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丛枝菌根真菌的抑病功能及其应用*

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摘 要 土传病害是引发连作障碍的关键因素, 严重制约着我国集约化农业(特别是种植业)的可持续发展. 丛枝菌根(Arbuscular mycorrhizal, AM)真菌能够提高宿主抗病性、抑制病原物生长及侵染发病, 是农业生产上防控土传病害的重要有益资源, 探索其抑病机制和应用技术是近年来的研究热点, 但一直缺乏比较系统的理论认识. 通过梳理相关研究进展发现, AM真菌主要在宿主根系、根际与植株等3个层面发挥抑病作用, 其中根系防御主要包括AM真菌与病原物竞争生态位和构建机械防御屏障, 根际防御主要包括调节根系分泌物与次生代谢产物及与拮抗菌协同抗病, 而植株防御主要包括促进宿主对养分与水分的吸收和诱导宿主产生系统防御体系, 因而提出AM真菌的"根系-根际-植株三级防御"理论. 在应用技术方面, 着重分析通过接种AM真菌或调动土著AM真菌来防控土传病害的技术研究现状, 并对应用中存在的问题及其发展前景进行展望, 一方面可通过建立AM真菌种质资源库或构建转基因工程菌来解决接种有效期及效果稳定性等问题, 另一方面可通过改变施肥模式和调整耕作制度来高效调动土著AM真菌的抑病活性, 旨在为利用AM真菌防控土传病害、促进集约化种植业可持续发展提供理论依据. (图1 参157)

关键词 土传病害; 连作障碍; 丛枝菌根真菌; 抑病机制; 接种; 施肥
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The function and potential application of disease suppression by arbuscular mycorrhizal fungi*

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Abstract Soil-borne pathogens are among the key factors preventing continuous cropping, which severely restricts the sustainable development of intensive agriculture (notably plant industries) in China. Arbuscular mycorrhizal fungi (AMF), which can improve the disease resistance of their host plants and inhibit growth and infection by pathogens, are important beneficial resources that can prevent and/or control soil-borne diseases. Although the disease-suppression mechanisms and technological application of AMF have become hot topics for research in recent years, there is a relative lack of a systematic theoretical understanding of these topics. Based on a search and review of the relevant literature, the present study found that AMF act in disease suppression at three main points: in the root, the rhizosphere, and the plant. The root defense pathway of AMF involves niche competition and the construction of a physical defensive barrier against infection. The rhizosphere pathway involves the regulation of root exudates and secondary metabolites and the interaction with other antagonists. The plant pathway involves the improvement of nutrient and water uptake by AMF and the induction of the host's systemic defenses. Therefore, a "three-level defense" theory of AMF is proposed, i.e. the root-rhizosphere-plant defense system. Based on current research on soil-borne disease suppression via inoculation with AMF or stimulating indigenous AMF, the problems and developmental prospects facing the application of AMF were also discussed. One approach that has been suggested to solve

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some of the problems association with the application of AMF, such as the limited term over which treatments remain effective and the low stability of their effects, is the establishment of a germplasm bank of AMF, or the construction of transgenic fungi. On the other hand, stimulating the disease suppression activity of indigenous AMF by changing fertilization patterns and/or the farming system used may also help to solve these problems. These efforts should be made to provide a theoretical basis for the exploiting of AMF for the prevention and control of soil-borne diseases, and the acceleration of the sustainable development of an intensive plant production industry in China.

Keywords soil borne disease; continuous cropping obstacle; arbuscular mycorrhizal fungi; disease suppression mechanism; inoculation; fertilization

