank first proposed the idea of mycorrhiza in 1885, fossil evidence indicates that these interactions began more than 400 million years ago, when vascular plants diverged [2,3]. The dynamic area that surrounds plant roots, known as the rhizosphere, is abundant in biochemical activity and microbial diversity. Plant health and nutrient cycling are significantly impacted by this environment, which is formed by interactions between plant roots, soil characteristics, and microbial communities. AM fungi are thought to be crucial for fostering plant growth and improving microbial interactions among the different organisms that live in this zone. A hotspot for these interactions is the soil microenvironment known as the "mycorrhizosphere," which is impacted by both root exudates and AM fungal hyphae [4]. AMF and soil bacteria work in concert to improve plant resistance to environmental stressors like drought, salinity, heavy metal toxicity, soil compaction, and pathogens. This is demonstrated by numerous studies [5-8]. By reducing the negative impacts of biotic and abiotic stress, these fungi serve as natural bio-protectants that promote plant growth and increase crop productivity.

Table 1. Common genera of Arbuscular Mycorrhizal Fungi [9].

S. No.	Genus	Representative Species	Characteristics	Reference
1	*Glomus*	*G. intraradices*	Forms abundant arbuscules, efficient P uptake	[9]
2	*Rhizophagus*	*R. irregularis*	Widely used in biofertilizers	[10]
3	*Funneliformis*	*F. mosseae*	Commonly used in sustainable agriculture	[11]
4	*Claroideoglomus*	*C. claroideum*	Tolerant to varioussoil stresses	[12]
5	*Gigaspora*	*G. margarita*	Large spores, low colonization rate	[13]
6	*Scutellospora*	*S. calospora*	Forms vesicles and auxiliary cells	[14]
7	*Acaulospora*	*A. scrobiculata*	Good drought tolerance	[15]
8	*Ambispora*	*A. leptoticha*	Intermediate spore development traits	[16]
9	*Entrophospora*	*E. infrequens*	Produces spores withinroots	[17]
10	*Paraglomus*	*P. occultum*	Small spores, limited distribution	[18]

***Correspondence:** Dr. Kapil Gupta, Department of Biotechnology, Siddharth University, Uttar Pradesh, India. e-mail: kapilgupta190184@gmail.com

11	*Redeckera*	*R. fulva*	Low host specificity	[12]
12	*Diversispora*	*D. epigaea*	Colonizes disturbed soils	[16]
13	*Septoglomus*	*S. deserticola*	Adapted to arid conditions	[19]
14	*Cetraspora*	*C. helvetica*	Produces ornamented spores	[20]
15	*Pacispora*	*P. robigina*	Forms spores in loose clusters	[16]
16	*Oehlia*	*O. diaphana*	Recently described genus,limited data	[12]
17	*Kuklospora*	*K. colombiana*	Spores with laminated walls	[21]
18	*Intraspora*	*I. schenckii*	Intracellular spore formation	[18]
19	*Otospora*	*O. bareae*	Spore with double wall layers	[20]
20	*Dominikia*	*D. indica*	Highly efficient colonizer	[21]

Importance of AM Fungi

Almost 80% of terrestrial plant species, including many crops of agricultural importance, depend on arbuscular mycorrhizal (AM) fungi for growth and survival [22]. Their functional and ecological contributions span a number of areas, such as stress tolerance, nutrient uptake, and ecosystem sustainability. Improving plant access to vital nutrients, especially in nutrient-poor soils, is one of their main functions. AM fungi enhance phosphorus and other less-mobile mineral absorption, promoting plant growth and nutrition. Furthermore, they produce glomalin, a glycoprotein that improves soil stability and structure, which aids in soil aggregation [23,24].

Additionally, these fungi increase a plant's resistance to biotic and abiotic stresses such salt, drought, and pathogenic invasions. AM fungi promote long-term ecosystem resilience and productivity by helping plants better handle environmental shocks. According to van der [25], their symbiotic networks promote plant cohabitation, which boosts biodiversity and stabilizes plant communities [12].

AM symbiosis starts with a molecular conversation between the fungus and the plant. According to Akiyama K et al. strigolactones released by plants into the rhizosphere promote AM fungal spore germination and hyphal branching [26].

In exchange, the fungus releases lipo-chito-oligosaccharides called Myc factors, which trigger the rhizobial symbiosis-related common symbiosis signaling pathway (CSSP) [27]. After making physical contact, fungal hyphae pierce the cortical cells and root epidermis to create vesicles, which act as storage bodies, and arbuscules, which are the main location for nutrient transfer.

Additionally, the fungi generate extra-radical hyphae that penetrate the surrounding soil, significantly expanding the surface area available for absorbing nutrients and water. The AM connection is complicated and highly adaptable because this interaction is tightly controlled by feedback processes involving environmental conditions, fungal colonization patterns, and plant carbon allocation.

Table 2. Benefits of AMF to Host Plants [28].

S. No.	Benefit	Description
1	Enhanced nutrient uptake	Especially phosphorus (P), nitrogen (N), zinc (Zn),and copper (Cu)
2	Improved drought resistance	Increased water absorption and regulation of osmotic balance
3	Disease resistance	Induced systemic resistance and competition with pathogens
4	Soil structure improvement	Hyphal networks stabilize soil aggregates and improve porosity
5	Increased biomassand yield	Better nutrientuptake leads to healthier and more productive plants

Biology of AM fungi

Taxonomy and diversity of AM fungi (Phylum Glomeromycota)

Arbuscular mycorrhizal fungi (AMF) belong to the phylum Glomeromycota, which is a group of obligatory symbionts that produce enormous, multinucleate spores through asexual reproduction and coenocytic (non-septate) hyphae. According to Schüßler et al. (2001), this phylum comprises a single class, Glomeromycetes, which is further classified into multiple families, such as Glomeraceae, Acaulosporaceae, Gigasporaceae, and Diversisporaceae [29].

