

丛枝菌根结构与功能研究进展*

田 蜜¹ 陈应龙² 李 敏¹ 刘润进^{1**}

(¹青岛农业大学菌根生物技术研究所, 山东青岛 266109; ²School of Earth and Environment/UWA Institute of Agriculture, University of Western Australia, WA 6009, Perth, Australia)

摘 要 丛枝菌根(arbuscular mycorrhiza, AM)是陆地生态系统中分布最广泛、最重要的互惠共生体之一,对提高植物抗逆性、修复污染生境、保持生态系统稳定与可持续生产力的作用显著. AM结构特征是判断菌根形成的主要指标,与其功能密切相关. 本文总结了AM丛枝结构、泡囊结构、菌丝结构和侵入点结构等发育特征;分析了A型丛枝结构、P型丛枝结构、泡囊结构和根外菌丝结构与促进寄主植物养分吸收和生长、提高植物抗旱性、耐涝性、耐盐性、抗高温、拮抗病原物、提高植物抗病性、抗重金属毒性、分解有毒有机物、修复污染与退化土壤等功能的关系,及其所发挥的重要作用;探讨了影响AM结构与功能的因子,以及基于AM不同结构所发挥功能的作用机制. 旨在为系统研究AM真菌发育特征、AM真菌效能机制,以及评价和筛选AM真菌高效菌种提供依据.

关键词 丛枝菌根 丛枝菌根真菌 侵染 寄主植物

文章编号 1001-9332(2013)08-2369-08 **中图分类号** Q949 **文献标识码** A

Structure and function of arbuscular mycorrhiza: A review. TIAN Mi¹, CHEN Ying-long², LI Min¹, LIU Run-jin¹ (¹*Institute of Mycorrhizal Biotechnology, Qingdao Agricultural University, Qingdao 266109, Shandong, China*; ²*School of Earth and Environment/UWA Institute of Agriculture, University of Western Australia, WA 6009, Perth, Australia*). -*Chin. J. Appl. Ecol.*, 2013, 24(8): 2369–2376.

Abstract: Arbuscular mycorrhiza (AM) is one of the most widely distributed and the most important mutualistic symbionts in terrestrial ecosystems, playing a significant role in enhancing plant resistance to stresses, remediating polluted environments, and maintaining ecosystem stabilization and sustainable productivity. The structural characteristics of AM are the main indicators determining the mycorrhizal formation in root system, and have close relations to the mycorrhizal functions. This paper summarized the structural characteristics of arbuscules, vesicles, mycelia and invasion points of AM, and analyzed the relationships between the Arum (A) type arbuscules, Paris (P) type arbuscules, vesicles, and external mycelia and their functions in improving plant nutrient acquisition and growth, enhancing plant resistance to drought, waterlogging, salinity, high temperature, diseases, heavy metals toxicity, and promoting toxic organic substances decomposition and polluted and degraded soil remediation. The factors affecting the AM structure and functions as well as the action mechanisms of mycorrhizal functions were also discussed. This review would provide a basis for the systemic study of AM structural characteristics and functional mechanisms and for evaluating and screening efficient AM fungal species.

Key words: arbuscular mycorrhiza (AM); arbuscular mycorrhizal fungi; colonization; host plant.

丛枝菌根(AM)真菌在侵染植物根系形成共生体过程中,通过参与植物生理生化代谢与基因调控,改善植物营养、提高植物抗逆性、改善生态环境安全

性、保持和增强生态系统可持续生产力. 众所周知,任何有生命的有机体和无生命的无机体的结构往往决定了其所具备的功能. 基于“结构决定功能”的理念和思路,尤其是前人研究结果所给出的有关迹象或证据^[1-2],作者提出AM结构特征与其功能密切相关的科学假设. 越来越多的试验结果表明,AM真

* 国家自然科学基金项目(31272210)和山东省科技发展计划项目(2012GNC11010)资助.

** 通讯作者. E-mail: liurj@qau.edu.cn

2013-10-29 收稿,2013-06-22 接受.

菌所具有的促进植物吸收养分、增强植物对干旱、水涝、高温、高盐、重金属毒害和土传病害等抗逆性、促进植物生长、分解有毒有机物、修复和改良污染土壤等功能与其菌根结构发育特征密切相关^[3-5]。那么, AM 不同结构特征是否具备与以往认识所不同的功能? AM 各结构,特别是菌根侵染率与其功能之间到底是什么关系?影响 AM 结构发育和功能的关键因素有哪些?深入系统地探讨这些问题,对于建立高效的菌种评价体系和指导高效菌种的筛选与应用具有一定的理论和实际意义。

1 丛枝菌根结构特征

AM 真菌侵染植物根系,首先形成附着泡和侵入点结构,随后侵染菌丝进入根内,扩展成胞间菌丝和胞内菌丝。其中一部分根内菌丝与根外(表)真菌结构相连,另一部分顶端膨大形成泡囊(vesicles)或/和菌丝二分叉式生长形成丛枝结构。研究表明,AM 真菌可形成不同形态结构的丛枝,其中,Arum(A)型和 Paris(P)型最为典型^[6]。Szymon 等^[7]对 15 种药用植物观察发现,大多数植物 AM 形成 A 型,少数形成 P 型,部分是中间型。

AM 真菌可以从幼嫩根系任何部位侵染,多数情况下是从根系成熟区侵入,也可以从根尖(即根冠、分生区或/和伸长区)侵入,形成丛枝、泡囊、根内菌丝等典型的菌根结构。分支级次越高的根尖,菌根侵染率也越高^[8]。舒玉芳等^[9]观察到 AM 真菌侵染的桑树根尖,单条根系侵染率在 0~100%,82% 的根尖形成了 AM,包括典型的泡囊、丛枝和根内孢子等 AM 结构。该结果支持了早期的研究结论^[8]。AM 真菌侵染根尖的特性,表明该真菌的生态位与土传病原物相同,这就为拮抗病原物创造了得天独厚的条件^[10]。更为重要的是,由根内伸展至根外于土壤中形成的巨大菌丝网络,以及由此形成的菌根网路为其发挥生理生态功能(如水分养分吸收等)奠定了坚实的生物学和生态学基础。