随着我国农业产业结构的调整，农作物种植趋于规模化、产业化，这在一定程度上解决了农业增产与农民增收问题[1]. 但由于集约化农业强调土地的高强度利用，且作物种植单一、复种指数高，随着栽培年限延长难免会出现作物生长滞缓、土传病害加剧、产量和品质下降等连作障碍问题[2-4]，严重制约农业的可持续发展. 连作障碍的成因十分复杂，但主要是土壤、植物、病原物三重因素综合作用的结果，包括土壤理化性质劣化、植物自毒作用、土传病原物激增等[5-7]. 其中，土传病原物是引起连作障碍极为重要的因素，以真菌为主，也包括部分细菌、线虫和病毒，故主要表现为土壤微生物区系由“细菌型”向“真菌型”转变[8]，而真菌化则是土壤健康质量退化的标志[9]. 连作导致土壤微生物区系发生改变，如芽胞杆菌（*Bacillus*）和假单胞菌（*Pseudomonas*）等有益微生物的数量减少，尖孢镰刀菌（*Fusarium oxysporum*）等病原菌的数量增加[10-11]. 研究表明，70%的连作障碍是由土传病原物引起的[12]，如对连作土壤进行灭菌处理，则能有效缓解再植病害[13-14]. 然而，在生产实践上对连作土壤进行大规模灭菌存在实施难度和经济制约，且灭菌对土体结构及土壤有益微生物的破坏表明并非一种可持续手段，因而有必要挖掘土壤自身的抑病功能及关键抑病资源.

在土壤生态系统中，有些微生物在抑制土传病原物、促进作物健康生长方面扮演着重要角色，如丛枝菌根（Arbuscular mycorrhizal，AM）真菌正是这样的生防菌[15]. AM真菌能与80%以上高等植物建立互惠共生关系[16]，能增强植物对非生物胁迫的抗逆性[17-19]，而且在防控土传病害方面也有显著的作用效果[20-21]. 自Safir首次发现接种AM真菌摩西管柄囊霉（*Funneliformis mosseae*）能降低由土棘壳孢（*Pyrenochaeta terrestris*）引起的洋葱根腐病的发病率[22]以来，众多研究表明AM真菌能帮助宿主抵御病原物的侵染发病[23-25]，如对尖孢镰刀菌和白腐小核菌（*Sclerotium cepivorum*）等均有很好的生防能力[26]，对高山红景天根腐病、桉树幼苗青枯病、茄子黄萎病、玉米纹枯病等均有明显的防治效果[27-29]. 尽管国内外已有大量学者关注AM真菌与土传病原物之间的相互作用，且对其抑病功能展开了长期而丰富的研究，但对其抑病机制和应用技术缺乏系统的整理和认识. 因此，本文对AM真菌防控土传病害的作用机制与应用技术研究进展进行梳理总结，以期为利用AM真菌抑制病原物繁殖与侵染宿主、防控土传病害、缓解连作障碍、推动农业可持续发展提供一定参考.

1 AM真菌对土传病害的防控作用

AM真菌提高宿主抗病性是一个复杂的综合过程，既可能是局部作用，也可能产生系统性作用[30]. 综合来看，AM真菌对土传病害的防控作用源自其对植物根系的侵染，进而对宿主植物形成了一个“根系-根际-植株三级防御”体系（图1）：首先在根系通过竞争生态位和构建机械防御屏障直接排斥病原物对宿主的侵染，其次在根际通过调节根系分泌物与次生代谢产物及与其他拮抗菌产生协同作用来抑制病原物的生长，此外还通过改善宿主的养分与水分状况和诱导植株产生系统防御体系来弥补或减轻病原物侵染对作物造成的危害. 因此，在防控土传病害、缓解连作障碍方面表现出巨大的潜力. 当然，关于根系、根际与植株的作用位点划分不是绝对的，它们之间是存在交叉或关联的. 下面基于“根系-根际-植株三级防御”理论来归纳和讨论AM真菌对土传病害的防控原理.