Molecular investigations have shown significant functional and genetic diversity within morphologically identical taxa, despite the very little-known taxonomic diversity of AMF (around 300 identified species). The discovery of cryptic diversity by high-throughput sequencing and rDNA-based research suggests that AMF communities are more varied and complicated than previously thought [30].

Life cycle of AM fungi

Due to their obligatory biotrophic life cycle, AM fungus rely solely on their relationship with a host plant to complete their life cycle. Thick-walled spores that can linger in the soil for long periods of time germinate to start the symbiosis. The spores germinate and generate hyphae when the right environmental factors are present, such as enough moisture and host plant signals. These hyphae respond to chemical cues, such as strigolactones released by the host, by growing directionally toward plant roots. Myc factors, which are signaling molecules that prime plant roots for colonization, are released concurrently by AM fungus. The fungal hyphae enter the cortical region after penetrating the root epidermis, where they develop into arbuscules , which are

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finely branched structures specifically designed for nutrient exchange. Vesicles, which serve as intracellular storage structures, are also produced in certain species. During the symbiotic phase, the plant provides the fungus with essential soil minerals, including phosphate and micronutrients, and the fungus receives carbohydrates from the plant through photosynthesis. New spores are externally formed on the soil's fungal hyphae while the encounter continues. The life cycle can be completed by these huge, multilayered spores (which range in size from 50 to 500 μm) surviving until the conditions are right for germination. Curiously, despite the fact that AMF reproduce asexually, there is evidence that their genomes contain recombination-like mechanisms [31].

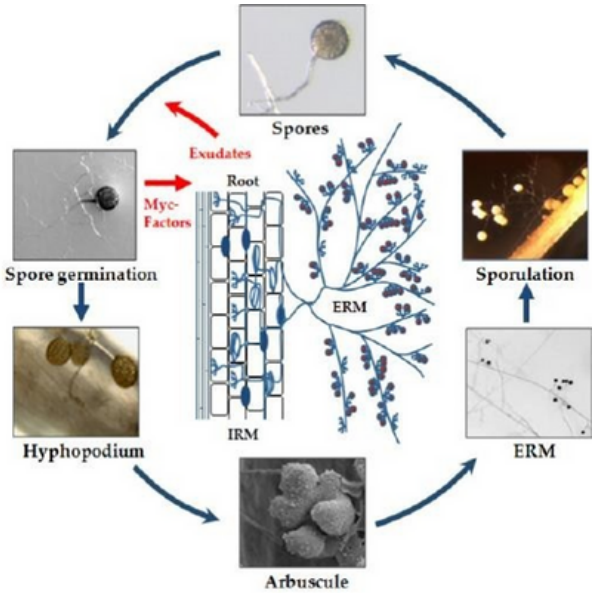

Figure 1. Life cycle of an AM fungus and the different steps during AM development.

Host specificity and compatibility

Because they associate with most vascular plant types, such as angiosperms, gymnosperms, and pteridophytes, AM fungi are well-known for their wide host range. Although the majority of AMF behave in a generalist manner, some taxa show host preferences, and the host-fungus pairing can greatly affect how efficient the symbiosis is [32]. Environmental factors and the spouses' genetic compatibility determine the extent of colonization and the advantages bestowed. Complex signaling cascades including particular receptor kinases, transcription factors, and downstream molecular responses mediate host recognition and compatibility [1]. Over evolutionary time, AM fungi and plants have co-adapted, leading to highly coordinated interactions that are finely regulated to balance mutual benefit with host control.

Mechanism of AMF symbiosis

Arbuscular mycorrhizal (AM) symbiosis is initiated and developed by a complex set of molecular signals that are transmitted between fungus spores and plant roots. Both partners release chemical cues that prepare them for engagement before they even make physical touch. Following their germination, the fungal spores develop hyphae that move toward the root under the direction of strigolactones and other signals emitted by the plant. After making contact, the fungal hyphae pierce the root's outer layers and arrive at the cortex, where they develop into highly branched arbuscules structures that are specifically designed to transport nutrients. Arbuscule formation necessitates extensive cellular remodeling in the cortical cells of the host root. The peri-arbuscular membrane (PAM), a specialized membrane-bound compartment that envelops the arbuscule and establishes the symbiotic interface, is one example of this.

The bidirectional flow of nutrients is made possible by this interface: the fungus may share mineral nutrients, especially phosphate, with the plant, and the plant can exchange carbon compounds with the fungus. The extraradical mycelium is formed by the fungus's external hyphae network extending into the surrounding soil. The root's ability to search soil volumes for water and nutrients is greatly enhanced by this mycelial system. The intraradical and extraradical fungal structures work together as an ongoing system to transport and acquire resources. A series of physiological and genetic reactions in the plant, especially in the root cortex, closely control symbiotic development. These reactions include the cytoskeletal reorganizations, membrane proliferation, metabolic modifications required to accommodate and sustain the fungal partner, and substantial transcriptional reprogramming to enable symbiosis [33,34].

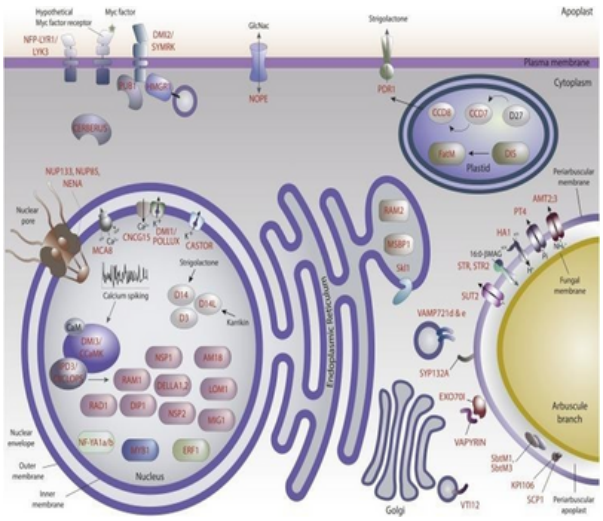

Figure 2. A brief overview of the essential plant proteins for AM symbiosis [35].

