Advances in Environmental Protection 环境保护前沿, 2025, 15(5), 852-861
Published Online May 2025 in Hans. https://www.hanspub.org/journal/aep
https://doi.org/10.12677/aep.2025.155096

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丛枝菌根真菌–植物–土壤互作网络的生态功能与调控机制研究进展

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收稿日期：2025年4月8日；录用日期：2025年5月10日；发布日期：2025年5月28日

摘 要

土壤微生物和植物–土壤系统之间的相互作用对于维持生态系统的功能与应对气候变化至关重要。丛枝菌根真菌(AMF)可以影响植物与土壤之间的物质交流，提高植物生产力和抗逆性，在改善土壤质量和养分循环方面发挥着重要作用。有研究表明，AMF与植物共生抑制植物产量积累，不利于维持土壤生态功能和可持续性。AMF在调控植物–土壤系统中表现出的作用不一致，这可能与环境条件有关。因此，需总结现有研究，系统的阐明AMF对植物–土壤系统生产力、抗逆性和养分循环的作用及其机理。本综述总结了AMF与植物–土壤系统共生关系和共生机理的研究进展；阐述了AMF对植物–土壤系统生产力和抗逆性的作用机制；提出AMF–植物–土壤系统共生领域中尚待系统深入研究的关键科学问题，并分析了当前该领域研究存在的不足与今后的研究方向，以期为农业生态系统的可持续发展提供新的思路。

关键词

丛枝菌根真菌，植物–土壤系统，生态功能

Research Advances in Ecological Functions and Regulatory Mechanisms of the Arbuscular Mycorrhizal Fungi-Plant-Soil Interaction Network

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Received: Apr. 8th, 2025; accepted: May 10th, 2025; published: May 28th, 2025

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文章引用: 于士惠, 刘佩勇, 刘云汇, 王雨琪. 丛枝菌根真菌-植物-土壤互作网络的生态功能与调控机制研究进展[J]. 环境保护前沿, 2025, 15(5): 852-861. DOI: 10.12677/aep.2025.155096

Abstract

The interactions between soil microorganisms and plant-soil systems are crucial for maintaining ecosystem functions and addressing climate change challenges. Arbuscular mycorrhizal fungi (AMF), through mediating material exchange between plants and soil, enhance plant productivity and stress resistance while playing pivotal roles in improving soil quality and nutrient cycling. However, studies have shown that AMF-plant symbiosis may inhibit yield accumulation and compromise soil ecological sustainability. The inconsistent performance of AMF in regulating plant-soil systems could be attributed to environmental conditions. Therefore, it is necessary to summarize the existing studies and systematically elucidate the role of AMF on the productivity, stress tolerance and nutrient cycling of plant-soil system and its mechanism. This review summarizes the progress of research on the symbiotic relationship between AMF and plant-soil systems and the mechanism of symbiosis, describes the mechanism of AMF on plant-soil system productivity and stress tolerance, and proposes the key scientific issues that need to be systematically and thoroughly researched in the field of AMF-plant-soil system symbiosis, as well as analyzes the shortcomings of the current research in this field and the direction of the future research, with the aim of providing new ideas for sustainable development of agroecosystems.

Keywords

Arbuscular Mycorrhizal Fungi (AMF), Plant-Soil System, Ecological Functions

1. 引言

全球耕地资源缩减、人口增长及气候变迁加剧对粮食安全构成多重威胁[1] [2]。工业化肥的过量施用虽提升作物产量，却导致土壤退化、环境风险加剧等问题[3]-[6]，推动农业向高产高效与低碳可持续转型[7]。土壤微生物作为生态调控的关键因子，通过影响植物生长、抗逆响应及物质循环等过程[8]-[11]，为破解上述困境提供了新思路。

AMF 作为与 90%以上被子植物共生的古老微生物[12]，因丧失有机物分解能力而完全依赖宿主[13] [14]。其通过构建根内丛枝结构和根外菌丝网络，显著增强宿主对水分及氮磷养分的吸收效率[12] [15]-[17]。这种共生体系赋予 AMF 多重生态功能：提升植物营养水平[18]-[20]、促进生长发育[20]-[22]、增强抗逆能力[22]-[24]并调控物质循环[25]-[28]。特别是菌丝网络可建立植物间资源共享通道，优化种间竞争关系[29] [30]。

