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评 述

中国菌根研究 60 年: 过去、现在和将来

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摘要　菌根(真菌根系)存在于大约 90%的植物中, 在促进土壤结构、植物养分与生长、元素生物地球化学循环和陆地生态系统结构与功能等方面具有重要作用. 过去 60 年尤其是近 30 年, 中国菌根研究成果举世瞩目, 如共鉴定出 20 种新种与 120 余种新记录种丛枝菌根真菌、30 种新种与 800 余种新记录种外生菌根真菌以及 10 种新种与 100 余种新记录种兰花菌根真菌. 同时, 在菌根真菌菌种丰富度与遗传结构、菌种生态分布与植物种群, 植物养分摄取与生长、植物修复与土地复垦、植物抗病性和与其他土壤微生物相互作用、菌根植物酶学性质及大气 CO_2 和 O_3 浓度升高对丛枝菌根多样性的影响等方面也取得重大进展. 本文选介中国菌根主要研究成就, 进行研究前景展望, 以促进我国菌根研究的深入开展.

关键词
中国
丛枝菌根
外生菌根
兰花菌根
菌根生理和生态功能
植物修复
物种多样性
国际合作

1　引言

1.1　中国植被简介

由于复杂的气候、地貌和土壤环境, 目前在中国 960 万平方公里国土上生长着超过世界总数 1/8 的 30000 多种植物(http://www.efloras.org/flora_page.aspx?flora_id=2), 其中数千种珍稀特有物种生长在 2 个(全球 25 个)生物多样性热点地域(图 1 的Ⅳ和Ⅵ区)[1]. 这些植物包括 7500 多种树木和灌木、2000 多种食用和 3000 多种药用植物. 仅见于中国的植物有银杉(*Cathaya argyrophylla*)、杉木(*Cunninghamia lanceolata*)、水松(*Glyptostrobus pensilis*)、珙桐(*Davidia involucrata*)、杜仲(*Eucommia ulmoides*)、福建柏(*Fokienia hodginsii*)、金钱松(*Pseudolarix amabilis*)、喜树(*Camplotheca acuminate*)、美味猕猴桃(*Actinidia deliciosa*)、水杉(*Metasequoia glyptostroboides*)、台湾冷杉(*Abies kawakamii*)和台湾松(*Pinus taiwanensis*)等、辽宁人参(*Panax ginseng*)、宁夏枸杞(*Lycium chinense*)、浙江银杏(*Ginkgo biloba*)和云南三七(*Panax notoginseng*)是闻名于世的传统中药材植物. 另一方面, 中国约有 8000 种大型真菌, 其中许多是土壤菌根真菌[2~4]. 辽阔的中国国土上植被和真菌资

英文版见: He X H, Duan Y H, Chen Y L, et al. A 60-year journey of mycorrhizal research in China: Past, present and future directions. Sci China Life Sci, 2010, 53: 1374−1398, doi: 10.1007/s11427-010-4096-z