2 丛枝菌根结构与功能的相关性

2.1 AM 真菌可以改善植物的营养状况

研究表明,AM 真菌可以改善植物对养分的吸收^[11-12]。例如,AM 真菌促进了黄花蒿(*Artemisia annu*)根系对养分的吸收,增加了各器官中 N、P、K 含量^[13]。摩西球囊霉(*Glomus mosseae*)对木薯(*Manihot esculenta*)的侵染率较高,菌根的形成增加了茎内 P 含量和植株的生长^[14]。接种 AM 真菌处理的番

茄叶片中的可溶性糖、可溶性蛋白、硝酸还原酶活性均比不接种处理有所增加,菌根侵染率与植株茎、根干质量及可溶性糖含量之间呈极显著正相关^[15]。AM 真菌与根系共生后,能显著促进根系对土壤矿质营养元素特别是 P 的吸收,甚至在土壤温度降低、植物生长和 P 吸收受抑的情况下,AM 真菌仍能增加植物体内 P 含量^[16]。¹⁴C 跟踪研究发现,碳水化合物在 AM 共生结构界面上的转移(从根系细胞到 AM 菌丝体)对 AM 吸收 P 及 P 在植物体内的运输有促进作用^[17]。

2.2 AM 真菌可以提高植物的抗旱性

AM 真菌可以促进植物水分吸收,提高水分利用率,特别是干旱条件下能增强植物的抗旱能力^[18-19]。接种 AM 真菌提高了叶片相对水分含量、木质部压力势、叶片气孔导度和光合速率,降低了永久凋萎点,从而提高其水分利用效率^[20]。在接种处理与对照植株体内磷含量和生长量无差异条件下,随着土壤的持续干旱,AM 真菌的侵染能提高土壤-根系水分导度^[21]。狗牙根(*Cynodon dactylon*)单接种聚球囊霉(*G. aggregatum*)或摩西球囊霉比两者的混合菌种有更高的侵染率和更好的抗旱性^[22]。AM 真菌的菌丝可以直接吸收水分^[23-24]。因此,AM 真菌改善植物水分状况与菌根发育数量有关。干旱条件下,随着菌根侵染率的提高,连翘(*Forsythia suspensa*)幼苗叶绿素和脯氨酸含量增加, SOD 活性增强,而丙二醛含量和膜透性降低,苗木枯死率下降^[25]。通过研究根内活性菌丝数量发现,具有磷酸酶活性的菌丝对于促进植物生长和提高抗旱性的作用最强^[26]。因此,大多数研究者通过测定菌根侵染率或/和根内外菌丝数量等来评价 AM 真菌的功能。

2.3 AM 真菌可以改善植物的耐涝性

有迹象表明,AM 真菌通过自身特有的方式可改善植物的耐涝性。具有繁殖功能的泡囊结构自身抗逆性强,当土壤水分含量过高时,AM 真菌增加了细叶百脉根(*Lotus tenuis*)泡囊结构数量^[27],在一定水涝逆境下泡囊结构仍可保存一定活力,当洪水退去后,存活下来的泡囊便又可生长发育,形成新的菌根结构,促进养分吸收,补偿植物涝灾时受到的损害。关于菌根结构与提高植物抗涝性的关系值得进一步试验。

2.4 AM 真菌可以增强植物耐盐性

AM 真菌可降低植物盐害程度,保护植物的正常生长^[28-29]。摩西球囊霉能降低大豆叶片 Na 含量,显著提高叶片 K⁺含量和 K/Na 比值,且随着盐浓度

升高而增大,从而增强了其抗盐性^[30]. Giri 等^[31]研究表明,金合欢(*Acacia farnesiana*)接种 AM 真菌后,其地上部 K/Na 比值增加,从而提高了金合欢的抗盐性. 高盐下(1.0%),接种 AM 真菌能促进番茄植株生长,增加叶片和根系的可溶性糖含量、叶片可溶性蛋白含量及根系脯氨酸含量,增强植株的耐盐能力^[32]. 盐胁迫下,菌丝对玉米植株 P 的贡献率由 45.3% 降为 42.6%,菌丝吸收的水分可缓解盐胁迫下的生理干旱^[33]. Jahromi 等^[34]研究发现,不同盐浓度下,根内球囊霉(*Glomus intraradices*)菌株能促进植物生长,可以作为耐盐 AM 真菌. 在今后筛选高效菌种过程中,应重视 AM 真菌侵染发育,尤其是根外菌丝数量.

2.5 AM 真菌可以提高植物抗高温能力

AM 真菌能保护植物免受高温伤害. 李思龙等^[35]研究表明,接种 AM 真菌能降低高温对牡丹(*Paeonia suffruticosa*)幼苗造成的伤害,接种后的根系活力显著增强,脯氨酸和可溶性糖含量明显增加,植株对高温逆境的忍耐力和适应性提高,植物细胞的保水能力增强,从而提高其对高温的抗性. 高温下接种 AM 真菌的玉米的光合效率、水分利用率升高;AM 真菌共生通过改善光性能和水的状态来保护玉米抵御高温胁迫^[36]. 10:00—12:00 高温阶段接种 AM 真菌后,彩叶草(*Coleus blumei*)叶片的净光合速率明显高于对照,且摩西球囊霉与地表球囊霉(*Glomus versiforme*)混合接种的侵染率高于单一菌种^[37].