自 19 世纪形态学研究以来[31]，分子技术的突破推动了 AMF 研究纵深发展。当前国际聚焦两大方向：一是解析植物–土壤–AMF 互作机制，阐明其对物质循环和植物生长的促进作用[31]；二是开发其在污染修复和抗逆调控中的应用[32]-[36]。尽管 AMF 已被证实是重要的养分调控通道[37]，现有研究仍缺乏从植物–AMF–土壤系统视角全面解析其综合作用机制。本文系统综述 AMF 多样性特征、共生机制及其生态功能研究进展，为农业可持续发展提供理论支撑。

2. 丛枝菌根真菌(AMF)的生物学特性

2.1. 进化历史与分类学特征

AMF 隶属于球囊菌门(Glomeromycota)，是陆地生态系统中最广泛的共生微生物之一，与 80%以上的

陆地植物形成共生关系[38] [39]。作为专性共生体，其进化历史可追溯至前寒武纪[40]，化石证据显示 4 亿年前 Rhynie Chert 地层的植物根系已存在类似丛枝结构[41] [42]，而泥盆纪分化出的球状体、巨孢菌类[43]和芽孢菌类[44]孢子进一步印证了球囊菌门在地质时期的辐射演化。AMF 的起源时间与植物登陆事件(奥陶纪至泥盆纪)高度同步[45]，表明其共生机制是早期植物适应陆地环境的关键驱动力。

基于形态学与分子系统发育，AMF 被划分为球囊菌纲(Glomeromycetes)下的 5 目(球囊霉目、类球囊霉目等)、14 科、26 属，涵盖 300 余种[46]。球囊霉属(Glomus)因其广布性成为全球土壤优势类群。AMF 多样性呈现显著生态梯度，热带森林与草地丰富度最高，温带及受干扰生境逐渐降低。中国已记录 145 个 AMF 虚拟种(8 科 12 属)，与 800 余种植物形成共生体系[39]。尽管环境因子影响共生建立，但 AMF 的遗传谱系与进化历史共同驱动其多样性分布。当前分类学仍面临形态与分子种区分难题，环境驱动模型的局限性导致全球多样性评估偏差[40] [42]，需结合 DNA 扩增技术与分子标记解析遗传多样性。

2.2. 典型的结构与功能

(1) 丛枝(Arbuscule)

丛枝由根内菌丝(IH)在植物根皮层细胞内形成树状分支结构，分为 Arum 型(线性菌丝扩展，增加交换表面积)和 Paris 型(细胞内盘状扩散，增强结构稳定性)定殖模式[47]。二者均通过复杂分支吸器实现宿主与真菌间的营养交换(图 1)，是碳－磷互惠的核心场所。

(2) 泡囊(Vesicle)

泡囊由 IH 末端膨大形成，80%的 AMF 可产生，主要储存脂类与碳水化合物[48]。其形态因属而异(Glomus 球状、Acaulospora 裂片状等)，部分物种(如 Glomus 属)的泡囊兼具繁殖功能。泡囊形成时间因种而异，可在根内停留数月至数年，但 Gigaspora 和 Scutellospora 等类群不产生泡囊。

(3) 菌丝(Anastomosis)网络

菌丝网络通过孢子丝共生体间化学交换或附着胞定植建立。外生菌丝(EH)延伸至根际外形成“养分高速公路”，吸收磷、氮等元素，并通过菌丝连接实现遗传物质交换[49]。EH 细胞壁较 IH 更厚，赋予其抗土壤微生物胁迫的能力。其生长受土壤 pH、有效磷及宿主－AMF 互作特性调控，功能涵盖侵染、吸收与繁殖。