1.1 AM真菌的根系防御作用

1.1.1 AM真菌与土传病原物竞争生态位 引起土传病害的最根本原因是土壤微生物区系失调、病原物激增[31]. AM真菌可与病原物竞争生态位，通过抑制病原物繁殖达到防控土传病害的目的[32]. 生态位竞争主要包括侵染位点和营养能源两个方面. 从侵染位点来看，AM真菌侵染宿主根系形成菌根后，其菌丝会迅速占据相应的生态位点，从而减少病原物的侵染位点并降低其数量. 例如，在沉香（一种药材）根际接种聚生球囊霉（*Glomus fasciculatum*），根系侵染位点被AM真菌占据，可减轻瓜果腐霉菌（*Pythium aphanidermatum*）的侵染，降低植株病情指数[33]；在番茄根际接种摩西管柄囊霉，引起根腐病的寄生疫霉（*Phytophthora parasitica*）在菌根化根系中的入侵位点数明显少于对照[32]. 研究发现，丛枝结构的发育状况和植物抗病性呈正相关关系，根内根生囊霉（*Rhizophagus irregularis*）侵染后丛枝着生数量与病情指数呈负相关[34]. 从营养能源来看，AM真菌和病原物的生长都依赖宿主植物提供能量和营养，故存在直接竞争关系[35]. 当来自宿主根系的光合产物首先被AM真菌利用时，病原物获取的机会无疑会减少，从而限制病原物的生长和繁殖. 此外，病原菌及其代谢产物也会抑制AM真菌的生长发育及菌根共生体的形成[36]. 与之相反，AM真菌还会通过产生拮抗类或营养螯合类物质抑制病原物生长，这则是两者之间具体的竞争策略和竞争手段.

1.1.2 AM真菌在根系构建机械防御屏障 AM真菌侵染

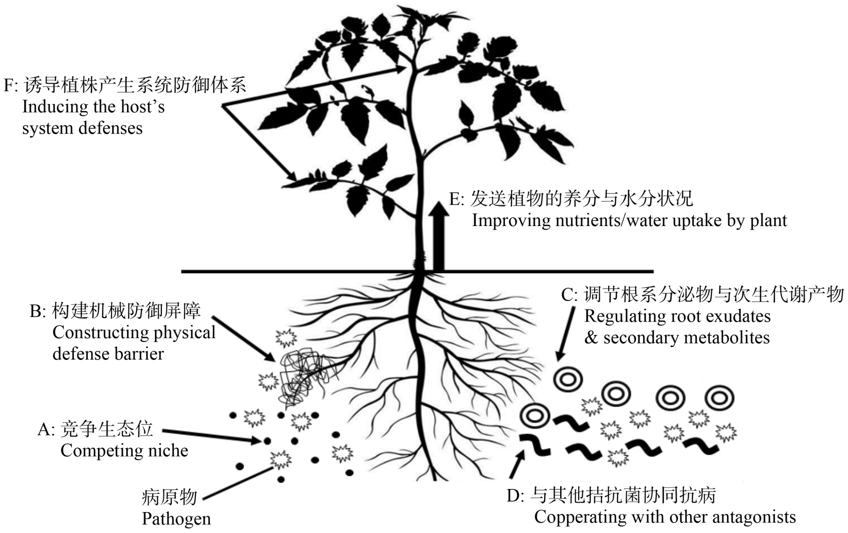

图1 AM真菌对土传病害的"根系–根际–植株三级防御"体系示意图.
Fig. 1 The schematic diagram of "three-level (root-rhizosphere-plant) defense" system of AM fungi to soil-borne diseases.

植物根系形成菌根后，根内与根外蔓延交错的菌丝网建立起一套天然的机械防御屏障，增加病原物侵染植物根系的难度[37]. 菌根化后根尖表皮会加厚，细胞层数会增加，随着表皮细胞壁物质不断积累，其木质化、硅质化程度不断提高[38-39]，且在病原物侵染时会诱导富含羟基脯氨酸的糖蛋白启动快速防御反应使根系细胞壁强度增大，不易被病原物分解的蛋白酶、纤维素酶、半纤维素酶等分泌增强[40]，侵染难度随之加大[41]. 例如，向番茄幼苗单独接种寄生疫霉，根尖分裂组织细胞的分裂活性降低，根尖直径变小，具分裂活性的细胞及细胞核降解或坏死；而同时接种摩西管柄囊霉，根尖分裂组织细胞仍然具有分生能力，根尖变长，直径增大，根皮层相应变厚，对病原菌入侵形成机械屏障，能保护植物根系正常生长[42]. 利用转移Ri T-DNA胡萝卜根器官双重培养技术研究发现，尖孢镰刀菌菊花专化型（*F. oxysporum* f. sp. *chrysanthemi*）可在非菌根化根系包括维管束中柱等在内的大部分器官中大量繁殖，却被限制在菌根化根系的表皮和外皮层部分[43].