2.6 AM 真菌可以增强植物抗病性

AM 真菌可以不同程度地抑制土传病原细菌、真菌和线虫的生长、繁殖和危害,提高植物的抗病性^[38–40];但由于寄主-AM 菌种及病原物组合不同以及生长环境的变化,AM 发育特征对植物抗病性会产生不同的影响^[41]. AM 表面着生和延伸着大量的根上菌丝与根外菌丝组成的庞大菌丝网络系统,对病原物入侵构成机械屏障,而且 AM 真菌通过与病原真菌在侵染中进行活力竞争,提高植物抗病性^[42]. AM 真菌丛枝结构的发育和植物抗病性有关,AM 丛枝着生数量(%)与植物抗病性呈正相关关系^[43]. 唐明和陈辉^[44]调查了 24 个杨树种和无性系的溃疡病自然发病情况,结果表明,7—8 年生杨树外生菌根的侵染率与病情指数呈负相关. Thygesen^[45]认为,根内球囊霉降低发病率的效果比近明球囊霉(*Glomus claroideum*)更显著,并且与其菌根发育数量相关. 本课题组在调查设施黄瓜根结线虫

危害时也观察到,黄瓜栽培品种“津优 35 号”同一根系内存在 P 型和 A+P 混合型两种类型的 AM 形态,而且还发现一条没有线虫侵染危害的根系丛枝结构为 P 型(未发表数据). 初步推测 P 型丛枝结构可能具有独特的生理代谢功能,尤其是在防御性酶基因表达和酶活性方面值得深入研究.

2.7 AM 真菌可以促进植物生长

研究表明,菌根侵染率与植物生长呈正相关^[15]. 例如,玉米接种摩西球囊霉 30、45、60 和 75 d 后,植株高度与侵染率呈正相关^[46];大须芒草(*Andropogon gerardii*)的 AM 真菌侵染率与总干质量等呈正相关. 也有少量试验结果例外,可能与植物种类以及 AM 真菌种类等因素有关^[47–48].

2.8 AM 真菌可以改善植物耐重金属毒害

AM 真菌自身对重金属具有较强的耐性,为其提高植物耐重金属毒害奠定了生物学基础. 根内球囊霉能显著提高铅胁迫下玉米的生物量^[49]. 重金属污染下,AM 发育降低了植物体内尤其是地上部的重金属浓度,有利于植物生长. 摩西球囊霉减少 Cd 向玉米植株地上部运输,将更多 Cd 固持于菌根中^[50]. 因此,菌根发育越多,固持的重金属数量就越多,使植物不受重金属毒害^[51]. AM 真菌还能通过菌丝对重金属的过滤、菌丝固持等降低重金属对植物组织造成的伤害^[52–53]. 从垃圾焚烧厂的植物根围土壤中提取的土壤球囊霉素相关蛋白与 AM 真菌侵染率呈正相关^[54]的研究结果,间接证明了 AM 发育与提高植物耐重金属毒害的效应是正相关关系. AM 真菌生物量越多,所具备的吸附重金属能力和容量就可能越大,可见,它们之间存在一定正相关关系的生物学基础,这有待进一步直接给予试验证明.

2.9 AM 真菌可以分解有毒有机物,修复污染与退化土壤

业已证实,AM 真菌能在不同程度上分解石油、有机磷(氯)农药、多环芳烃(PAHs)等有毒有机物^[55]. 接种 AM 真菌能促进土壤中 PAHs 的降解^[56]. 接种苏格兰球囊霉(*Glomus caledonium*)促进对土壤中苯并[a]芘的降解,接种处理比不接种最大可提高 34% 的 B[a]P 降解^[57]. 石油污染土壤中缩球囊霉(*Glomus constrictum*)对三叶草(*Trifolium subterraneum*)根系的侵染率达到 83%,显著促进三叶草生长^[58]. 对矿区脆弱地带的新疆杨(*Populus bolleana*)和白蜡(*Fraxinus chinensis*)幼苗混合接种摩西球囊霉和幼套球囊霉(*Glomus etunicatum*)后,其侵染率在 80% 以上,接种后根围孢子数量较多,

对矿区环境修复和生态恢复起到了重要作用^[59]. 接种 AM 真菌显著提高球囊霉素相关土壤蛋白含量和土壤水稳性大团聚体数量;接种处理提高了土壤的平均质量直径和几何平均直径,降低了土壤分形维数^[60]. 而球囊霉素与孢子密度和总定殖率呈极显著正相关^[61]. 因此,AM 真菌所具有的促进植物吸收养分、生长、改良退化土壤、提高土壤质量与健康状况等功能必然与其菌根结构发育特征密切相关^[62].

综上所述,不同生态条件、不同农艺措施下,各类 AM 真菌特别是高效菌种的菌根发育特征及其数量与其功能的关系,值得系统深入研究.

3 影响丛枝菌根结构发育及其功能的因素

丛枝结构发育特征是由寄主植物和 AM 真菌共同决定的^[6]. 亚麻(*Linum usitatissimum*)上 6 种不同 AM 真菌均形成 A 型;而野生番茄上根内球囊霉等形成 A 型,副冠球囊霉(*G. coronatum*)等则形成 P 型^[63]. *Gigaspora rosea* 等在日本常春藤(*Hedera rhombea*)上形成 P 型,在茅莓(*Rubus parvifolius*)上形成 A 型;分子生物学测定表明,球囊霉科的幼套球囊霉和近明球囊霉多分布于茅莓(*Rubus parvifolius*)和蔷薇(*Rose multiflora*)根内形成 A 型;而巨孢囊霉科的巨盾孢囊霉(*Scutellospora erythropha*)多分布于日本常春藤根内形成 P 型^[64].