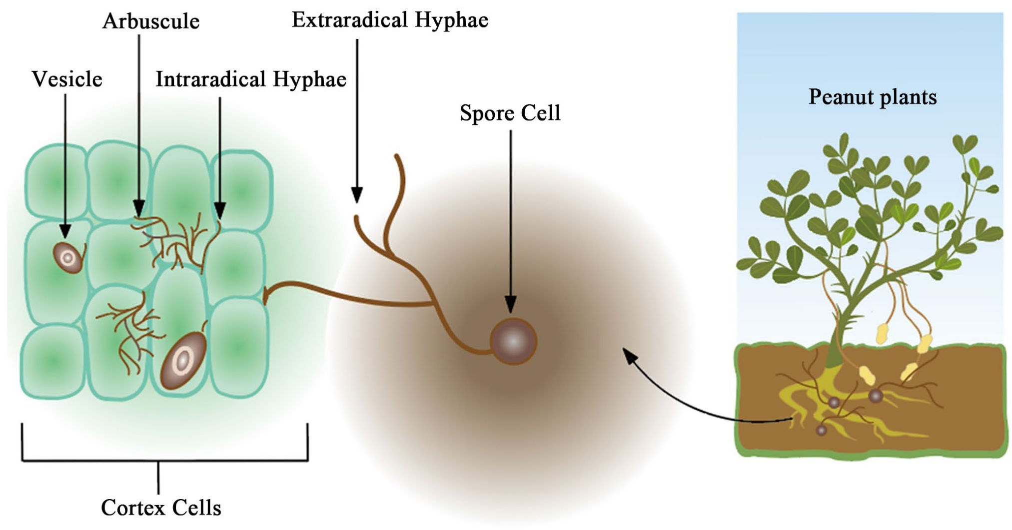

Figure 1. Main structure of AMF
图 1. AMF 的主要结构

3. 丛枝菌根真菌与植物–土壤系统共生关系的发展

3.1. 丛枝菌根真菌的多样性

菌根与植物的共生关系是陆地生态系统中最广泛的互惠形式[50]。1885 年德国植物学家 Frank 通过观察橡树与山毛榉根系共生现象，首次系统提出菌根概念[51]。其本质是双向物质交换：真菌依赖宿主获取碳水化合物，植物则通过菌丝网络增强矿质元素吸收。根据形态特征，菌根分为七大类，其中丛枝菌根与 72%维管植物共生，其标志性结构为根内泡囊和丛枝。部分真菌虽缺失泡囊形成能力，但依然保留丛枝发育特性，此类菌种被统称为丛枝菌根真菌[52] [53]。

3.2. 丛枝菌根真菌与植物–土壤系统共生的分子基础

分子生物学技术推动 AMF 研究从分类描述转向分子互作机制解析[54]。AMF 共生过程可分为五阶段：信号识别→侵染位点形成→外皮层穿透→丛枝分化→孢子发育[55]。宿主分泌独角金内酯激活 AMF 释放菌根因子(Myc 因子)，通过钙信号级联调控基因表达促进菌丝增殖[56]。Shi 团队发现植物磷饥饿响应因子(PHRs)整合根系吸收与菌根共生双途径调控磷代谢[57] [58]。传统认为糖类是主要碳源[59]，但 Jiang 等[60]在《Science》发表的研究颠覆了这一认知，证实脂肪酸才是共生过程中碳转移的核心载体。

成熟共生体系中，丛枝结构作为碳–磷交换枢纽，根外菌丝形成“养分高速公路”[61]，实现跨物种资源联通。WRI5a 转录因子通过协同激活 STR 与 PT4 基因，成为营养交换的分子开关[62]。AMF 多样性受遗传与环境因子共同驱动[63]，土壤水肥条件对共生建立具决定性影响。未来研究需重点关注不同土壤养分梯度下 AMF 介导的营养信号传导机制，以深入解析共生系统的调控网络。

4. 丛枝菌根真菌对植物–土壤系统生产力和抗逆性的作用及机制

4.1. 丛枝菌根真菌对植物–土壤系统生产力的影响及其机制

大量研究表明，AMF 在与植物根系建立共生关系时，可通过调控宿主生理代谢及基因表达途径，显著增强植物对养分的吸收能力、促进籽粒发育及地上部生物量积累，从而提升生态系统的可持续生产力。接种摩西球囊霉可使小麦生物量提升 26%，籽粒增产 15% [26]。玉米–山黧豆间作体系中，AMF 优化种间资源竞争，系统产量提高 19% [22]。其机制包括：(1) 菌丝网络扩展增强氮磷吸收；(2) 根系分泌物激活土壤有机质矿化。但部分研究显示 AMF 可能抑制生长：Mortimer 等发现共生呼吸消耗 30%光合产物[64]，Xavier 证实碳同化与呼吸消耗相抵消[65]。这些矛盾提示 AMF 效应受菌种多样性、土壤肥力等调控(图 2)。