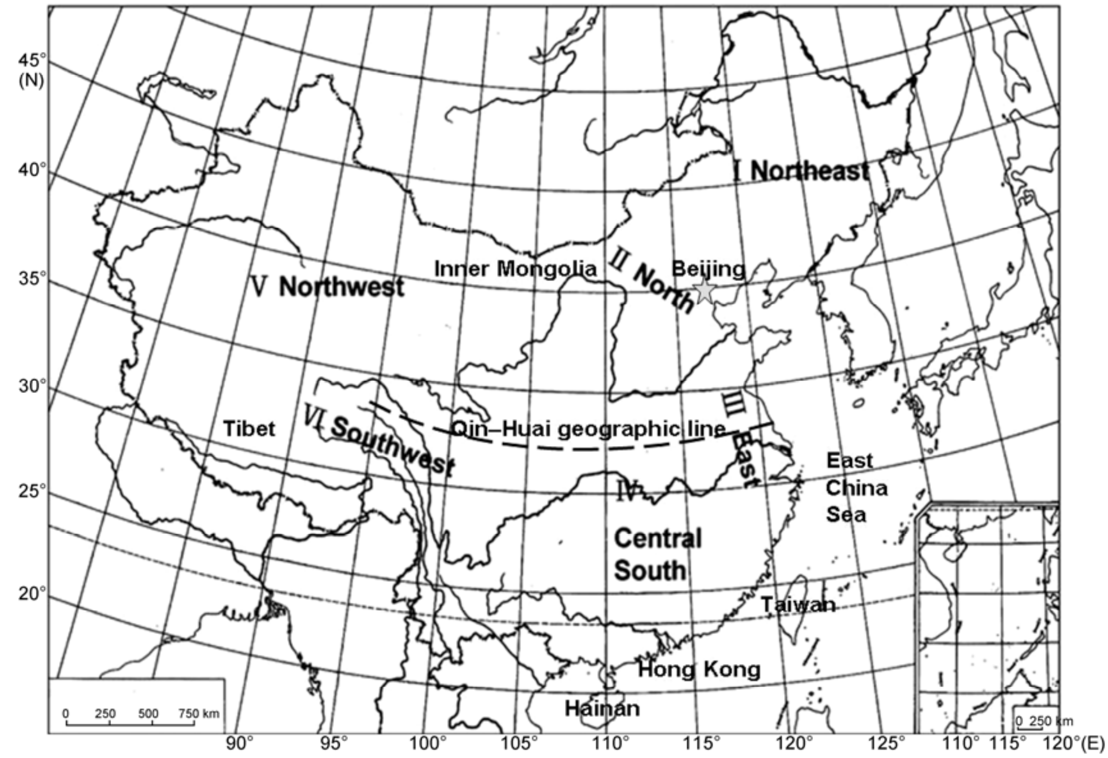

图 1　中国六大地理区域示意图

改编自盖京苹等人[63]并得到原作者和 Springer 许可

源丰富多样, 广泛分布着菌根共生现象.

1.2　菌根共生简介

大约 90%陆地植物能和土壤菌根真菌共生形成菌根(顾名思义, 真菌根系)[5,6]. 菌根在土壤结构、植物养分吸收与生长、生物多样性及农业和自然生态系统的生产力等方面具有重要作用[6]. 根据形态结构的不同, 菌根分为 6 类: (1) 丛枝菌根(Arbuscular mycorrhiza, AM), (2) 浆果鹃类菌根(Arbutoid mycorrhiza), (3) 外生菌根(Ectomycorrhiza, EM), (4) 欧石南类菌根(Ericoid), (5) 石晶兰类菌根(Monotropoid mycorrhiza), (6) 兰花菌根(Orchid mycorrhiza). 其中最普遍且最有经济价值的两大类当属与农业中绝大部分的谷类作物、蔬菜和水果等共生的丛枝菌根和与树木及灌木共生的外生菌根[7].

2　中国菌根研究简史

自 120 年前德国人 Frank[8]提出“菌根”概念以来已有数以万计菌根科学论文在全世界发表. 自第二次世界大战至 2010 年初, 我国菌根研究共有约 200 多篇论文在 62 种英语期刊和约 2000 多篇论文在 350 余种中文期刊(图 2, 表 1)上发表. 因此, 国际菌根学界对大量的中国菌根研究几无所知. 同时, 与国际菌根研究相比, 中国菌根研究水平亟待更上一层楼. 本文首先回顾中国菌根研究的过去状况和现在进展, 旨在向国际, 特别是非华裔学者推介中国菌根研究所取得的重要成果, 展望今后需要加强的研究领域和前景, 以促进我国菌根研究的深入开展和进一步的国际合作.

根据论文发表数量, 中国菌根研究可以分为 3 个不同阶段: 初始零星第一阶段(1950~1980)、缓慢恢复第二阶段(1981~1990)与蓬勃发展第三阶段(1991 年后至今).