一些生态因子也影响到 AM 结构发育及其与植物抗逆性的关系. 如土壤类型影响 AM 真菌侵染及生理效应. 棕壤中玉米根侵染率最高,为 71.1%,低磷草甸土次之,高磷草甸土最差. 各类黄潮土中 AM 真菌侵染率以两合土最高,盐碱土最低^[65]. 不同土壤类型、土壤质地显著影响菌根侵染率、菌根侵染强度和丛枝丰度^[66-67]. 土壤含水量^[68]、磷含量和 pH 值与菌根形成的关系最为密切,速效磷含量过高往往抑制菌根形成^[69-70]. 这也必然影响到 AM 结构与功能的关系. 另外,季节、接种试验中接种物类型、数量和采样测定时间^[69,71],以及测定侵染率的不同方法^[72]均影响到 AM 侵染率,也必须给予足够的重视.

从单纯的数理分析角度来看,表面上 AM 结构发育特征或数量与其功能存在相关性. 其实,这恰恰是这两者之间具备本质的密切关联性、因果机制性和相互依存性的反映.

4 基于丛枝菌根结构所发挥功能的作用机制

作为 AM 的主要功能结构,丛枝是 AM 真菌与

植物之间进行养分交换与拮抗病原物诱导植物抗病性的核心构造. 因此,丛枝结构特征与数量会直接影响到 AM 真菌的生理生态效应. 根据试验结果推理认为,P 型中假如菌丝和菌丝圈作用不同,那么二者比率不同就会导致功能的强弱产生差异^[73]. 由于 A 型和 P 型发育特点各异——P 型 AM 发育较 A 型慢^[63],二者吸收养分与促进植物生长效应,以及防御基因表达和介导的防御反应亦可能不同^[6,74]. 虽然已观察到丛枝结构与抑制植物病原物的侵染和扩展有关,但遗憾的是,相关的观察并没有区分这些丛枝是属于哪些类型的丛枝结构.

土壤中 AM 网络通过菌丝将不同植物根系连成一体,进行养分、能量物质和信息的传递与交换,促进各种植物高效利用有限的信息和资源. AM 菌丝体能够提高土壤团聚体的水稳定性,改善土壤结构^[75]. AM 真菌的根外菌丝可穿过土壤颗粒间极细小的孔隙,由于根外菌丝与土壤颗粒密切接触,其分泌的有机小分子物质可以作为土壤颗粒的黏着吸附剂,促进土壤颗粒形成团聚体,提高其水稳性,使土壤保持较好的水渗透速率、耕作条件和通气状况,从而抵抗风和水的侵蚀^[76]. Wang 等^[77]观察到 *Glomus caledonium* 提高了重金属污染土壤中磷酸酶和脲酶活性,改善了土壤质量. 可见,AM 真菌调控土壤酶活性也是其提高植物抗逆性的机制之一.

AM 真菌的菌丝内聚磷酸盐可能参与改善植物耐毒性机制. Cd²⁺胁迫作用下,聚磷酸盐含量降低而菌丝密度随着该盐的升高而升高,表明聚磷酸盐在减弱重金属毒性方面发挥了重要作用^[78]. 此外,庞大的菌丝网络可以作为屏障,阻止金属向根部运输,从而减轻重金属毒害^[79]. 接种 AM 真菌提高蜈蚣草(*Nephrolepis cordifolia*)根部吸收和积累砷,抑制砷向地上部分运输^[80]. 铬和锌污染下,接种 AM 真菌增加了紫花苜蓿(*Medicago sativa*)根内重金属积累,减少地上部的积累,间接地减轻了重金属对地上部的毒害作用^[81-82].

5 研究展望

菌根真菌接种试验及野外菌根调查都涉及到菌根结构观察与侵染率等测定,这可以明确菌根发育状况,更重要的是可为结果分析、确定菌根结构及数量与其功能的关系提供数理依据. 然而,多数试验缺乏针对菌根结构及数量与其功能进行直接的数理相关分析,因此不能全面认识 AM 结构与功能的关系. 因此,今后工作中,可采用生物化学、组织化学、激光

共聚焦显微镜技术、分子原位杂交等技术与方法, 深入系统开展以下几项工作:

1) 进一步加大野外自然调查研究力度、深度和广度, 注重菌根形态结构的观察, 善于探索和发现新的菌根结构特征, 同时对菌根侵染率、根内和根外菌丝发育数量、丛枝着生数量、泡囊数、孢子数量等进行定量精确测定, 为后续室内试验研究提供依据和技术基础;

2) 有计划的顺序开展逐步深入的室内接种效应试验, 通过这些菌根发育数量与其生理效应(功能)作相关和回归分析, 为诠释菌根真菌的生理生态功能机制奠定基础;

3) 于上述基础上, 进一步开展一些专门研究菌根结构与功能的试验, 例如, 在 AM 真菌介导植物拮抗病原物的机制研究中, 应着重研究不同类型丛枝结构可能具备的不同生理功能; 一种植物根内 A 型/P 型比率不同的生物学意义及其与 AM 真菌功能的关系; 通过测定 A 型、P 型或/和 A+P 混合型丛枝结构状况、吸收养分与促进生长发育的效应, 特别是抑制根结线虫的生理与分子基础研究, 应结合数理分析, 探讨其抑制根结线虫的作用机制. 这将有助于深化了解丛枝结构的生理功能及其作用机制, 大大推动菌根结构与功能关系的研究和进展.