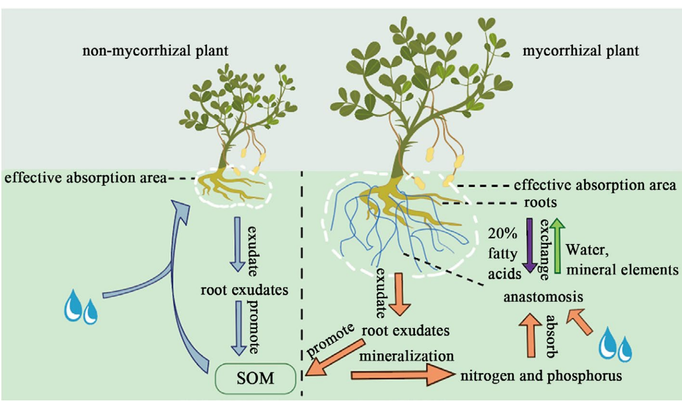

Figure 2. Diagrammatic sketch of the mechanism of promoting plant biomass accumulation through symbiosis between arbuscular mycorrhizal fungi and plants
图 2. 丛枝菌根真菌和植物共生促进植物生物量积累机制示意图

AMF 与植物的互作本质上是宿主对环境响应的适应性权衡(trade-off)。当共生收益超过碳成本时，植物倾向于维持强共生关系；反之则会弱化互作强度。Zhang 等[17]近期揭示了这一权衡的分子机制：AP2/ERF 家族蛋白 ERM1/WRI5a 与 ERF12-TOPLESS 转录复合体形成双向调控网络，通过正–负反馈环动态调节脂质转运与丛枝发育。具体而言，ERM1 和 WRI5a 在共生初期正向调控养分交换，而在后期通过激活 ERF12 抑制脂质过度输出，防止植物自身资源的无效输出。

4.2. 丛枝菌根真菌对植物–土壤系统抗逆性增强机制

AMF 通过多维度调控机制显著增强植物–土壤系统抗逆性，其作用涵盖干旱、盐碱、重金属及病原菌等胁迫响应。作为优质微生物菌肥，AMF 能激活植物激素介导的系统性抗性[57]，提升抗氧化酶活性与渗透调节能力[66]，促进光合作用[67]及养分吸收，并通过分泌球囊霉素相关土壤蛋白(GRSP)改良土壤结构[68]。与根瘤菌、放线菌等益生菌的协同作用已获初步验证[69]-[71]，但其互作机制仍需深入解析。值得注意的是，AMF 对植物生产力的影响存在菌种特异性，部分研究显示接种会导致生长抑制[60] [61]，这可能与共生呼吸消耗 30%光合产物相关[64]，且碳同化与呼吸消耗的平衡关系受 AMF 多样性、土壤水肥条件等多因素调控[65]。

在干旱胁迫下，AMF 通过菌丝网络优化水分再分配，显著提高作物抗旱能力。摩西球囊霉在 40%田间持水量条件下使小麦生物量和籽粒产量分别提升 22%~25% [21]，而异形根孢囊霉与根内根孢囊霉对番茄抗旱能力的提升则呈现菌种特异性差异。其作用机制涉及提高叶片净光合速率与气孔导度、增加渗透调节物质降低氧化损伤[35]、调控激素分泌优化根系构型[72]，以及通过 RiHog1-RiMsn2-STREs 分子模块诱导抗旱基因表达[73]。例如，木豆–小米间作系统中 AMF 菌丝网络实现深层水向表层跨层输送，使浅根作物存活率提升 30% [74]。当前研究多聚焦生理生化层面，未来需结合多组学技术解析干旱信号转导中的分子调控网络，并筛选区域优势菌种以优化菌剂开发。

针对盐碱胁迫，AMF 通过调节渗透物质、维持离子平衡及保护光系统等途径增强植物耐盐性。在中度盐胁迫(100 mmol/L NaCl)下，摩西球囊霉处理使碱蓬碳氮积累量提升 35%，生物量增加 27% [32]，混合 AMF 可使花生叶绿素含量提高 15%~22% [75]。紫花苜蓿接种 AMF 后，超氧化物歧化酶(SOD)、过氧化物酶(POD)和过氧化氢酶(CAT)活性分别增强 40%、32%和 28%，有效清除活性氧[76] [77]。极端盐胁迫(24.36 g/kg NaCl)下，AMF 处理组棉花和玉米矿质元素含量仍保持对照组的 82%~90% [78]。碱性胁迫环境中，混合球囊霉属菌种在高 HCO_3^- 度(10.0 g/mol)下使长春花光合速率提升 28% [79]。值得注意的是，AMF 通过多胺代谢途径改变柑橘根系构型，使菌根侵染率提升 2.3 倍[80]，但菌种筛选与宿主互作特异性仍需系统研究。