1.2 AM真菌的根际防御作用

1.2.1 AM真菌调节根系分泌物与次生代谢产物 植物根系因化感作用所分泌的自毒物质会抑制植株防御酶活性[44-45]，且可为土传病原物增殖提供所需的营养能源，如番茄、黄瓜、豌豆等根系分泌的苯甲酸、肉桂酸、水杨酸等酚酸类自毒物质会导致病原物侵染作物[46]，而外源添加肉桂酸可显著促进尖孢镰刀菌菌丝发育，提高蚕豆枯萎病的病情指数[47]. 研究发现，AM真菌侵染能减少宿主根系分泌的自毒物质[48]，如连作西瓜土壤中酚酸类物质的含量[49]. 究其原因，根系自毒物质本可直接分泌到土壤中，但菌根形成后会对分泌物进行过滤，其中一部分会被真菌作为营养利用和代谢，所以送达土壤的分泌物会发生很大变化[50-51]. 同时，菌根化植物的根系分泌物及渗出物（如氨基酸、有机酸等）的数量与质量也会发生变化，进一步改变根际微生物区系[52]，如菌根化棉花根际真菌的数量在整个生长期一直低于对照，其发病率也随之降低[53]；接种地表球囊霉（*Glomus versiforme*）的番茄根际细菌数量高于对照，而番茄青枯菌（*Rastonia solanacearum*）的数量却显著低于对照[54]. 此外，AM真菌能调节植物产生次生代谢产物，如通过提高植株体内苯丙氨酸解氨酶的活性[40]来促进和抗病性有关的次生代谢物质（如植保素、生物碱、胼胝质、酚类化合物和类黄酮）的合成[55]，在抵御病原菌入侵过程中可降解真菌细胞壁，抑制孢子萌发与菌丝体生长[56]；而有的次生代谢产物可产生毒素，抑制病原物的生长繁殖甚至直接杀死病原物[57-58]. 研究发现，AM真菌既能提高不同连作年限西瓜根内总酚含量，增强西瓜根系抗病性[49]；也能诱导西瓜根系产生植保素，显著降低根内和根际土壤中尖孢镰刀菌的数量以及西瓜枯萎病的发病率和病情指数[59]；还能促进棉花根系产生大量酚类化合物，提高棉花抵御大丽轮枝菌（*Verticillium dahliae*）的能力[60]. 另一方面，适宜浓度的次生代谢产物对菌根共生体的建立也能起到促进作用[61].

1.2.2 AM真菌与其他拮抗菌协同抑制病原物 AM真菌可与土壤有益微生物产生协同抑病作用，如刺激对土传病原物有拮抗作用的微生物（即拮抗菌）的活性，通过吸引木霉（*Teichoderma*）、链霉菌（*Streptomyces*）、粘帚霉（*Gliocladium*）等大量有益拮抗菌到根际定殖，进而消耗大量碳源及其他营养物质[62-63]，降低病原物在根际的定殖能力[64]. 例如，在番茄根际接种摩西管柄囊霉和根内根生囊霉均能增加根际有益拮抗菌数量、抵御病原菌侵染宿主[65]；在连作蚕豆根际接种摩西管柄囊霉、扭形球囊霉（*Glomus tortuosum*）和幼套球囊霉（*G. etunicatum*）可不同程度地提高根际细菌的碳源利用能力及多样性指数，同时降低蚕豆枯萎病的病情指数[66]. 此外，拮抗菌对AM真菌侵染、菌根生长发育及功能发挥也有一定促进作用，如蒙氏假单胞菌（*Pseudomonas monteilii*）能明显促进AM真菌对刺槐的侵染[67]，而强壮类芽胞杆菌（*Paenibacillus validus*）可为根内根生囊霉侵染胡萝卜根系提供信号物质[68]，这为AM真菌与拮

抗菌协同抑病提供了具体路径.