参考文献

- [1] Macculidwin AE, Bird GW, Safir GR. Influence of *Glomus fasciculatum* on *Meloidogone hapla* infecting *Allium*. *Journal of Nematology*, 1985, **17**: 389–395
- [2] Von Reichenbach HG, Schonbeck F. Influence of VA-mycorrhiza on drought tolerance of flax (*Linum usitatissimum* L). I. Influence of VAM on growth and morphology of flax and on physical parameters of the soil. *Angewandte Botanik*, 1995, **69**: 49–54
- [3] Bonfante P, Genre A. Mechanism underlying beneficial plant-fungus interactions in mycorrhizal symbiosis. *Nature Communications*, 2010, **1**: 48
- [4] Abdel-Latef AAH, He CX. Arbuscular mycorrhizal influence on growth, photosynthetic pigments, osmotic adjustment and oxidative stress in tomato plants subjected to low temperature stress. *Acta Physiologiae Plantarum*, 2011, **33**: 1217–1225
- [5] Serfoji P, Rajeshkumar S, Selvaraj T. Management of root-knot nematode, *Meloidogyne incognita* on tomato cv Pusa Ruby by using vermicompost, AM fungus, *Glomus aggregatum* and mycorrhiza helper bacterium, *Bacillus coagulans*. *Journal of Agricultural Technology*, 2010, **6**: 37–45
- [6] Dickson S. The Arum-Paris continuum of mycorrhizal symbioses. *New Phytologist*, 2004, **163**: 187–200
- [7] Szymon Z, Janusz B, Waldemar B. Fungal root endo-phyte associations of medicinal plants. *Nova Hedwigia*, 2012, **94**: 525–540
- [8] Liu RJ, Li M, Wang WH. Colonization of AM fungi in meristematic zone and cap cells of plant roots. *Mycosystema*, 2001, **1**: 116–121
- [9] Shu Y-F (舒玉芳), Ye J (叶 娇), Pan C-Y (潘程远), et al. Developmental features of mycorrhiza and its promotion effect on growth of mulberry saplings in Three Gorges Reservoir Region. *Science of Sericulture* (蚕业科学), 2011, **37**(6): 978–984 (in Chinese)
- [10] Li J-X (李俊喜), Li H (李 辉), Wang W-H (王维华), et al. Effects of arbuscular mycorrhizal fungal arbuscule development on soybean cyst nematode diseases. *Journal of Qingdao Agricultural University* (青岛农业大学学报), 2010, **27**(2): 95–99 (in Chinese)
- [11] Baidengsha M (白灯莎·买买提艾力), Zhang S-M (张少民), Sun L-B (孙良斌). Effect of inoculation of arbuscular mycorrhizal fungi on growth and yield of micropropagated potato. *Soil and Fertilizer Sciences in China* (中国土壤与肥料), 2011(1): 80–82 (in Chinese)
- [12] Shi W-Q (石伟琦), Ding X-D (丁效东), Zhang S-R (张士荣). Effects of arbuscular mycorrhizal fungi on *Leymus chinensis* growth and soil carbon. *Acta Botanica Boreali-Occidentalia Sinica* (西北植物学报), 2011, **31**(2): 357–362 (in Chinese)
- [13] Huang J-H (黄京华), Tan J-F (谭钜发), Jie H-K (揭红科), et al. Effects of inoculating arbuscular mycorrhizal fungi on *Artemisia annua* growth and its official components. *Chinese Journal of Applied Ecology* (应用生态学报), 2011, **22**(6): 1443–1449 (in Chinese)
- [14] Su F-X (苏凤秀), Liu J-A (刘君昂), Luo X-Y (罗晓莹), et al. The effects of AM fungi on the growth of cassava. *Chinese Agricultural Science Bulletin* (中国农学通报), 2012, **28**(25): 229–233 (in Chinese)
- [15] He Z-Q (贺忠群), He C-X (贺超兴), Zhang Z-B (张志斌), et al. Physiological study of tomato growth effects induced by different arbuscular mycorrhizal fungus (AMF) strains. *Journal of Shenyang Agricultural University* (沈阳农业大学学报), 2006, **37**(3): 308–312 (in Chinese)
- [16] Karasawa T, Hodge A, Fitter AH. Growth, respiration and nutrient acquisition by the arbuscular mycorrhizal fungus *Glomus mosseae* and its host plant *Plantago lanceolata* in cooled soil. *Plant, Cell and Environment*, 2012, **35**: 819–828
- [17] Bücking H, Shachar-Hill Y. Phosphate uptake, transport and transfer by the arbuscular mycorrhizal fungus *Glomus intraradices* is stimulated by increased carbohydrate availability. *New Phytologist*, 2005, **165**: 899–912
- [18] Farahani A, Lebaschi H, Hussein M, et al. Effects of arbuscular mycorrhizal fungi, different levels of phosphorus and drought stress on water use efficiency, relative water content and proline accumulation rate of Coriander (*Coriandrum sativum* L.). *Journal of Medicinal*