Parniske coined the term "accommodation program," which describes the host's proactive participation in promoting fungal colonization [36]. Plant genetics research has revealed important genes whose disruption results in less or unsuccessful colonization. For instance, the fungus releases signal molecules that cause calcium oscillations in the plant nucleus. Signalling proteins then interpret these oscillations and control the expression of downstream genes. Enzymes involved in lipid production, membrane transporters embedded in the PAM, and different transcriptional regulators are some of the essential elements. These elements facilitate a sustainable and effective exchange of nutrients by coordinating the development and operation of the symbiotic interface [36].

AM pre-symbiotic signaling initiates symbiosis

Arbuscular mycorrhizal (AM) symbiosis starts with a chemical exchange that takes place prior to the fungal spores and plant roots physically interacting. Certain chemicals that start and coordinate the colonization preparation processes

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are released into the rhizosphere by both symbiotic partners [37,38].

Strigolactones, a class of hormones produced from carotenoid pigments, are released into the soil by plants that are phosphate-deficient. Both controlling plant growth and serving as signals to draw in AM fungal partners are the two roles of these chemicals [26,39,40].

The fungi detect strigolactones, which increase the possibility of physical contact with neighboring plant roots by stimulating hyphal branching and growth and activating mitochondrial activities [41,42].

The importance of these early signals is shown by the fact that mutant plants with compromised strigolactone synthesis or export usually exhibit decreased AM colonization [39,43].

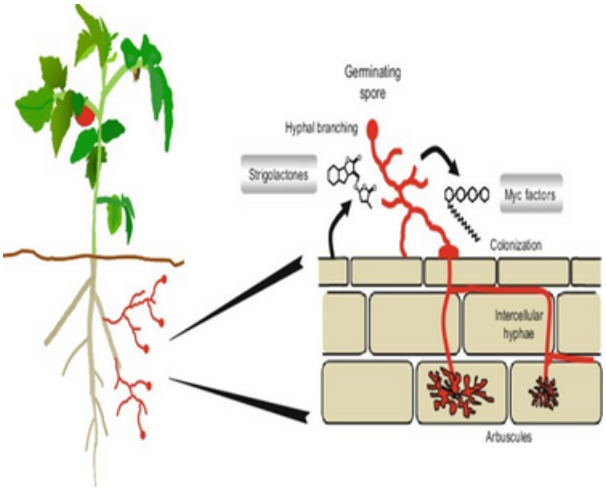

Figure 3. Pre-Symbiotic signalling.

NO PERCEPTION1 (NOPE1) is a transporter protein found in maize and rice that has recently been discovered to be crucial for priming the fungus prior to contact. It is thought that NOPE1 transports a molecule based on N-acetylglucosamine from the plant to the fungus, triggering the expression of fungal genes linked to the start of symbiosis. NOPE1-deficient plants exhibit little fungal colonization and are unable to stimulate fungal transcription, indicating that pre-contact communication is mediated by molecules other than strigolactones [44].

D14L forms a complex with the F-box protein MAX2 to control protein degradation and functions similarly to KARRIKIN INSENSITIVE2 (KAI2), a receptor involved in karrikin signaling. According to genetic research, AM colonization is significantly hampered by the absence of D14L or its downstream components [45].

According to one theory, D14L might detect a new signaling substance from the fungus that is connected to strigolactones or karrikins possibly an undiscovered "KAI2 ligand" (KL). According to Conn and Nelson and Gutjahr et al., this signaling pathway may be evolutionarily conserved and essential to the development of symbioses [46,47].

In summary, the initiation of AM symbiosis is governed by a sophisticated pre-contact communication system involving strigolactones, NOPE1-mediated signals , and KAI2-like perception pathways. These early molecular events prepare both the plant and fungus for the physical and physiological transformations required for successful colonization.

The Signaling Pathway for Common Symbiosis

The nitrogen-fixing symbiosis between legumes and rhizobia and the arbuscular mycorrhizal (AM) symbiosis share a core set of signaling components. Underpinning crucial communication events in both partnerships, this same system known as the Common Symbiosis Signaling Pathway (CSSP) was appropriated during the development of rhizobial symbiosis [27]. Three separate steps can be used to understand this pathway: transcriptional activation, signal transmission, and perception.

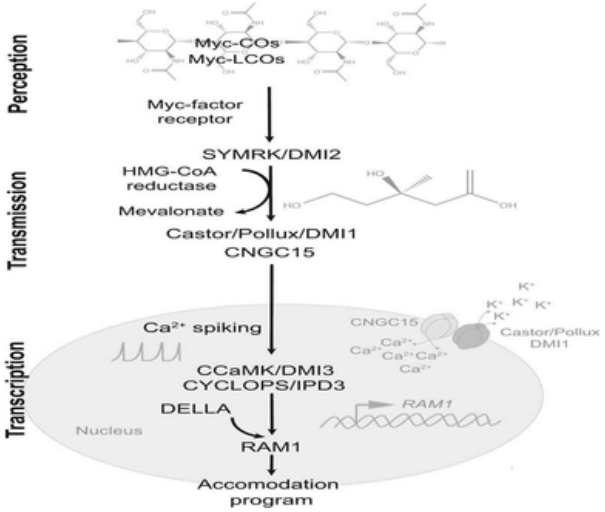

Figure 4. Establishment of AM symbiosis involves a three-tiered response of the host to accommodate its fungal partner, comprising perception, transmission, and transcription [35].

Perception

Early on in the connection, plant roots are able to identify compounds originating from fungi, including short-chain chitin oligomers (Myc-COs) and lipo-chitooligosaccharides (Myc-LCOs). LysM-type receptor-like kinases, including MtLYK3 (Medicago truncatula), SlLYK10 (tomato), LjNFR1 (Lotus japonicus), and OsCERK1 (in rice), facilitate this sensing. Furthermore, integrating these exterior cues and starting intracellular reactions depend on a receptor-like kinase termed SYMRK (also known as DMI2) [48].