1.3 AM真菌的植株防御作用

1.3.1 AM真菌改善植物的养分与水分状况 AM真菌能够通过根外菌丝扩大根系吸收范围，有效提高宿主对环境中养分与水分的吸收利用，同时对不同植物间的水分和养分进行再分配[69]，从而增加宿主生物量，在一定程度上补偿因病原物侵染而造成的生物量损失和根系功能损伤[70]，而健壮的植株也间接提高了抵御病原物侵染的能力[71-72]. AM真菌还有助于宿主植物对铁、锌、钴、铜、锰和镍等微量元素的吸收[73-74]. 例如，发病植株经常表现硼、氮、铁、镁、锌的匮缺[75]，而在发生西瓜枯萎病的大田接种AM真菌能促进西瓜对氮、磷、硼和锌等矿质营养的吸收，增加西瓜生物量，降低枯萎病发病率与病情指数[59]；给连作番茄接种AM真菌，番茄的叶片中可溶性糖、可溶性蛋白含量显著提高，植株干重随AM真菌侵染率升高而升高[76]. 研究发现，利用地表球囊霉将黄瓜菌根化育苗后再接种尖孢镰刀菌，壮苗指数较对照提高0.22倍，病情指数较对照降低26.6% [77]；民勤绢蒿（*Seriphidium minchiinense*）接种摩西管柄囊霉后叶片可溶性糖与可溶性蛋白含量显著增加，有利于宿主保持较低的渗透势，促进宿主吸收水分，提高其保水能力[78]. 连作条件下菌根化根系输水能力显著高于普通根系，可以降低植株的萎蔫系数[79].

1.3.2 AM真菌诱导植物产生系统防御体系 AM真菌能诱导植物更加迅速地产生防御酶类以抵御病原物入侵，其中过氧化氢酶、过氧化物酶和超氧化物歧化酶等可作为植物抗病性的生理生化指标[80-81]. 研究发现，接种根内根生囊霉可以提高橄榄苗根系超氧化物歧化酶和过氧化物酶活性，从而抑制病原菌大丽轮枝菌的生长[82-83]；在葡萄连作土壤接种AM真菌，葡萄叶片与根系超氧化物歧化酶活性均提高，根系活力增强[84]. 此外，AM真菌侵染作物根系能诱导植株合成内源信号物质，如生长素、细胞分裂素、赤霉素、油菜素内酯、茉莉酸、水杨酸、乙烯、脱落酸等，激活植物的系统防御体系，提高其抗病性[85-86]. 例如，接种摩西管柄囊霉同时施加外源水杨酸能有效抑制尖镰孢对番茄的侵染，降低病情指数[87]；向已感染尖镰孢菌（*F. oxysporum* f.sp. *cucumarinum*）的番茄幼苗根系接种聚生球囊霉和大果球囊霉（*Glomus macrocarpum*），茎叶中茉莉酸的含量提高8倍，且发病指数下降75%-78% [88]. AM真菌能提高宿主相关防御基因的转录水平，并通过菌丝桥诱导邻近植株的基因转录[89]. 病程相关蛋白是植物体内受病原体或其他因子胁迫而诱导表达的一类蛋白，在植物抵御病害方面发挥着重要作用[90]. 研究发现，丹参接种地表球囊霉后其防御基因*PR1*和*WRKY*的表达量显著增加，抗病性显著提高[91]；与仅接种早疫病病原菌的对照相比，摩西管柄囊霉侵染的番茄根系中抗病基因的转录水平显著升高，与其有菌丝桥连接的番茄根系中抗性基因的表达量也显著提高[92]. 通过嫁接试验体系证实，受AM真菌感染诱导的抗病信号甚至还可以从砧木根系远距离传导至地上部接穗的茎叶，进而激发地上部的抗病性[93].