- Plant Research*, 2008, **2**: 125–131
- [19] Birhane E, Frank J, Sterck FM, *et al.* Arbuscular mycorrhizal fungi enhance photosynthesis, water use efficiency, and growth of frankincense seedlings under pulsed water availability conditions. *Oecologia*, 2012, **169**: 895–904
 - [20] Caravaca F, Diaz E, Barea JM, *et al.* Photosynthetic and transpiration rates of *Olea europaea* subsp. *sylvestris* and *Rhamnus lycioides* as affected by water deficit and mycorrhiza. *Biologia Plantarum*, 2003, **46**: 637–639
 - [21] Gonzalez-Dugo V. The influence of arbuscular mycorrhizal colonization on soil-root hydraulic conductance in *Agrostis stolonifera* L. under two water regimes. *Mycorrhiza*, 2010, **20**: 365–373
 - [22] Zeng X-H (曾秀华), Ye S-P (叶少萍), Bai C-J (白昌军), *et al.* Effects of arbuscular mycorrhizal fungi on the drought resistance of bermudagrass under different phosphorus application rates. *Chinese Journal of Tropical Crops* (热带作物学报), 2011, **32**(6): 1069–1074 (in Chinese)
 - [23] Kaya C, Higgs D, Kimak H. Mycorrhizal colonization improves fruit yield and water efficiency in watermelon (*Citrullus lanatus* Thunb.) grown under well-watered and water-stressed conditions. *Plant and Soil*, 2003, **253**: 287–292
 - [24] Poreel R, Barea M, Ruiz-Lozano JM. Antioxidant activities in mycorrhizal soybean plants under drought stress and their possible relationship to the process of nodule senescence. *New Phytologist*, 2003, **157**: 135–143
 - [25] Zhao P-J (赵平娟), An F (安锋), Tang M (唐明). Effects of arbuscular mycorrhiza fungi on drought resistance of *Forsythia suspense*. *Acta Botanica Boreali-Occidentalia Sinica* (西北植物学报), 2007, **27**(2): 396–399 (in Chinese)
 - [26] Tang M (唐明), Chen H (陈辉), Shang H-S (商鸿生). Effects of arbuscular mycorrhizal fungi (AMF) on *Hippophae rhamnoides* drought-resistance. *Scientia Silvae Sinicae* (林业科学), 1999, **35**(3): 48–52 (in Chinese)
 - [27] García I, Mendoza R, Pomar MC. Deficit and excess of soil water impact on plant growth of *Lotus tenuis* by affecting nutrient uptake and arbuscular mycorrhizal symbiosis. *Plant and Soil*, 2008, **304**: 117–131
 - [28] Al-Karaki GN. Nursery inoculation of tomato with arbuscular mycorrhizal fungi and subsequent performance under irrigation with saline water. *Science Horticulture*, 2006, **109**: 1–7
 - [29] Abo-Ghaila HH, Khalafallah AA. Responses of wheat plants associated with arbuscular mycorrhizal fungi to short-term water stress followed by recovery three growth stages. *Applied Scientific Research*, 2008, **4**: 570–580
 - [30] Li T (李涛), Liu R-J (刘润进), Chen M (陈敏), *et al.* Effects of arbuscular mycorrhizal fungi on growth and ionic content of *Glycine max* seedlings under saline conditions. *Mycosystema* (菌物学报), 2009, **28**(3): 410–414 (in Chinese)
 - [31] Giri B, Kapoor R, Mukerji KG. Improved tolerance of *Acacia nilotica* to salt stress by arbuscular mycorrhiza, *Glomus fasciculatum* may be partly related to elevated K/Na ratios in root and shoot tissues. *Microbial Ecology*, 2007, **54**: 753–760
 - [32] He Z-Q (贺忠群), He C-X (贺超兴), Zhang Z-B (张志斌), *et al.* Study on osmotic adjustment mechanism of tomato salt tolerance enhanced by arbuscular mycorrhizal fungi. *Acta Horticulturae Sinica* (园艺学报), 2007, **34**(1): 147–152 (in Chinese)
 - [33] Feng G (冯固), Li X-L (李晓林), Zhang F-S (张福锁), *et al.* Effect of AM fungi on water and nutrition status of corn plants under salt stress. *Chinese Journal of Applied Ecology* (应用生态学报), 2000, **11**(4): 595–598 (in Chinese)
 - [34] Jahromi F, Aroca R, Porcel R, *et al.* Influence of salinity on the in vitro development of *Glomus intraradices* and on the in vivo physiological and molecular responses of mycorrhizal lettuce plants. *Microbial Ecology*, 2008, **55**: 45–54
 - [35] Li S-L (李思龙), Zhang Y-G (张玉刚), Chen D-M (陈丹明), *et al.* Effect of arbuscular mycorrhizal fungi on physiology and biochemistry of tree peony under high temperature stress. *Chinese Agricultural Science Bulletin* (中国农学通报), 2009, **25**(7): 154–157 (in Chinese)
 - [36] Zhu XC, Song FB, Liu SQ, *et al.* Effects of arbuscular mycorrhizal fungus on photosynthesis and water status of maize under high temperature stress. *Plant and Soil*, 2011, **346**: 189–199
 - [37] Han T-T (韩婷婷), Wang W-H (王维华), Guo S-X (郭绍霞). Effects of arbuscular mycorrhizal fungi on photosynthetic characteristics of *Coleus blumei*. *Journal of Qingdao Agricultural University* (Natural Science) (青岛农业大学学报·自然科学版), 2011, **28**(1): 9–12 (in Chinese)
 - [38] Li M (李敏). Effects of Arbuscular Mycorrhiza on Resistance to Fusarium Wilt by Watermelon (*Citrullus lanatus*) and Related Mechanisms. PhD Thesis. Beijing: China Agricultural University, 2005 (in Chinese)
 - [39] Elsen A, Gervacio D, Swennen R, *et al.* AMF-induced biocontrol against plant parasitic nematodes in *Musa* sp.: A systemic effect. *Mycorrhiza*, 2008, **18**: 251–256
 - [40] Affokpon A, Coyne DL, Lawouin L, *et al.* Effectiveness of native West African arbuscular mycorrhizal fungi in protecting vegetable crops against root-knot nematodes. *Biology and Fertility of Soils*, 2011, **47**: 207–217
 - [41] Liu R-J (刘润进), Chen Y-L (陈应龙). Mycorrhizology. Beijing: Science Press, 2007: 1–447 (in Chinese)
 - [42] Vigo C, Norman JIL, Hooker JE. Biocontrol of the pathogen *Phytophthora parasitica* by arbuscular mycorrhizal fungi is a consequence of effects on infection loci. *Plant Pathology*, 2000, **49**: 509–514
 - [43] Liu RJ. Effects of vesicular-arbuscular mycorrhizal fungi on verticillium wilt of cotton. *Mycorrhiza*, 1995, **5**: 293–297

