



Research Progress on the Symbiotic Relationship between Rice and Arbuscular Mycorrhizal Fungi

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Abstract

The symbiotic system formed between Arbuscular Mycorrhizal Fungi (AMF) and rice (*Oryza sativa* L.) holds significant potential for sustainable rice production. Based on domestic and international research literature, this paper systematically reviews the progress in molecular regulatory mechanisms, AMF community diversity and its influencing factors, symbiotic functional effects, and field applications of the rice-AMF symbiosis. At the molecular level, rice mycorrhizal symbiosis involves complex networks including strigolactone signal recognition, calcium oscillation transduction, and downstream transcriptional regulation. Key components such as *OsCERK1*, *CCaMK*, and *CYCLOPS* play central roles in the symbiotic signaling pathway, while the nutrient exchange phase relies on the collaborative participation of transporters such as *STR1/STR2* and *OsAMT3;1*. At the ecological level, AMF community structure is comprehensively regulated by multiple factors including water management, soil physicochemical properties, agricultural cultivation practices, and host genotypes. Functionally, AMF enhance rice tolerance to stresses such as drought, salinity, heavy metals, and pests by promoting nutrient uptake (especially phosphorus and nitrogen), regulating plant hormone balance, and inducing systemic resistance. However, AMF effects exhibit high host dependency and environmental specificity; the stability and controllability of their field application remain major challenges. Future research should integrate multi-omics technologies and synthetic biology tools to promote the precise application of AMF in green rice production.

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1. Introduction

Rice (*Oryza sativa* L.) is the staple crop for more than half of the global population, and its stable and high yield is directly related to world food security^[1]. Current rice production relies heavily on the large-scale input of chemical fertilizers and pesticides. While this intensive model ensures yield, it also brings environmental problems such as soil degradation, water eutrophication, and increased greenhouse gas emissions. In this context, exploring and utilizing beneficial microbial resources to build resource-saving and sustainable agricultural production systems has become an important direction in plant science and agronomy.

Arbuscular mycorrhizal fungi are among the most widely distributed plant symbiotic microorganisms in the soil, capable of establishing symbiotic relationships with approximately 80% of terrestrial plants^[2]. AMF belong to the subphylum Glomeromycotina and are obligate biotrophs that form arbuscule structures within the cortical cells of plant roots, serving as the primary site for nutrient exchange^[3]. In this relationship, AMF transport mineral nutrients such as phosphorus and nitrogen absorbed from the soil to the host plant, while obtaining photosynthetic carbon sources from the host^[4].

For a long time, rice was considered less dependent on AMF symbiosis due to its typical wetland growth environment. However, research over the past two decades has gradually revealed that rice roots can be colonized by AMF under both aerobic and flooded conditions ^[5]. This discovery has changed the traditional understanding of the relationship between rice and AMF and prompted researchers to systematically investigate the ecological and agronomic significance of this symbiotic system in rice agriculture. In recent years, with the rapid development of molecular biology, multi-omics, and ecological methods, research on the rice-AMF interaction has made significant progress, covering symbiotic signal transduction, community ecology, stress physiology, and field application ^[6]. This paper aims to systematically review the important research achievements in this field, focusing on the molecular basis of symbiosis establishment, AMF diversity distribution patterns, functional effects, and regulatory factors, and looking forward to future research directions and application prospects.

2 Molecular Regulatory Mechanisms of Rice-AMF Symbiosis

2.1. Signal Recognition and Transduction in Symbiosis Establishment

The establishment of the symbiotic relationship between rice and AMF begins with molecular dialogue between the roots and the fungi ^[7]. This process involves a complex signal recognition network, in which strigolactones secreted by plant roots are key signaling molecules that stimulate AMF spore germination and hyphal branching ^[8]. Studies have shown that the biosynthesis of rice strigolactones is regulated by the *D3 F-box* protein and *NSP1/NSP2* GRAS transcription factors; mutants *d3* and *nsp1/nsp2* both exhibit significantly decreased mycorrhizal colonization rates ^[9]. Interestingly, natural variation in rice strigolactone biosynthesis is related to the deletion of two *MAX1* homologous genes, which may explain differences in mycorrhizal symbiotic capacity among different rice varieties ^[10]. Seto *et al.* ^[11] further identified carlactone as an endogenous precursor for strigolactone biosynthesis, providing important clues for understanding this hormonal pathway.