Transmission

HMG-CoA reductase, which binds to SYMRK and is thought to generate mevalonate, a chemical that activates downstream components, is involved in the internal cascade that transmits the signal after recognition [49]. By interacting with nuclear ion channels like CASTOR and POLLUX (also called DMI1), mevalonate helps to regulate the calcium influx that is mediated by CNGC15 cyclic nucleotide-gated channels by promoting a potassium efflux. A defining feature of symbiotic signal transduction, this ion exchange results in distinctive nuclear calcium oscillations (Ca2+ spiking) [50].

Transcription

CCaMK (Calcium and Calmodulin-dependent Kinase) binds to calmodulin and becomes activated , decoding the calcium

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oscillations. CCaMK phosphorylates CYCLOPS, a crucial transcriptional regulator, when it is activated. They work together to activate downstream targets, such as transcription factors of the GRAS family like DELLA, which in turn trigger the expression of genes like RAM1, which are necessary for the production of arbuscules [51]. Remarkably, DELLA proteins have been appropriated for symbiotic signaling after being discovered as repressors in gibberellic acid (GA) signaling. By encouraging the expression of RAM1 and other symbiosis-related genes, their stability in phosphate-deficient environments aids in the formation of AM [52,53]. Their crucial significance has been highlighted by mutational studies that have demonstrated that stabilizing DELLA proteins or overexpressing RAM1 can restore impaired arbuscule formation in symbiotic mutants [51].

Other GRAS domain proteins, including RAD1, MIG1, NSP1, and NSP2, in addition to RAM1, also play a role in symbiotic control by impacting processes like root development and strigolactone production [54].

Even though these regulators are recognized to be important, more research is still needed to determine which genes they specifically regulate and the full scope of their functions.

According to phylogenetic investigations, GRAS proteins have conserved residues associated with small-molecule binding, indicating that they descended from a bacterial progenitor. Their classification within the Rossmann fold methyltransferase superfamily is confirmed by structural studies, which also provide novel insights into their regulatory roles [55].

In conclusion, the host plant is able to successfully establish and maintain AM symbiosis thanks to the CSSP's coordination of a precisely calibrated network of perception, signaling, and gene regulation. The evolutionary and functional integration of microbial partnerships in plant biology is demonstrated by this common pathway.

Table 3. Key structures formed in AM symbiosis.

S. No.	Structure	Location	Function
1	Arbuscule	Inside root corticalcells	Siteof nutrient exchange betweenfungus and plant
2	Vesicle	Inside or between cells	Storage of lipids andnutrients; reproductive structure in some AM fungi
3	Extraradical Hyphae	Soil surrounding roots	Absorb nutrients(P, N, micronutrients) and transport them to the plant
4	Intraradical Hyphae	Inside root cortex	Penetrate root cells and form arbuscules or vesicles
5	Spores	In soil or root surface	Reproductive structures; aid in dispersal and survivalof AM fungi

Nutrient Exchange

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Phosphorus (P) uptake

The improved uptake of phosphorus, a nutrient that is frequently limited in terrestrial ecosystems, is one of the most well-established advantages of AM symbiosis. For phosphorus uptake, mycorrhizal plants use two different pathways: a mycorrhizal channel mediated by fungal hyphae and a direct approach via root epidermal cells [56]. The fungal hyphal network explores extensive soil volumes beyond the depletion zone of roots, accessing inorganic phosphate that would otherwise remain unavailable. This expanded reach is critical for plant survival in phosphorus-deficient soils [9].

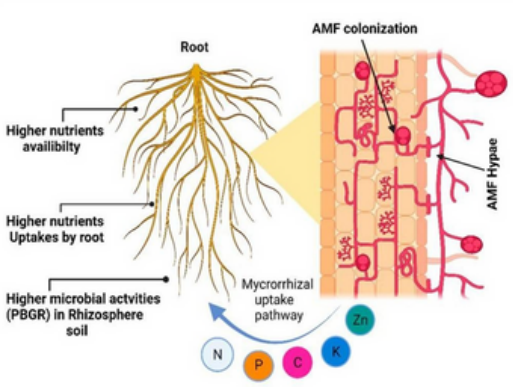

Figure 5. Scientific figure on researchgate for nutrient exchange between plants and AMF.

Transfer of nitrogen (N)

AM fungi help plants acquire nitrogen in addition to phosphorus, particularly in situations when nitrogen is limited or poorly mobile because of dryness, acidity, or low organic matter. In certain situations, these fungi help mobilize organic nitrogen from complex soil molecules like amino acids and peptides. They also aid in the uptake of both inorganic nitrogen forms, nitrate (NO_3^-) and ammonium (NH_4^+). According to research, under such circumstances, AM fungi can contribute significantly (24–42%) to a plant's overall nitrogen content [57].

Supply of carbon (C)

In return for improved mineral uptake, AM fungi depend on their host plants for organic carbon. They receive 10–30% of the plant's photosynthetic products, mainly in the form of sugars [58]. This carbon is critical for fungal growth and development

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within the root system. A high-affinity monosaccharide transporter, located on the fungal side of the interface, facilitates carbon uptake from the peri-arbuscular space [59]. Additionally, carbon fuels the production of fungal storage structures and the extension of hyphae into surrounding soil.

Essential nutrients

Beyond phosphorus and nitrogen, AM fungi also enhance the uptake of additional nutrients, including potassium, sulfur, and various microelements [9,1]. Sulfur, for instance, is vital for amino acid and protein synthesis, while potassium plays a role in osmotic regulation and stress tolerance. Although the role of AM symbiosis in potassium acquisition is less extensively studied, it is increasingly recognized for its contribution, especially in potassium-limited soils [60].

These nutrient exchanges are orchestrated at the peri-arbuscular membrane (PAM), a specialized plant-derived structure that envelops the fungal arbuscule. Nutrient transporters embedded in this membrane mediate the movement of mineral nutrients from the interface space into the host root cell cytoplasm [61].