- [44] Tang M (唐 明), Chen H (陈 辉). The relationship between poplar canker and mycorrhiza. *Acta Pedologica Sinica* (土壤学报), 1994, **31**(suppl.): 218–223 (in Chinese)
- [45] Thygesen K, Larsen J, Bødker L. Arbuscular mycorrhizal fungi reduce development of pea root-rot caused by *Aphanomyces euteiches* using oospores as pathogen inoculum. *European Journal of Plant Pathology*, 2004, **110**: 411–419
- [46] Zhang GY, Zhang LP, Wei MF, *et al.* Effect of arbuscular mycorrhizal fungi, organic fertilizer and soil sterilization on maize growth. *Acta Ecologica Sinica*, 2011, **31**: 192–196
- [47] Zai X-M (宰学明), Xia L-Q (夏连全), Yan D-L (闫道良), *et al.* Effects of arbuscular mycorrhizal fungi on the rooting, growth and enzymatic activity relating to disease resistance of beach plum (*Prunus maritima*) cuttings. *Guihaia* (广西植物), 2011, **31**(3): 393–397 (in Chinese)
- [48] Liu J-F (刘建福), Zhang Y (张 勇), Xie L-Y (谢丽源), *et al.* Effects of arbuscular mycorrhizal fungi on the growth and development of *Macadamia* plantlets. *Chinese Journal of Tropical Crops* (热带作物学报), 2005, **26**(3): 16–19 (in Chinese)
- [49] Sudová R, Vosátka M. Differences in the effects of three arbuscular mycorrhizal fungal strains on P and Pb accumulation by maize plants. *Plant and Soil*, 2007, **296**: 77–83
- [50] Liu L-Z (刘灵芝), Zhang Y-L (张玉龙), Li P-J (李培军), *et al.* Effect of arbuscular mycorrhizal fungi (*Glomus mosseae*) on Cd accumulation in maize plants. *Chinese Journal of Soil Science* (土壤通报), 2011, **42**(3): 568–572 (in Chinese)
- [51] Göhre V, Paszkowski U. Contribution of the arbuscular mycorrhizal symbiosis to heavy metal phytoremediation. *Planta*, 2006, **223**: 1115–1122
- [52] Janouskova M, Vosatka M. Response to cadmium of *Daucus carota* hairy roots dual cultures with *Glomus intraradices* or *Gigaspora margarita*. *Mycorrhiza*, 2005, **15**: 217–224
- [53] Christie P, Li X, Chen B. Arbuscular mycorrhiza can depress translocation of zinc to shoots of host plants in soils moderately polluted with zinc. *Plant and Soil*, 2004, **261**: 209–217
- [54] Stefano B, Alessandra T, Chiarafrancesca R. Molecular characterization and glomalin production of arbuscular mycorrhizal fungi colonizing a heavy metal polluted ash disposal island, downtown Venice. *Soil Biology and Biochemistry*, 2010, **42**: 758–765
- [55] He Y (何 翊), Wei W (魏 薇), Wu H (吴海). Research on mycorrhiza bioremediation technique in oil contaminated soil. *Chemical Engineering of Oil and Gas* (石油与天然气化工), 2004, **33**(3): 217–218 (in Chinese)
- [56] Liu W-W (刘魏魏), Yin R (尹 睿), Lin X-G (林先贵), *et al.* Interaction of phytoremediation-microorganism to remediation of aged polycyclic aromatic hydrocarbons (PAHs) polluted soils. *Soils* (土壤), 2010, **42**(5): 800–806 (in Chinese)
- [57] Liu S-L (刘世亮), Luo Y-M (骆永明), Ding K-Q (丁克强), *et al.* Enhanced phytoremediation of benzo[a] pyrene contaminated soil with arbuscular mycorrhizal fungi. *Acta Pedologica Sinica* (土壤学报), 2004, **41**(3): 336–342 (in Chinese)
- [58] Geng C-N (耿春女), Li P-J (李培军), Chen S-H (陈素华), *et al.* Effects of different arbuscular mycorrhizal fungi on oil tolerance of *Trifolium subterraneum* L. *Chinese Journal of Applied and Environmental Biology* (应用与环境生物学报), 2002, **8**(6): 648–652 (in Chinese)
- [59] Du S-Z (杜善周), Bi Y-L (毕银丽), Wu W-Y (吴王燕), *et al.* Ecological effects of arbuscular mycorrhizal fungi on environmental phytoremediation in coal mine areas. *Transactions of the Chinese Society of Agricultural Engineering* (农业工程学报), 2008, **24**(4): 113–116 (in Chinese)
- [60] Peng S-L (彭思利), Shen H (申 鸿), Guo T (郭涛). Influence of mycorrhizal inoculation on water stable aggregates traits. *Plant Nutrition and Fertilizer Science* (植物营养与肥料学报), 2010, **16**(3): 695–700 (in Chinese)
- [61] He X-L (贺学礼), Wang L (王 雷), Niu K (牛凯), *et al.* Seasonal distribution of AM fungi and glomalin in the rhizosphere of *Dendranthema morifolium*. *Acta Agriculturae Boreali-Occidentalis Sinica* (西北农业学报), 2013, **22**(1): 162–167 (in Chinese)
- [62] Li Y, Chen YL, Li M, *et al.* Effects of arbuscular mycorrhizal fungal communities on soil quality and growth of cucumber seedlings in a greenhouse soil continuously planted to cucumber. *Pedosphere*, 2012, **22**: 79–87
- [63] Cavagnaro TR, Smith FA, Kolesik P, *et al.* Arbuscular mycorrhizas formed by *Asphodelus fistulosus* and *Glomus coronatum*: Three-dimensional analysis of plant nuclear shift using laser scanning confocal microscopy. *Symbiosis*, 2001, **30**: 109–121
- [64] Ahlu EM, Andoh H, Nonaka M. Host-related variability in arbuscular mycorrhizal fungal structures in roots of *Hedera rhombea*, *Rubus parvifolius*, and *Rosa multiflora* under controlled conditions. *Mycorrhiza*, 2007, **17**: 93–101
- [65] Hua X-Y (华秀英), Chen X-S (陈锡时), Shen Y (沈 音). Effects of soil and crop in Shenyang on VA mycorrhiza. *Acta Pedologica Sinica* (土壤通报), 1990, **21**(3): 137–139 (in Chinese)
- [66] Gai J-P (盖京苹), Liu R-J (刘润进). Ecological distribution of arbuscular mycorrhizal fungi on wild plants in different vegetation regions of Shandong. *Chinese Journal of Ecology* (生态学杂志), 2000, **19**(4): 18–22 (in Chinese)
- [67] Wang F-Y (王发园), Liu R-J (刘润进), Lin X-G (林先贵), *et al.* Comparison of diversity of arbuscular mycorrhizal fungi in different ecological environments. *Acta Ecologia Sinica* (生态学报), 2003, **23**(12): 110–119 (in Chinese)