2 AM真菌在防控土传病害中的应用

AM真菌防控土传病害的应用技术，可主要分为接种AM真菌和调动土著AM真菌两大方向. 在应用前最好先测定土著AM真菌的活性及数量，若土著AM真菌拥有高数量且活性强，则应该采取保护措施从而更有效地利用土著菌的作用，若土著AM真菌数量少且活性差，则可以考虑引入外来菌种[94]. 接种AM真菌既可单独接种，也可与其他有益菌（含生防菌）联合接种. 调动土著AM真菌主要通过调整施肥模式或改变栽培制度等途径，如通过合理减少氮肥与磷肥投入、增施有机肥以及构建间作系统等来调动土著AM真菌的促生抗病活性[95-96]，在防控土传病害上具有较大挖掘潜力.

2.1 接种AM真菌

2.1.1 单接种AM真菌 研究发现，接种幼套球囊霉显著降低黄瓜枯萎病病情指数和发病率，根际真菌减少，细菌增多，降低了病原菌侵害宿主的机率[97]；接种摩西管柄囊霉能降低西瓜枯萎病病情指数、根内和根际土壤尖孢镰刀菌数量[98]；接种根内根生囊霉和摩西管柄囊霉可以推迟烤烟青枯病发病时间，降低发病率和病情指数[99]；接种地表球囊霉则抑制根际大丽轮枝菌的繁殖，缓解棉花枯萎病发生[100]. 但是，AM真菌的来源也会影响其接种效应，如在土壤不灭菌条件下接种源自供试土壤本身的AM真菌在增强植物抗病性上显著优于外源的摩西管柄囊霉[101]，这与所接种AM真菌的环境适应性有关，也可能是由于土著菌与外源菌之间存在竞争. 国内外针对接种单一AM真菌防控土传病害已进行了深入的研究，但目前关于接种AM真菌混合菌剂抑制土传病原物的研究仍不多见. 接种混合菌剂往往能更有效地促进宿主吸收营养[102]，提高生物量[103]，并更有效地抑制土传病原物侵染[104]. 例如，接种苏格兰管柄囊霉（*Funneliformis caledonium*）与混合菌剂（*Glomus* spp.和*Acaulospora* spp.等）均显著提高AM真菌侵染率，但仅混合菌剂提高黄瓜生物量、降低枯萎病发病率，并达到与未接种尖孢镰刀菌处理相当的产量水平[105]；以地表球囊霉和混合菌剂*Glomus* spp.分别对番茄进行菌根化育苗，混合菌剂对番茄青枯病的抑制优于单一菌剂[106]. 此外，对鹰嘴豆预先接种摩西管柄囊霉、聚生球囊霉和根内根生囊霉组合菌剂有效降低了枯萎菌的密度，病情指数下降高达90% [107].

2.1.2 AM真菌与其他有益菌双接种 根际促生菌（Plant growth promoting rhizobacteria，PGPR）是能在根际自由活动且通过固氮、溶磷、拮抗病原物等途径促进植物生长和防控土传病害的有益细菌[108]，也能诱导植物产生系统抗性增强抗病能力，目前发现的有假单胞菌、芽胞杆菌、根瘤菌（*Rhizobium*）、农杆菌（*Agrobacterium*）、沙雷氏菌（*Serratia* Bizio）等属[89]. PGPR与AM真菌双接种，两者之间可通过协同抑制病原物或提高植物抗病性来共同发挥对土传病害的生防功能[109-110]，主要的PGPR有假单胞菌和芽胞杆菌[111-112]. 研究发现，利用摩西管柄囊霉、根内根生囊霉和地表球囊霉与5个PGPR菌株混合接种，黄瓜根际尖孢镰刀菌数量显著减少、枯萎病发病率有效降低[113]. 与之相似，摩西管柄囊霉与枯草芽胞杆菌（*Bacillus subtilis*）双接种显著降低秋季草莓冠腐病病情指数、根坏疽程度及恶疫霉合子数[114]，地表球囊霉与芽胞杆菌双接种能减轻树番茄根系病害发生程度[115]，根内根生囊霉与杰氏假单胞菌（*Pseudomonas jessenii*）或类黄假单胞菌（*P. synxantha*）双接种能提高防御性酶活性，降低