Role of Plant Hormones

In order for arbuscular mycorrhizal (AM) symbiosis to form, grow, and function, plant hormones are essential regulators. By altering plant physiology and root architecture, these signaling chemicals affect several phases of the interaction, from initial colonization to the development and upkeep of arbuscules.

Auxin

Auxin is an essential hormone for root growth and for establishing the ideal environment for AM fungus colonization. In order to accommodate the fungal structures within the root, it controls processes such cell elongation, cortical cell division, and the development of root hair [33]. Because it facilitates cortical cell development and increases root vulnerability to fungal penetration, elevated auxin activity encourages the formation of arbuscules.

Abscisic acid (ABA)

Abscisic acid (ABA) is primarily associated with plant responses to abiotic stress, particularly drought. In the context of AM symbiosis, ABA helps modulate root architecture and symbiotic signaling pathways under water-limiting conditions. It can either promote or inhibit AM colonization depending on its concentration and the environmental context [62]. ABA also influences the plant's sensitivity to fungal signals, affecting the efficiency of symbiotic establishment during periods of stress.

Strigolactones

Plant roots create strigolactones, a family of terpenoid lactones, particularly when phosphorus levels are low. These substances are crucial signaling molecules during the initial phases of AM symbiosis. They increase the likelihood of successful colonization by promoting hyphal branching and stimulating spore germination in AM fungus [63]. In addition to their function in fungal recruitment, strigolactones also affect the architecture of the root system, which increases the likelihood of fungal contact.

AM's Ecological Functions and Roles

Fungi By promoting plant productivity, improving nutrient dynamics , and preserving ecological balance , arbuscular mycorrhizal (AM) fungi are crucial in forming terrestrial ecosystems. Biodiversity, soil structure, and ecosystem resilience are greatly enhanced by their interactions with soil, plants, and microorganisms.

Fertility and soil structure

The main way that AM fungi improve soil structure is by generating glomalin and other extracellular polymeric substances (EPS), which hold soil particles together. These substances encourage the development of stable soil aggregates, which enhance water retention, aeration, and erosion resistance [23,64]. This structural improvement fosters an environment that is conducive to microbial activity and root growth. Furthermore, by aiding in the absorption of vital nutrients like phosphorus, nitrogen, and other micronutrients, AM fungi improve soil fertility [65]. Plants can access nutrient pools outside of the rhizosphere thanks to their extraradical hyphal networks, which increase the functional root surface area [1].

Cycling of nutrients and bioavailability

AM fungi have an important role as mediators in the biogeochemical cycling of important elements such as carbon, nitrogen, sulfur, and phosphorus. AM fungus can access bound or insoluble forms of inorganic phosphorus in phosphorus-deficient soils and transfer them to the plant, increasing bioavailability [66]. They can access nutritional zones that are unavailable to plant roots alone thanks to their vast hyphal systems. By assisting plants in obtaining organic nitrogen and promoting mineralization processes, these fungi also aid in the nitrogen cycle [9]. Additionally, they aid in the mobilization of sulfur, which is essential for plant defense and protein synthesis [67,68]. Regarding carbon cycle, AM fungi help sequester carbon in the soil by obtaining carbohydrates from their host plants. They aid in preserving organic carbon in the soil matrix and minimizing the loss of CO_2 from the atmosphere by stabilizing soil aggregates and slowing down the pace of decomposition.

Impact on plant biodiversity and ecosystem stability

AM fungi affect competitive dynamics and improve nutrient access, which promotes plant species diversity and environmental stability. Certain plant species are more dependent on AM fungus than others, which can change their competitive advantages and make it easier for them to coexist in situations with low nutrient levels [25]. AM fungi also improve ecosystem recovery after disturbances by promoting plant health and stress tolerance. Their function in maintaining soil structure enhances resistance to environmental stresses such erosion, flooding, and drought.

Furthermore, by affecting invasive species' capacity to form symbioses, AM fungus may have an impact on their success. AM connections often benefit native plant species more than invading ones, helping to limit invasive populations and preserve native biodiversity [69].

Interaction with Biotic Factors

Arbuscular mycorrhizal (AM) fungi engage in diverse interactions with other living organisms in the soil ecosystem, including pathogens, beneficial microbes, and neighboring plants. These biotic interactions significantly influence plant health, community structure, and overall ecosystem dynamics.

Interaction with pathogens

AM fungi are known to enhance plant defense mechanisms

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against a range of soil-borne pathogens. One of their key ecological roles is acting as bioprotective agents, providing a layer of defense through multiple strategies. These include competition for root colonization sites, nutrient resources, and in some cases, the production of antifungal compounds.

Additionally, AM fungi can induce systemic resistance in host plants, a defense strategy known as Induced Systemic Resistance (ISR). This involves the activation of the plant's immune system, leading to the production of phytoalexins and pathogenesis-related (PR) proteins, which collectively enhance resistance to a wide range of pathogens including those causing root rot [70].

By colonizing root surfaces, AM fungi occupy niches that would otherwise be vulnerable to pathogenic invasion. This competitive exclusion not only limits pathogen establishment but also promotes a healthier rhizospheric environment [71].

Communication with other microbes

Other soil microbes like rhizobia, plant growth-promoting rhizobacteria (PGPR), and actinomycetes cohabit and frequently work in concert with AM fungus. Depending on the state of the microbial community and the environment, these interactions can either promote or hinder plant development and nutrient uptake.

For instance, a tripartite symbiosis between AM fungi and rhizobia in leguminous plants greatly increases plant access to nitrogen (by rhizobia) and phosphorus (via AMF), leading to improved growth and nutrient absorption [72]. Similar collaboration between PGPRs and AM fungus facilitates nutrient solubilization and provides pathogen defence. Competition for carbon supplies or root colonization locations, however, can occasionally make these collaborations less effective, especially in situations where microbial densities are high [73,63]. Both plant roots and AM fungal hyphae impact the soil zone known as the mycorrhizosphere, which is frequently enhanced with a variety of microbial communities. By modifying root exudation patterns and encouraging microbial diversity, AM fungus can influence this microbial community and enhance the resilience and health of the soil [74].