尽管 AMF 在抗逆调控中展现出显著潜力，其实际应用仍面临菌种特异性强、环境效应复杂等挑战。未来需构建多尺度研究体系，结合合成群落(SynComs)策略组装功能模块，通过微生物组工程优化土壤碳固存与养分周转的级联效应。同时，需建立基于多组学的菌株资源库与数字孪生系统，动态模拟不同农艺措施下 AMF 功能表达轨迹，为退化土壤修复与农业可持续发展提供精准调控方案。

5. 菌种特异性–环境互作–宿主响应协同驱动的 AMF 负面效应机制解析

AMF 对植物的负面影响通常由菌种特异性、土壤环境异质性及宿主植物适应性共同驱动，具体机制可归纳为以下方面。

5.1. 菌种功能分化导致的负效应

不同 AMF 菌种对宿主碳分配策略的影响是一个复杂且多层次的过程。研究表明，植物可能从更为多样化的 AMF 群落中获益，因为 AMF 的功能互补性可能允许增加资源获取。此外，高 AMF 多样性增加

了植物与最佳 AMF 共生体匹配的概率[81]。在温室实验中，通过对植物和 AMF 进行放射性标记，研究人员发现，随着 AMF 物种丰富度的增加，植物通过 AMF 获取磷的能力增强，同时植物的生物量、磷含量和氮含量也随之增加[81]。

然而，值得注意的是，高侵染力的 AMF 菌种可能会过度消耗植物的光合产物，这可能导致宿主植物的生物量降低。这种现象可能是由于这些高侵染力菌种在与植物进行碳交换时，要求的碳成本较高，从而影响了植物的整体生长和资源分配策略[81]。因此，植物在与 AMF 共生时，选择合适的 AMF 菌种组合是至关重要的，以便在资源获取和碳成本之间达到最佳平衡。

5.2. 土壤环境因子的调控作用

养分阈值效应在植物与 AMF 的共生关系中扮演着重要角色。当土壤中的有效磷浓度超过某一阈值时，AMF 与植物的关系可能从互利共生转变为寄生关系。这种现象在多项研究中得到了验证。例如，在高磷条件下，植物可能会抑制 AMF 的定殖和功能，因为植物能够通过自身的根系满足磷的需求，而不再需要依赖 AMF 提供的磷[82]。此外，研究表明，AMF 在高磷环境下的菌丝网络可能成为植物碳的“陷阱”。在这种情况下，AMF 仍然从植物中获取碳水化合物，但由于植物不再需要 AMF 提供的磷，AMF 的存在对植物的益处减少甚至可能产生负面影响[83]。这种碳与养分交换的不平衡可能导致 AMF 在高磷条件下的功能性降低，甚至对植物生长产生抑制作用[84]。为了更好地理解这种现象，研究者们通过多种实验方法探讨了 AMF 在不同磷浓度下的行为变化。例如，通过对不同磷浓度下 AMF 菌丝生长和植物生长的观察，研究者发现，随着磷浓度的增加，AMF 的菌丝生长和植物的磷吸收效率呈现出不同的变化趋势[85]。这些研究结果提示我们，在农业实践中，应根据土壤磷浓度的变化调整 AMF 的应用策略，以避免因磷过量而导致的共生关系失衡。

6. 展望

针对未来研究方向的展望，本文建议在跨学科技术融合与数据驱动建模层面进行深化探索。在构建数字孪生系统方面，可依托多源数据集成技术，整合植物表型组、AMF 基因组、土壤理化参数及环境动态监测数据，通过高分辨率传感器网络与物联网技术实现实时数据采集。系统构建需开发多尺度耦合模型，结合机器学习算法(如深度神经网络)解析 AMF–植物–土壤互作的非线性关系，并利用高性能计算平台实现生态系统动态仿真。此外，动态模拟 AMF 功能表达轨迹需建立时空分辨的代谢通量模型，结合转录组与蛋白质组时间序列数据，量化共生过程中碳氮交换的动态阈值。此类模型的验证可通过可控微宇宙实验与田间原位观测相结合，利用同位素标记技术追踪光合产物分配与菌丝网络扩展的协同机制。为实现上述目标，需突破现有技术瓶颈，例如开发适用于根际环境的微型生物传感器、构建标准化 AMF 功能基因数据库，并通过跨学科协作(如计算生物学、环境信息学)推动技术落地。最终，数字孪生系统可服务于精准生态管理，例如优化 AMF 菌剂接种策略或预测气候变化下的共生网络稳定性，为农业可持续发展提供理论工具。

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