丙二醛含量[116]，苏云金杆菌（*Bacillus thuringiensis*）与5种AM真菌共同接种于齿叶薰衣草也有相同的功效[117]. 此外，马铃薯接种根内根生囊霉和PGPR（*Pseudomonas* sp.）可上调植株体内乙烯响应因子（Ethylene-responsive factor, EFR）的基因表达量，降低立枯丝核菌对马铃薯的危害[118]；两者双接种可协同增强黄瓜对病原菌的抗性，且改变病原菌相关防御基因的表达[119]. 由此可见，AM真菌与PGPR双接种是通过提高防御酶活性、促进合成抗病信号物质、上调防御基因表达和降低植株体内有毒物质等机制拮抗病原物和提高植物抗病性[120]. 因此，进一步探索和开发AM真菌与PGPR的抗病组合菌剂是十分有意义的.

2.2 调动土著AM真菌

2.2.1 改变栽培制度 目前国内外利用AM真菌防控土传病害的研究大多关注接种外源AM真菌，如能定向而高效地调动土著AM真菌，同样具有巨大的应用价值. 例如，AM真菌的群落组成会因土地利用方式、施肥模式、耕作制度及其他管理措施等的调整而发生演替[121]，也会因宿主植物不同而造成群落结构和侵染水平上的差异[122-123]. 研究发现，免耕能有效促进AM真菌根外菌丝生长并显著提高土壤碱性磷酸酶活性，4年持续免耕并不会造成土著AM真菌群落结构的退化[124]；免耕主要提高大粒径团聚体中AM真菌的种群丰度，且可通过提高球囊霉素等促进土壤团聚化[125]. 结果表明，免耕或可通过促进AM真菌的增殖和活性来提高其抑病功能. 传统的单一作物种植模式被认为会降低AM真菌的物种丰富度和侵染力，因为连作会抑制根际土著AM真菌的活性、减少定殖在作物根系的土著AM真菌数量[126]，而关于间作可提高AM真菌多样性的研究已愈来愈受重视[127]，但参与间作的作物种类也会深刻影响AM真菌群落[128]. 研究发现，间作能有效增加单位面积生物多样性，使土壤中AM真菌物种丰富度和种群多样性高于单作，可以直接促进AM真菌的侵染与菌根的形成[129]. 例如，间作韭菜可显著提高番茄根系AM真菌侵染率（比单作高出20%），且根际尖孢镰刀菌的数量显著降低[20]；间作玉米显著增加土壤中AM真菌的生物量（比马铃薯单作提高18%），土壤真菌与细菌的生物量比值下降，促进土壤向高肥效的"细菌型"土壤发展[130]. 事实上，间作本身就是防控土传病害、缓解连作障碍的有效手段，如间作辣椒处理西瓜枯萎病发病率降低24% [131]. 间作能够提高根际土壤养分的有效性、促进植物生长，提高植株体内防御酶活性、增强根系活力，降低根际病原菌（*F. oxysporum*）数量、提高植株抗病性[132]. 在间作系统中，AM真菌既能与病原物直接发生竞争关系，又能通过宿主间接发挥抗病作用，且与间作抑病有一定的叠加效应. 目前有关AM真菌在间作系统抑病过程中所发挥作用的认识十分匮乏，亟待开展系统研究.