Regarding fungal signal perception, the LysM receptor-like kinase *OsCERK1* plays a core role ^[12]. *OsCERK1* can perceive chitin oligosaccharide signals released by AMF and initiate the symbiotic signaling cascade. Research has also found that *OsCERK1* functions dually in immune and symbiotic signaling, and its natural variation may provide targets for the genetic improvement of rice mycorrhizal symbiotic capacity ^[12]. Additionally, ion channel genes such as *CASTOR* and *POLLUX* are indispensable for symbiotic signal transduction, likely participating in the calcium oscillations induced by symbiotic signals ^[13].

Downstream transduction of calcium signals depends on calcium/calmodulin-dependent protein kinase (*CCaMK*) and its substrate *CYCLOPS* ^[14, 15]. *CCaMK* achieves precise responses to symbiotic signals by decoding the frequency and amplitude of calcium oscillations. *CYCLOPS*, as a phosphorylated substrate of *CCaMK*, further activates downstream transcriptional reprogramming. Recent studies revealed that the *CCaMK-CYCLOPS-DELLA* complex can activate the expression of the *RAM1* transcription factor,

thereby regulating the formation of arbuscule branches ^[16]. Research by Yu *et al.* ^[17] showed that the *DELLA* protein complex plays a key regulatory role in mycorrhizal symbiosis, linking the gibberellin signaling pathway to mycorrhizal development. Gobbato *et al.* ^[18] identified a GRAS transcription factor with specific functions in mycorrhizal signaling, further enriching the symbiotic signaling regulatory network. Furthermore, Das *et al.* ^[19] found that phosphate starvation response transcription factors can promote AMF symbiosis, revealing the regulatory link between phosphorus nutritional status and symbiosis establishment. At the cellular level, before AMF infection, rice epidermal cells undergo nuclear migration and cytoskeletal rearrangement, forming the so-called "pre-penetration apparatus" to prepare for fungal invasion ^[20].

2.2. Nutrient Exchange and Metabolic Regulation

Once the symbiotic relationship is established, nutrient exchange becomes the core of the interaction. AMF transport mineral nutrients, primarily phosphorus and nitrogen, to the host plant via arbuscule structures while obtaining carbon sources from the host ^[4]. In terms of phosphorus transport, the plant genome encodes multiple mycorrhiza-induced phosphate transporters, of which *OsPT11* is a key member of the rice mycorrhizal phosphorus absorption pathway ^[21]. Studies show that genetic diversity in rice phosphate transporters may be related to differences in mycorrhizal responses among varieties ^[21].

Regarding nitrogen transport, Courty *et al.* ^[22] systematically reviewed the mechanisms of inorganic nitrogen uptake and transport in beneficial plant-microbe interactions. Ammonium transporters such as *OsAMT3;1* are significantly induced during mycorrhizal symbiosis, participating in AMF-mediated nitrogen uptake. Koegel *et al.* ^[23] performed phylogenetic, structural, and functional characterization of *AMT3;1*, finding it specifically induced in mycorrhizalized Poaceae plants. In conjunction, *GS/GOGAT* genes in the nitrogen assimilation pathway are also up-regulated in mycorrhizalized rice roots.

The distribution of carbon sources from the host to the AMF is the energy basis for maintaining symbiosis. Studies show that AMF infection can lead to an increase in the photosynthetic rate of rice, partially compensating for the consumption of photosynthates by the fungi. *STR1* and *STR2*, encoded by the rice genome, are half-size ABC transporters indispensable for arbuscule development and material transport; *str1/str2* mutants cannot form normal arbuscule structures ^[24]. Additionally, Guo *et al.* ^[25] found that *OsADK1* encodes a novel kinase involved in regulating arbuscule development and nutrient exchange efficiency. Research by Nadal *et al.* ^[26] showed that the N-acetylglucosamine transporter *OsNPF4.5* is necessary for rice mycorrhizal symbiosis, possibly participating in the recognition of fungal signal molecules or sugar transport during nutrient exchange. The study by Markmann *et al.* ^[27] revealed that the functional adaptation of plant receptor kinases provided the genetic basis for intracellular symbiotic evolution, offering an important perspective on the evolution of rice-AMF symbiosis. These findings collectively outline the molecular framework of nutrient exchange in the rice-AMF symbiotic system, though many details remain to be elucidated.