Interaction with other plants

By creating common mycorrhizal networks (CMNs), which link the root systems of various plants, AM fungi also promote connections between plants. Neighboring plants can share nutrients, water, and chemical signals thanks to these subterranean fungal networks [75].

In order to facilitate cooperative resource sharing or the early activation of defense responses during environmental stress, plants can use CMNs to transmit signals relating to carbon, phosphorus, or stress to nearby individuals. Additionally, by lessening the adverse effects of allelopathic substances, AM fungi affect allelopathic interactions, which are chemical inhibition between plants. Because of their enhanced nutritional availability and general vigor, plants linked with AMF frequently exhibit increased resistance to allelopathic stress [76].

Additionally, these networks provide chemical communication between plants. For example, a plant can use signaling chemicals sent through the fungal hyphae to notify neighboring plants about herbivore attacks or environmental stress. Collective resilience is increased and community stability is supported by this interconnectedness.

AM's Mitigation of Abiotic Stress Fungi

Arbuscular mycorrhizal (AM) fungi are essential for increasing a plant's resistance to a range of abiotic stressors, such as salinity, drought, heavy metal toxicity, and severe temperatures. AM fungus help plants survive and produce in harsh environmental conditions by enhancing nutrient uptake, controlling water, and modifying biochemistry.

Tolerance for salinity and drought

The capacity of AM fungi to enhance plant function in drought situations is among their best-known advantages. The vast hyphal network of AM fungus expands the amount of soil that can be searched for water, giving host plants access to moisture that is outside the reach of their roots. In water-limited conditions, this improved water absorption aids in preserving plant hydration and turgor pressure [77]. Furthermore, AM fungi enhance root hydraulic conductivity, which increases the effectiveness of water transport within the root system and supports the maintenance of physiological processes in the face of drought [78].

By increasing water use efficiency and controlling ion uptake and compartmentalization, AM fungus reduce stress in saline environments. By encouraging selective ion transport and sequestration into vacuoles, they minimize ion toxicity and lessen sodium ion buildup in roots and shoots. Additionally, during salt stress, AM fungi aid in osmotic adjustment, which helps plants preserve cellular integrity and enzyme function [79].

Heavy metal detoxification

By reducing metal uptake and improving sequestration, AM fungi aid in the detoxification of soils tainted with harmful metals like copper, lead, or cadmium. Metals can be stored within fungal structures or immobilized in the rhizosphere by fungal hyphae, which stops them from moving into plant tissues [80]. Additionally, AM fungi aid in the production of metal-chelating substances including organic acids and glutathione, which attach to heavy metals and counteract their negative effects. Additionally, they can increase metal tolerance and lessen oxidative stress by causing host plants to express metal-binding proteins [81,82].

AM fungi aid in reducing cellular damage by promoting the activity of antioxidant enzymes like peroxidase, catalase, and superoxide dismutase (SOD), which help combat reactive oxygen species (ROS) produced following heavy metal exposure [83].

Adjustment to severe temperatures

Additionally, AM fungus help plants survive under extremes of heat and cold. When plant metabolism is otherwise inhibited, they assist root development and nutrient uptake by stabilizing cellular membranes and promoting osmotic balance at low temperatures [84]. During cold weather, these effects assist sustain metabolic function and lessen frost damage. AM fungi help protect plant cells under high-temperature conditions by increasing the synthesis of antioxidants and heat shock proteins (HSPs). These compounds lessen heat-induced oxidative damage and preserve protein structure. Furthermore, AM fungi enhance

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water uptake and root activity, both of which are essential for plants to withstand heat stress [85].

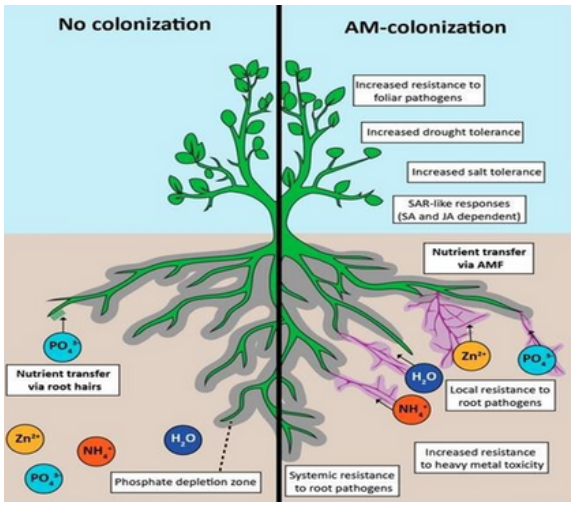

Figure 6. Positive effects of arbuscular mycorrhizal (AM) colonization[86].

Beyond the depletion zone (grey), the hyphal network of arbuscular mycorrhizal fungus (AMF) reaches a larger region of soil for phosphate uptake. Around AM hyphae, a mycorrhizal-phosphate depletion zone will eventually develop (purple). Zinc and nitrogen (ammonium) are two more nutrients that AM-roots have better absorption of. By fostering systemic acquired resistance, colonization can result in tolerances to a variety of biotic and abiotic stimuli [86].

AM's Use in Agriculture and Biotechnology Fungi

Arbuscular mycorrhizal (AM) fungi have a lot of potential to improve biotechnology and sustainable agriculture. They are useful tools in organic agriculture, environmentally friendly farming methods, and environmental remediation because of their capacity to promote soil fertility, improve plant nutrient acquisition, and boost resilience to environmental stress.

Application in organic farming and sustainable agriculture

In sustainable and organic farming systems, AM fungi play a crucial role by organically increasing soil health and lowering dependency on synthetic fertilizers. These fungi increase the availability of vital micronutrients while promoting nutrient recycling, particularly of nitrogen and phosphorus.

By improving plant nutrient uptake and productivity, AM fungi offer a crucial advantage in situations where external inputs are scarce [87,88].