2.1　菌根研究第一阶段(1950~1980)

第二次世界大战前后只有少许几例菌根研究[9,10], 此后大陆学者在 20 世纪 50~60 年代对木麻黄

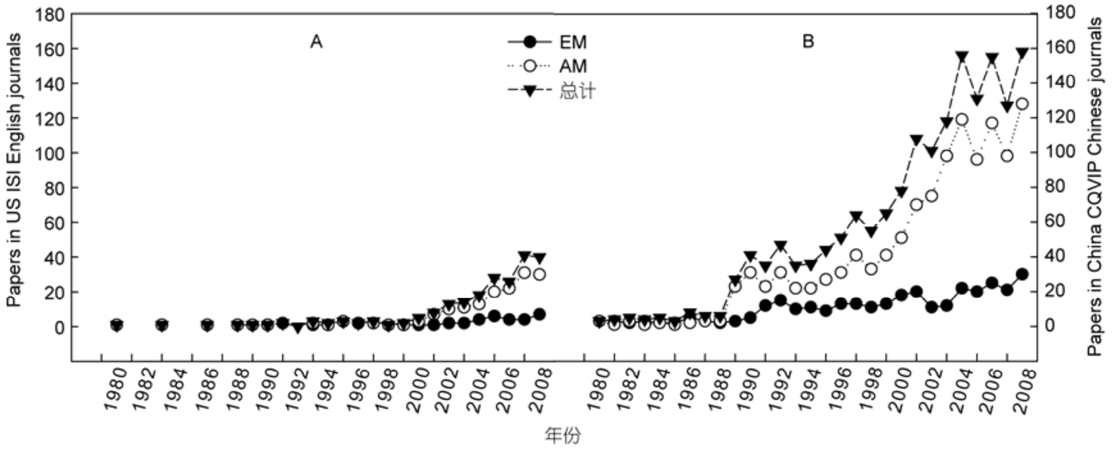

图 2 1980~2010 年间中国菌根研究论文发表概况(英文(A)和中文(B))

论文篇数统计源于 2010 年版美国"期刊引证报告®数据库"(http://apps.isiknowledge.com, 共约 7500 种期刊)和重庆"中国科技期刊数据库"(http://www.cqvip.com/asp/zksear.shtml, 共约 9200 种期刊). AM: 丛枝菌根; EM: 外生菌根; 总计: 丛枝菌根+外生菌根+兰花菌根

表 1 中国菌根研究论文被美国"期刊引证报告®数据库"收录的 64 种英文期刊目录及其学科引用影响简况 a)

期刊名录	论文发表数	学科类别	2009 年影响因子	学科内排名
Acta Agriculturae Scandinavica Section B	1	Agronomy; Soil Sciences	0.460	47/61; 28/31
African Journal of Biotechnology	1	Biotechnology & Applied Microbiology	0.565	131/150
Agriculture, Ecosystems and Environment	1	Agriculture, Multidisciplinary; Ecology; Environmental Sciences	3.130	1/44; 35/127; 28/180
Allelopathy Journal	4	Agronomy	0.793	31/61
Annals of Microbiology	1	Microbiology; Biotechnology & Applied Microbiology	0.358	92/94; 140/150
Applied Soil Ecology	9	Soil Science	2.122	9/31
Biologia Plantarum	1	Plant Sciences	1.656	60/172
Biology and Fertility of Soils	1	Soil Science	1.757	13/31
Bioresource Technology	1	Agricultural Engineering; Biotechnology & Applied Microbiology; Energy & Fuels	4.253	1/11; 21/150; 4/70
Botanical Studies (formerly Bot Bull Acad Sinica)**	2	Plant Sciences	0.781	113/172
Bull Environmental Contamination & Toxicology	2	Environmental Sciences	0.992	132/180
Chemosphere	13	Environmental Sciences	3.253	22/180
Communications in Soil Science and Plant Analysis	4	Argonomy; Soil Science	0.397	51/61; 29/31
Chinese Science Bull***	7	Multidisciplinary Sciences	0.898	20/48
Environ Sci Pollu Res	1	Environmental Sciences	2.411	50/180
Environmental Geochemistry and Health	1	Environmental Sciences; Public, Environmental & Occupational Health	1.622	82/180; 62/122
Environment International	1	Environmental Sciences	4.786	5/180
Environmental Pollution	5	Environmental Sciences	3.426	19/180
European Journal of Soil Biology	2	Soil Science	1.247	18/31
FEMS Microbiology Ecology	1	Microbiology	3.598	26/94
Forest Ecology and Management	4	Forestry	1.950	5/46
Functional Plant Biology	1	Plant Sciences	1.678	59/172
Fungal Diversity***	2	Mycology	3.803	2/19
Geoderma	2	Soil Science	2.461	5/31
International Journal of Phytoremediation	1	Environmental Sciences	1.321	108/180
International Review of Hydrobiology	1	Marine & Freshwater Biology	1.082	55/88
Journal of Arid Environments	1	Environmental Sciences	1.426	95/180