3. Diversity and Influencing Factors of Rice Mycorrhizal Symbiosis

3.1. Universality and Variety Differences in Rice Root AMF Colonization

Early studies suggested that the flooded environment of rice was unfavorable for AMF survival and colonization. However, increasing evidence shows that rice roots can be colonized by AMF under both traditional paddy and aerobic conditions^[5]. Investigations in major rice-producing areas in southern China show that the mycorrhizal colonization rate of lowland rice varies greatly, influenced by soil type, water management, and variety characteristics^[5]. Research by Wang *et al.*^[28] indicated that in high-input and intensive irrigation rice systems, the dynamic changes of AMF communities are significantly influenced by agricultural management practices. A study by Sarkodee-Addo *et al.*^[29] on AMF in Ghanaian rice found that regional geography and soil factors collectively influence AMF diversity and community assembly. Surendirakumar *et al.*^[30] detected abundant AMF taxa in the roots and rhizosphere soil of black rice in the terraces of Northeast India, further confirming the universality of rice mycorrhizal symbiosis.

There are significant differences in mycorrhizal colonization rates and response levels among different rice varieties. Research from Nigeria showed differences in the diversity of indigenous AMF in the rhizosphere of different rice varieties^[31]. Studies in Bangladesh also revealed systematic differences in AMF communities between modern high-yielding varieties and traditional rice varieties^[32]. This variety specificity provides potential for mycorrhizal breeding but also increases the complexity of field application of mycorrhizal inoculants.

3.2. Regulation of AMF Community Structure by Environmental Factors

Water management is a key environmental factor affecting rice mycorrhizal symbiosis. Research by Vallino *et al.* showed that flooded conditions significantly inhibit rice root branching and AMF colonization rates but do not affect the viability of the fungi themselves^[33]. Watanarajanapon *et al.* found that indigenous AMF community structures differ significantly between different rice cropping systems^[34]. Wang *et al.* comparatively studied the response differences of root AMF communities in aquatic and semi-aquatic rice varieties under different flooding regimes, finding that water status had a greater impact on AMF community composition than host genotype effects^[35]. Bao *et al.* further analyzed the interaction between rice and AMF under different flooding conditions from the perspective of carbon-water-phosphorus exchange^[36].

Soil physicochemical properties are also important regulatory factors. Alguacil *et al.* found that soil texture, pH, and organic matter content are the primary factors driving AMF community composition in semi-arid Mediterranean soils^[37]. Research by Klinnawee *et al.* showed that the inhibitory effect of flooding on rice mycorrhizal colonization exceeded the promoting effect of phosphorus availability on colonization^[38]. Studies by Parvin *et al.*^[32, 39] in Bangladesh found that soil salinity and arsenic pollution gradients significantly affected AMF community composition in rice roots, and systematic differences existed between traditional and modern varieties. Zhang *et al.*'s study on fungal communities under long-term rice cultivation in

sodic saline-alkaline soil in China showed that long-term rice planting altered soil fungal community structure, including the adaptive succession of AMF communities^[40].

3.3. Impact of Agricultural Management Practices

Agricultural cultivation systems have a profound impact on rice AMF communities. Ilag *et al.* reported early on the population dynamics of AMF in rice cropping systems^[41]. Lumini *et al.*'s study on Italian paddy fields showed that different cultivation practices and water management modes significantly affect soil AMF community structure^[42]. Panneerselvam *et al.* used the Illumina MiSeq platform to analyze changes in rice soil AMF communities under elevated CO₂ concentrations, revealing response trends under climate change^[43]. These studies collectively indicate that the composition and function of AMF communities are regulated by multiple environmental factors.

4. Regulation of Rice Nutrient Uptake and Growth by AMF

4.1. Efficient Acquisition of Phosphorus Nutrients

Phosphorus is an essential mineral nutrient limiting rice growth, and most phosphorus in the soil exists in forms difficult for plants to utilize. AMF greatly expand the nutrient absorption range of roots through their extensive hyphal networks, effectively acquiring soil phosphorus and transporting it to the host plant. The growth-promoting effect of AMF is particularly evident in low-phosphorus soils^[44]. Johnson *et al.* proposed the "mycorrhizal phenotype" concept, suggesting that the plant response to AMF depends on soil nutrient status and the plant's own nutrient acquisition strategy^[45].