AM fungi also aid in improving soil aggregation, which increases soil structure, improves water retention, and lessens erosion by promoting root development and microbial activity. In systems that rely on the natural function of soil, their hyphae's ability to bind soil particles reduces compaction and increases aeration. By improving plant access to immobile phosphorus reserves, AM fungus can significantly lower the need for phosphate fertilizers in phosphorus-deficient soils. This helps to preserve soil over the long term and reduces the environmental impact of agriculture [89].

Development and commercialization of Inoculants

One area of agricultural biotechnology that is expanding is the creation of mycorrhizal inoculants. These products are applied to seeds, soil, or hydroponic systems to promote mycorrhizal colonization and enhance plant performance. They are made using specific AM fungus species. In farms with degraded soils where chemical inputs or intensive farming have reduced natural AMF populations, inoculants are especially helpful [90,56].

Nowadays, a variety of crops, such as cereals, legumes, vegetables, and fruit trees, use commercial inoculants, particularly in low-input and organic systems. Their application can improve soil health generally, increase crop yields, and lessen reliance on fertilizers [91,92].

Biofertilizers for enhancing soil health

By acting as organic biofertilizers, AM fungus help soil nutrients be used more effectively. By extending the root absorption zone, their symbiotic relationship with plant roots allows plants to obtain nutrients particularly phosphorus and nitrogen that would not otherwise be available to them. This feature supports sustainable farming methods and lessens the demand for chemical fertilizers [93]. Moreover, AM fungi promote microbial diversity, improve soil structure, and raise the amount of organic matter. These enhancements promote healthier soils that are more robust, productive, and able to sustain agricultural use for an extended period of time. Additionally, they promote microbial symbiosis and nutrient cycling, which improves plant health and yield.

Phytoremediation role

The use of AM fungus in phytoremediation the process of restoring contaminated areas using plants and the bacteria that coexist with them is growing. By immobilizing heavy metals like lead, cadmium, and arsenic in fungal tissues or encouraging their sequestration in plant roots, these fungi aid in lowering their toxicity and mobility [80]. Additionally, they help remove excess nutrients like phosphorus and nitrogen from overfertilized soils, which is a prevalent problem in eutrophication-affected areas [94]. Furthermore, by promoting plant detoxifying enzymes or microbial interactions in the rhizosphere, AM fungi may improve the breakdown of organic contaminants, such as pesticides and petroleum residues [95].

Table 4. Applications of AMF.

S.N.	AMF Genus	Application	Reference(s)
1	*Rhizophagus*	Enhances nutrientuptake and growthin crops like soybeanand cotton	[96,97]
2	*Gigaspora*	Improves phosphorus uptake in onion and tomato	[98]
3	*Ambispora*	Enhances growth in asparagus	[99]
4	*Funneliformis*	Increases drought tolerancein alfalfa	[100]
5	*Glomus*	Enhances growth in tobacco and chili	

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6	*Claroideoglomus*	Improves nutrient uptakein various plants	
7	*Diversispora*	Enhances plant growth under stressconditions	[101]
8	*Acaulospora*	Improves growth in various plants	[102]
9	*Glomus geosporum*	Enhances growthin sea wormwood andchamomile	
10	*Glomus intraradices*	Improves growth in mung bean and cashew	[103]
11	*Rhizophagus irregularis*	Enhances growth in Medicago truncatula	
12	*Funneliformis mosseae*	Improves growth in chickpea	[74]
13	*Glomus aggregatum*	Enhances phosphorus uptakein maize	[104]
14	*Rhizophagus clarus*	Increases yield in soybean and cotton	[96]
15	*Gigaspora margarita*	Enhances growth in onion and tomato	[98]
16	*Ambispora granatensis*	Improves growth in asparagus	
17	*Rhizophagus irregularis*	Enhances growthin Vicia faba and Robinia pseudoacacia	[105]
18	*Glomus versiforme*	Improves growth in Robinia pseudoacacia	[105]
19	*Rhizophagus iranicus var. tenuihypharum*	Enhances growthin various agricultural crops	
20	*Glomus macrocarpum*	Improves growth in tobacco and chili	

Table 5. AMF species and their symbiotic plants.

S.N.	AM Fungi Species	Symbiotic Plant(s)	Reference(s)
1	*Rhizophagus clarus*	Strawberry, Maize, Soybean,Cotton,Tomato	[96,97]
2	*Gigaspora margarita*	Onion, Tomato,Soybean, Corn, Clover	[98]
3	*Ambispora granatensis*	Asparagus officinalis	[106]
4	*Rhizophagus irregularis*	Vicia faba,Robinia pseudoacacia	[105]
5	*Glomus macrocarpum*	Tobacco, Chili	
6	*Rhizophagus iranicus var. tenuihypharum*	Various Agricultural Crops	
7	*Funneliformis mosseae*	Alfalfa (Medicago sativa)	[100]
8	*Glomus versiforme*	Robinia pseudoacacia	[105]
9	*Claroideoglomus etunicatum*	Various Plants	[107]
10	*Diversispora epigaea*	Various Plants	
11	*Acaulospora laevis*	Various Plants	[102]
12	*Glomus geosporum*	Sea wormwood, Sea plantain, Salt aster,Chamomile	
13	*Glomus intraradices*	Mung bean, Cashew	[103]
14	*Rhizophagus irregularis*	Medicago truncatula	
15	*Funneliformismosseae*	Cicer arietinum (Chickpea)	[74]

Difficulties and Restrictions in AMF Studies

Arbuscular mycorrhizal fungi (AMF) are important for agriculture and the environment, yet there are many scientific and technical barriers to their research and use. These obstacles, which include host heterogeneity, environmental limitations, and cultivation hurdles, all impede broad adoption and advancements in research.

Mandatory cultivation and biotrophy barriers

The obligate biotrophic nature of AMFs, which necessitates a living plant host for survival and reproduction, is a significant study restriction. Since AMF cannot be cultivated on synthetic media like many other fungi, it is challenging to investigate their physiology separately [108]. This restriction inhibits the development of uniform cultivation procedures and makes laboratory trials more difficult.