- [68] Gong MG, Tang M, Chen H, *et al.* Effects of two *Glomus* species on the growth and physiological performance of *Sophora davidii* seedlings under water stress. *New Forests*, 2013, **44**: 399–408
- [69] Sivakumar N. Effect of edaphic factors and seasonal variation on spore density and root colonization of arbuscular mycorrhizal fungi in sugarcane fields. *Annals of Microbiology*, 2013, **63**: 151–160
- [70] Liu RJ, Li Y, Diao ZK, *et al.* Effects of soil depth and season variation on community structure of arbuscular mycorrhizal fungi in greenhouse soils planted with watermelon. *Pedosphere*, 2013, **23**: 350–358
- [71] Liu RJ, Diao ZK, Li JX, *et al.* The relationship between colonization potential and inoculum potential of arbuscular mycorrhizal fungi. *Mycosystema*, 2006, **25**: 408–415
- [72] Sheng P-P (盛萍萍), Liu R-J (刘润进), Li M (李敏). Methodological comparison of observation and colonization measurement of arbuscular mycorrhizal fungi. *Mycosystema* (菌物学报), 2011, **30**(4): 519–525 (in Chinese)
- [73] Ahlu EM, Nakata M, Nonaka M. Arum- and Paris-type arbuscular mycorrhizas in a mixed pine forest on sand dune soil in Niigata Prefecture, central Honshu, Japan. *Mycorrhiza*, 2005, **15**: 129–136
- [74] Ruiz-Lozano JM, Bonfante P. Identification of a putative P-transporter operon in the genome of a burkholderia strain living inside the arbuscular mycorrhizal fungus *Gigaspora margarita*. *Journal of Bacteriology*, 1999, **181**: 4106–4109
- [75] Bever JD, Schultz PA, Pringle A, *et al.* Arbuscular mycorrhizal fungi: More diverse than meets the eye, and the ecological tale of why. *Bioscience*, 2001, **51**: 923–931
- [76] Li Q-L (李秋玲), Ling W-T (凌婉婷), Gao Y-Z (高彦征), *et al.* Arbuscular mycorrhizal bioremediation and its mechanisms of organic pollutants-contaminated soils. *Chinese Journal of Applied Ecology* (应用生态学报), 2006, **17**(11): 2217–2221 (in Chinese)
- [77] Wang FY, Lin XG, Yin R. Effects of arbuscular mycorrhizal inoculation on the growth of *Elsholtzia splendens* and *Zea mays* and the activities of phosphatase and urease in a multi-metal-contaminated soil under sterilized conditions. *Applied Soil Ecology*, 2006, **31**: 110–119
- [78] Yang R-H (杨瑞恒), Yao Q (姚青), Guo J (郭俊), *et al.* Influence of P and Cd on the spore germination, hyphal growth and polyphosphate accumulation in extraradical hyphae of *Glomus intraradices*. *Mycosystema* (菌物学报), 2010, **29**(3): 421–428 (in Chinese)
- [79] Liang Z-C (梁振春), Huang Y (黄艺), Ao X-L (敖晓兰). Pb-tolerance of ectomycorrhizal fungi from polluted and unpolluted sites under different P levels. *Chinese Journal of Applied Ecology* (应用生态学报), 2006, **17**(6): 1081–1085 (in Chinese)
- [80] Leung HM, Ye ZH, Wong MH. Interactions of mycorrhizal fungi with *Pteris vittata* (As hyper accumulator) in As-contaminated soils. *Environmental Pollution*, 2006, **139**: 1–8
- [81] Huang J (黄晶), Ling W-T (凌婉婷), Sun Y-D (孙艳娣), *et al.* Impacts of arbuscular mycorrhizal fungi inoculation on the uptake of cadmium and zinc by alfalfa in contaminated soil. *Journal of Agro-Environment Science* (农业环境科学学报), 2012, **31**(1): 99–105 (in Chinese)
- [82] Chen X, Wu CH, Tang JJ, *et al.* Arbuscular mycorrhizae enhance heavy metal lead uptake and growth of host plants under a sand culture experiment. *Chemosphere*, 2005, **60**: 665–671

作者简介 田蜜,女,1989年生,硕士研究生.主要从事蔬菜栽培生理与菌根学研究. E-mail: tmfling@126.com

责任编辑 李凤琴