In the context of reduced phosphorus fertilizer application, the efficient phosphorus acquisition function of AMF has significant application value. AMF can maintain rice yields under conditions of reduced chemical phosphorus fertilizer input. Research by Jeong *et al.* suggests that genetic diversity in rice phosphate transporters may be related to mycorrhizal phosphorus absorption efficiency^[21]. These studies indicate that AMF can serve as a biotechnological tool for efficient phosphorus utilization, supporting sustainable agricultural development.

4.2. Absorption of Nitrogen and Other Nutritional Elements

In addition to phosphorus, the contribution of AMF to rice nitrogen nutrition is increasingly emphasized. Ammonium transporters such as *OsAMT3;1* are significantly induced during mycorrhizal symbiosis, indicating the functional importance of AMF-mediated nitrogen uptake pathways in rice^[22, 23]. Research by Pérez-Tienda *et al.* further confirmed the activation effect of AMF on the rice nitrogen assimilation pathway at the transcriptional level^[46]. Courty *et al.* systematically reviewed inorganic nitrogen uptake and transport mechanisms in beneficial plant-microbe interactions, pointing out that the contribution of AMF to nitrogen nutrition might be underestimated^[22].

AMF can also promote the absorption of other meso- and micronutrients in rice. Zhang *et al.* found that mycorrhizal inoculation altered carbon-nitrogen distribution patterns in rice, improving grain yield and nutritional quality^[47]. These studies suggest that AMF possess multiple functions in comprehensive rice nutritional management.

4.3. Growth Promotion and Bidirectional Effects

Although most studies show that AMF promote rice growth, some have found that AMF may inhibit host growth, particularly under conditions of nutrient sufficiency or carbon supply limitation^[48]. This growth-inhibition phenomenon reminds us that the relationship between AMF and plants is not always mutualistic; its effect depends on environmental conditions and the physiological states of both parties. Field trials by Diedhiou *et al.* clearly observed specific responses of rice ecotypes to AMF inoculation, further confirming the condition-dependence of symbiotic benefits^[49]. Therefore, understanding the benefit-tradeoff mechanism of mycorrhizal symbiosis is the theoretical basis for promoting AMF field application.

5. The Role of AMF in Rice Response to Stress

5.1. Drought and Saline-Alkaline Stress

Drought is a major abiotic stress factor limiting rice production. AMF enhance rice drought resistance through various mechanisms: improving water absorption, inducing the accumulation of osmotic regulation substances, increasing antioxidant enzyme activities, and regulating stomatal conductance^[50]. Chareesri *et al.* found that increased mycorrhizal colonization could significantly reduce yield loss under drought conditions^[51]. Research by Tisarum *et al.* respectively confirmed the alleviation effects of AMF inoculation on water deficit and salt stress in colored rice varieties, pointing out that AMF enhance stress tolerance by increasing photosynthetic pigment content and osmotic regulation capacity^[52].

Regarding saline-alkaline stress, Parvin *et al.* compared the effects of single and mixed AMF species on salt tolerance in Bangladeshi rice varieties, finding that mixed inoculation was superior to single inoculation^[53]. Field trials by Norouzinia *et al.* further confirmed the improved effects of combined application of AMF and plant growth-promoting bacteria (*Pseudomonas*) on the physiological and agronomic traits of rice under salt stress^[54]. Overall, there is substantial experimental evidence for the protective role of AMF in rice under drought and saline-alkaline stresses.

5.2. Heavy Metal and Metalloid Stress

With industrialization and the large-scale use of agricultural chemicals, soil heavy metal pollution is becoming increasingly severe, and rice accumulation of cadmium (Cd) and arsenic (As) is of particular concern. AMF show unique potential in remediating heavy metal-polluted soil and reducing heavy metal accumulation in rice.

Regarding cadmium stress, Li *et al.* studied the effect of AMF on redox homeostasis in rice under cadmium stress, finding that the antioxidant system was activated and membrane lipid peroxidation was reduced in mycorrhizalized plants^[55]. Luo *et al.* further revealed the impact of AMF on cadmium absorption and chemical forms in rice during different growth stages, noting that AMF altered the distribution and occurrence forms of cadmium within the plant^[56]. These studies indicate that AMF mitigate cadmium toxicity through multiple mechanisms including physical adsorption, chemical precipitation, and antioxidant defense.