2.2.2 调整施肥模式 集约化农业生产中高养分投入是最显著的特征，但氮肥、磷肥对土著AM真菌侵染率、孢子密度、菌根发育存在抑制作用，会使宿主植物大量削减或者停止向AM真菌分配光合产物，导致AM真菌侵染势降低[133]，影响AM真菌发育[134]. 研究发现，AM真菌侵染率和孢子密度随磷肥施用量的增加而减少[135]，即使是中等施磷水平也大大降低土壤中AM真菌孢子的数量[136]. AM真菌的侵染势在供氮水平较低时随磷含量的增加而降低[137]，在供氮充足情况下该变化会更加明显[138]. 与之相反，长期缺施磷肥能够保持较高的AM真菌侵染率，即AM真菌的活性更高，植物依赖性也更大[139]. 施用氮肥也会改变土壤中AM真菌的种类和群落组成[140-141]，但磷肥的影响有时较小[142]. 研究发现，施用大量的氮、磷肥不仅能降低AM真菌的侵染率，也会改变AM真菌的多样性，一般球囊霉属的数量会增加，而其它属的数量会减少[143]. 另一方面，土壤含有丰富的有机质也会对丛枝菌根的形成产生正效应，增加AM真菌的多样性[144-145]，而适量有机质也有利于提高AM真菌的孢子数[146]. 因此，向贫瘠或缺肥土壤中施有机肥往往可通过增加土壤有益微生物[147]和改善土壤质地[148]等途径来促进AM真菌菌丝生长和侵染[149]，提高其多样性与功能[150]. 例如，在利用有机肥改良的沙土中AM真菌菌丝的生长加快且侵染率明显提高[151-152]，菌丝、泡囊和总侵染率均与土壤有机质含量呈正相关[153]. 通过长期定位试验发现，潮土中施有机肥能显著增加AM真菌的种群数量、物种丰富度与多样性[154]，但也会降低AM真菌侵染率[155]，这应该与土壤肥力状况、宿主植物类型、AM真菌种类和施肥水平等有关[144]. 有盆栽试验发现，当有机肥用量低于2.0 g/kg时，摩西管柄囊霉的侵染率、孢子密度均高于不施肥处理，且随有机肥水平的提高而逐渐增高，但当有机肥用量超过2.0 g/kg时，各项指标则与对照处理相当或显著低于对照处理[156].

3 问题与展望

综上可知，AM真菌在提高植物防御和抵抗病原物侵染的能力、防控土传病害与缓解连作障碍方面表现出巨大的应用前景与生产价值. 尽管目前关于AM真菌与病原物之间的互作研究已经取得了丰富进展，但要将AM真菌规模应用于集约化农业生产中，仍有一些亟待解决的理论与技术问题.

（1）AM真菌防控连作土传病害的研究大多关注其抗病效果，但对防控机制方面的研究不够深入，究竟起主要作用是哪些机制，起次要作用的又是哪些过程，目前还没有认识清楚. 因此，利用同位素标记、分子生物学和激光共聚焦扫描显微等技术探究植物防御体系与根际微生物群落变化的研究亟待加强，进而探明AM真菌的抑病机制、对各种信号途径的影响过程以及各个信号物质间的相互联系，明晰AM真菌对土传病原物的"根系–根际–植株三级防御"体系之间的交叉、关联与协调机制.

（2）目前关于接种AM真菌的活性有效期及效果稳定性难以保证. AM真菌的积极防效依赖于较高的侵染率[157]，但受宿主基因型、AM真菌种类与病原菌接种时间等因素影响. 未来一方面应开展广泛的大田和保护地试验以及长期定位试验，深入研究能够使宿主受益最大化的最佳接种条件与管理措施，建立AM真菌生防效果评价标准；另一方面应对AM真菌菌种甚至菌株进行甄别筛选，建立AM真菌种质资源库，为在不同的宿主–病原物系统中接种相应的AM真菌创造条件. 此外，还可提取、纯化抗病性AM真菌菌株的抗菌物质（如抗菌蛋白、抗生素等），克隆、分离能够表达抗菌物质的基因，通过遗传工程技术，构建高效、多抗转基因工程菌.

（3）AM真菌是一类严格共生菌，目前不能单独进行纯

培养，只能通过侵染宿主植物根系进行扩繁，使AM菌剂的规模化生产难以完成，这严重限制了AM真菌菌剂的推广应用. 因此，如何通过改变施肥模式和调整耕作制度等方式来定向调动和充分发挥土著AM真菌的抑病功能，应是未来需要倍加重视和努力推进的研究方向.

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