There are restrictions on the commercial manufacture of AMF on a large scale. The manufacturing of inoculants is hampered by the absence of sterile, economical, and effective mass production techniques [109]. Additionally, varied growth circumstances across AMF species necessitate customized approaches, making industrial use more challenging [110].

Variability and host dependency

As AMF have different levels of host compatibility, not every plant species gains the same advantages from colonization. While certain plant-fungus combinations exhibit limited symbiotic activity, others provide extremely effective nutrient exchange [111].

In field applications, this host specificity restricts the consistency and predictability of results. Different cultivars of the same AM fungus strain may react differently, even within a single plant species. Inconsistent performance across habitats is also a result of AMF's genetic diversity. According to van der Heijden et al., these features make it more difficult to design universal inoculants and emphasize the necessity of host-specific matching techniques [112].

The impact of soil and environmental conditions

AM fungal colonization and functionality are significantly influenced by environmental factors. For instance, when plants become less dependent on fungal support in nutrient-rich environments, soils with a high phosphorus content can inhibit mycorrhizal colonization. In high-input agricultural systems, where phosphorus is frequently applied in large quantities, this

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poses a significant constraint. AMF performance is also influenced by the pH of the soil. While extremely acidic or alkaline soils can prevent spore germination and root colonization, the majority of AM fungi prefer slightly acidic to neutral soils [113]. In a similar vein, water availability is crucial; while AMF might increase a plant's resistance to drought, the fungus themselves need enough soil moisture to grow and thrive [5].

Prospects for AMF Research in the Future

Research on arbuscular mycorrhizal fungi (AMF) is progressing, creating new opportunities to restore degraded ecosystems, increase ecosystem resilience, and improve sustainable agriculture. However, a number of practical, technical, and scientific obstacles must be overcome before AMF's full potential may be realized. In order to further our comprehension and use of AM symbiosis, future studies must combine molecular, ecological, and agronomic methodologies.

Genetic and molecular studies

The molecular mechanisms behind AM symbiosis are being clarified by ongoing studies in transcriptomics and genomes. Gene families involved in food exchange, signaling, and host contact have been better understood thanks to the sequencing of AM fungal genomes, including Rhizophagus irregularis [10]. despite the intricacy of AMF genomes which are distinguished by limited sexual reproduction, multinucleate cells, and substantial genetic variability continues to present analytical difficulties. In order to understand the gene functions and regulatory pathways within AM fungus, future research should focus on creating better tools for gene editing and functional analysis, such as CRISPR-based techniques.

Engineering more successful symbiotic partnerships will need an understanding of the signaling networks and molecular conversations between AM fungus and plant hosts, including the function of effector proteins, short RNAs, and post-transcriptional alterations [114].

Innovation in biotechnology and synthetic biology

The creation of altered AM fungal strains or host plants with increased symbiotic effectiveness may be made possible by advancements in synthetic biology. More stable and productive soil microbiomes for agriculture may result from the creation of artificial microbial consortia that contain AM fungus, bacteria that promote plant growth, and other advantageous organisms.

Biotechnological methods, such as the utilization of immobilized spores, carrier-based formulations, and bioreactor systems for mass production, may also improve the scalability of AMF inoculants. One of the important areas for innovation is making sure these products are viable, effective, and have a long shelf life in a variety of field situations.

Incorporation into ecological agriculture systems

AM fungus must be a fundamental part of climate-smart and regenerative strategies in agricultural systems of the future. Optimizing AMF treatments in field settings should be the main goal of research, especially in light of crop rotation, less tillage, lower fertilizer input, and organic amendments. The reliability of results will be improved by creating region-specific AMF formulations that are tailored to the local soil types and climates.

To evaluate how AMF affects crop productivity, soil fertility, and resilience under a variety of environmental circumstances, long-term field research is required. To learn more about their ecological compatibility, these studies should also assess how AMF interacts with other soil biota, such as pathogens and mutualists.

Policy and education

Programs for awareness, farmer education, and policy support will be necessary for the effective integration of AMF into conventional agriculture. The long-term advantages of using AMF in lowering chemical inputs, enhancing crop health, and advancing environmental sustainability must be communicated to stakeholders. For research to be translated into reality, networks of scientists, agricultural extension agencies, and industry stakeholders must work together. To facilitate broad adoption, infrastructure and training investments for AMF production, use, and monitoring will be required.

Conclusions

An essential part of terrestrial ecosystems, arbuscular mycorrhizal (AM) fungi provide vital advantages for soil fertility, plant health, and ecological resilience. Their significance in both natural and agricultural systems is highlighted by their ability to improve stress tolerance, boost biodiversity, and improve nutrient uptake. With most land plants, AM fungi establish complex symbiotic interactions that allow for the effective exchange of carbon from plants for phosphorus, nitrogen, and other vital minerals. AM fungi have an important role in soil structure, carbon sequestration, and defense against pathogens and environmental stressors in addition to nutrient dynamics. They are essential to climate-resilient food systems, restoration ecology, and sustainable agriculture because of their diverse functions. But even after decades of study, scientists still don't fully grasp the biology, diversity, and function of AM fungi. Both scientific research and real-world implementation are constrained by issues like their obligatory biotrophic lifestyle, host-specific reactions, and environmental variability. It will take coordinated efforts integrating genetics, molecular biology, soil ecology, and agronomic innovation to overcome these obstacles. Enhancing large-scale inoculant production, developing molecular tools for functional analysis, and customizing AMF use for particular crop and soil systems should be the main goals of future AMF research. Promoting their broad use in ecological restoration and regenerative farming will also require increasing awareness, education, and policy backing. In summary, AM fungi offer a promising pathway toward more sustainable and resilient agricultural practices. Continued research and application of this ancient symbiotic partnership will be essential for meeting the growing demands of food security, environmental stewardship, and global climate adaptation.

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