Regarding arsenic stress, as a typical flooded crop, rice absorption and accumulation of arsenic is particularly prominent^[57]. The protective role of AMF under arsenic pollution has received extensive attention. Zhang *et al.* found that water management, rice variety, and AMF inoculation

interactively influenced the concentration and form of arsenic in rice grains^[58]. Research by Li *et al.* showed that AMF could reduce the ratio of inorganic to organic arsenic in rice grains, thereby lowering health risks^[59]. Spagnoletti and Lavado found that *Rhizophagus intraradices* could reduce arsenic toxicity in soybean plants, providing a model for understanding AMF-arsenic interaction^[57]. At the molecular level, González-Chávez *et al.* and Maldonado-Mendoza *et al.* respectively identified transporter genes in AMF induced by arsenic stress^[60, 61], providing molecular evidence for understanding fungal-mediated arsenic detoxification mechanisms.

5.3. Biotic Stress from Pests and Diseases

The impact of AMF on soil-borne and foliar diseases is a hotspot in plant-microbe interaction research. In rice, the interaction between AMF and rice blast (*Magnaporthe oryzae*) has been studied extensively. Campo *et al.* found that AMF rhizosphere colonization could promote rice growth and enhance resistance to rice blast^[62]. Tian *et al.* compared transcriptomic differences in mycorrhizalized roots of wild and cultivated rice under challenge from the rice blast fungus, revealing the molecular basis of mycorrhiza-induced resistance^[62]. Regarding pests, Cosme *et al.* found that AMF (*Glomus intraradices*) could influence the egg-laying behavior of the rice water weevil (*Lissorhoptrus oryzophilus*), though this effect varied by variety^[63]. Bernola *et al.* found that in some cases, AMF inoculation instead increased rice sensitivity to pests, suggesting that mycorrhiza-mediated resistance is highly specific^[64]. Overall, research on the application of AMF in rice disease management still requires more systematic assessment under field conditions.

6. Conclusion

Research on the rice-AMF interaction has made significant progress over the past two decades. At the molecular level, a relatively complete symbiotic signaling and functional regulation network has been revealed, spanning signal recognition (strigolactones-*OsCERK1*), calcium signal transduction (*CCaMK-CYCLOPS*), transcriptional regulation (*RAM1-DELLA*), and nutrient transport (*OsPT11*, *OsAMT3;1*, *STR1/STR2*)^[8, 9, 12, 14, 16, 21, 24]. These findings not only deepen our understanding of plant-microbe symbiosis mechanisms but also provide targets for the genetic improvement of rice mycorrhizal symbiotic capacity. Kamel *et al.* systematically explained the biological and evolutionary mechanisms of AMF symbiosis from a genomic perspective, providing an important reference for understanding the evolutionary framework of rice-AMF interactions^[65]. However, compared to root nodule symbiosis in legumes, there are still many gaps in the molecular regulatory network of rice mycorrhizal symbiosis, particularly key issues such as carbon source allocation and the balanced regulation of immunity and symbiosis.

At the ecological level, research has clarified that AMF communities are collectively regulated by water regimes, soil types, cultivation practices, and host genotypes. Rice mycorrhizal symbiosis is not an accidental phenomenon under aerobic conditions but a universal ecological process^[5, 34, 35, 39, 42]. Climate change factors such as elevated CO₂ concentrations also affect AMF community composition^[43], providing an entry point for predicting mycorrhizal function under future environmental changes.

At the application level, the promoting effect of AMF on rice nutrient uptake and their protective functions under drought, salinity, and heavy metal stresses have been widely verified, demonstrating the potential of mycorrhizal technology in green agricultural production [51, 55, 56, 66]. However, the transformation from laboratory to field still faces significant bottlenecks. The host specificity and environmental dependence of mycorrhizal effects require future research to focus more on verification under field conditions and the development of regional application schemes.

Looking forward, several aspects deserve focused attention:

1. using single-cell sequencing and spatial transcriptomics to resolve the refined regulatory network of arbuscule development and function;
2. based on genome-wide association studies of rice germplasm resources, mining superior alleles that regulate mycorrhizal symbiotic efficiency [10];
3. developing AMF inoculant formulas and application techniques suitable for paddy field environments;
4. integrating AMF into comprehensive rice nutrient management and green pest control systems, evaluating their synergistic effects with reduced chemical fertilizer and pesticide application.

With the continuous development of multi-omics, gene editing, and synthetic biology methods, research on rice-AMF symbiosis will enter a new stage of deeper mechanism resolution and more precise application transformation, providing new solutions for global food security and sustainable agricultural development.

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