续表 1

期刊名录	论文发表数	学科类别	2009年影响因子	学科内排名
Journal of Agricultural and Food Chemistry	1	Food Science & Technology; Chemistry, Applied	2.469	10/118; 8/64
Journal of Environmental Sciences-China***	7	Environmental Sciences	1.412	98/180
Journal of Integrative Plant Biology (Acta Bot Sin)***	1	Plant Sciences	1.395	77/172
Journal of Microbiology	1	Microbiology	1.463	75/94
Journal of Phytopathology	1	Plant Sciences	0.983	98/172
Journal of Plant Nutrition	11	Plant Sciences	0.512	141/172
Journal of Plant Nutrition and Soil Science	1	Agronomy; Soil Science	1.595	18/61; 14/31
Micorbiology–SGM	1	Micorbiology	3.025	32/94
Molecular Ecology	1	Ecology	5.960	6/127
Mycologia	5	Mycology	1.587	10/19
Mycological Research	2	Mycology	2.921	4/19
Mycorrhiza	31	Mycology	2.650	5/19
Mycotaxon	12	Mycology	0.574	18/19
Nature	1	Multidisciplinary Sciences	34.480	1/48
New Forests	2	Forestry	0.728	27/46
New Phytol	3	Plant Sciences	6.033	8/172
Pedosphere***	9	Soil Science	1.103	19/31
Pedobiologia	1	Ecology; Soil Science	2.414	45/127; 6/31
Physiological and Molecular Plant Pathology	1	Plant Sciences	1.407	74/172
Phytopathology	1	Plant Sciences	2.223	44/172
Planta	1	Plant Sciences	3.372	20/172
Plant and Cell Physiology	1	Plant Sciences	3.594	17/172
Plant Growth Regulation	2	Plant Sciences	1.530	66/172
Plant and Soil	24	Agronomy; Plant Sciences; Soil Sciences	2.517	4/61; 41/172; 4/31
Plant Ecology	1	Ecology; Forestry; Plant Sciences	1.567	67/127; 10/46; 64/172
Progress in Natural Science***	2	Multidisciplinary Sciences	0.704	24/48
Restoration Ecology	1	Ecology	1.665	64/127
Science in China Series C-Life Sciences***	2	Biology	0.691	54/73
Science in China Series D-Earth Sciences***	1	Geosciences, Multidisciplinary	0.880	111/53
Science of the Total Environment	3	Environmental Sciences	2.905	31/180
Scientia Horticulturae	2	Horticulture	1.197	8/30
Soil Biology and Biochemistry	4	Soil Sciences	2.978	1/31
Soil Science and Plant Nutrition	1	Agronomy; Soil Sciences	0.989	29/61; 23/31
Sydowia	1	Mycology	0.786	15/19
Symbiosis	2	Microbiology	1.052	80/94
Trees-Structure and Function	2	Forestry	1.603	9/46
Trends in Plant Science	1	Plant Science	9.883	4/172

a) 资料来源: 美国"期刊引证报告®数据库"(2010版). *: 2009年 5年期刊影响因子; **: 期刊编辑部在中国台湾; ***: 期刊编辑部在中国大陆

(*Casuarina equisetifolia*)、辽东栎(*Quercus liaotungensis*)、白皮松(*Pinus bungeana*)、樟子松(*P. sylvestris*)和油松(*P. tabulaeformis*)等树木的外生菌根真菌组成[11~13], 外生菌根真菌对白皮松、油松、马尾松(*P. massoniana*)、金钱松(*Pseudolarix amabilis*)、加拿大杨(*Populus canadensis*)与钻天杨(*P. nigra* var. *italica*)等树木生长和丛枝菌根真菌对柑桔与玉米的磷素营养及生长进行了研究[13,14]. 香港学者报道了7种外生真菌菌株对樟子松生长的影响[15]. 台湾学者报道了台湾松与彩色豆马勃(*Pisolithus tinctorius*)和乳牛肝菌(*Suillus bovinus*)共生形成外生菌根[16]和柑桔及玉米与丛枝菌根真菌共生形成丛枝菌根的研究[17].

2.2 菌根研究第二阶段(1981~1990)

大陆于1978年文革结束后恢复菌根研究, 1981~1990年间年均中英文论文仅为10和1篇(图2), 1989年第一本中文菌根学术专著出版[13]. 在此阶段共发现6种新种和大约100种新记录种丛枝菌根真菌[18~23]. 在广西、四川和云南天然林(图1的Ⅳ区)与东喜马拉亚山地区(图1的Ⅵ区), 发现了约300余种外生菌根真菌,

包括 11 个新种, 如橙香牛肝菌(*Boletus citrifragrans*)、鳞柄牛肝菌(*B. squamulistipes*)、长白乳菇(*Lactarius changbainensis*)、温泉乳菇(*L. wenquanensis*)、拟菱红菇(*Russula pseudovesca*)、红边绿菇(*R. viridirubrolimbata*)、裸皱松塔牛肝菌(*Strobilomyces glabellus*)、阔裂松塔牛肝菌(*S. latirimosus*)、微茸松塔牛肝(*S. subnudus*)、短绒松塔牛肝菌(*S. velutinus*)、青冈松口蘑(*Tricholoma quercicola*)[24~39]. 此外, 研究了鹅膏属(*Amanita*)、蜡蘑属(*Lactarius*)和松茸群(Matsutake)的形态分类和地理分布[29,37,38].

研究表明, 丛枝菌根真菌促进白藤(*Calamus tetradactylus*)、格氏栲(*Castanopsis kawakamii*)、白花泡桐(*Paulownia fortunei*)和杉木及玉米、大豆和小麦等的生长[13]. 对北细辛(*Asarum heterotropoides*)、曼陀罗(*Datura stramonium*)、人参(*Panax ginseng*)、蓝靛果忍冬(*Lonicera edulis* Turcz.)等药用植物及软枣猕猴桃(*Actinidia arguta*)和茶(*Camellia sinensis*)丛枝菌根真菌组成进行了研究[40~43]. 同时发现, 磷或铁和外生菌根真菌对柑桔和松树生长具有交互作用[13], 接种丛枝菌根真菌对苹果、玉米和大豆磷摄取[44~49], 对柑桔钙和铁摄取[50~51]或对苹果和绿豆水分摄取及生长产生积极影响[48,52]. 此外, 发现螺旋状或胞质螺旋样生物能够在丛枝菌根真菌菌内生长[53,54]和紫萁小菇(*Mycena osmundicola*)可促进天麻(*Gastrodia elata*)种子萌发[55].

2.3 菌根研究第三阶段(1991~2010)

中国学者从 1991~2000 年间在国际英文期刊年均发表菌根研究论文两篇(共 23 篇)增加到 2001~2010 年间年均 20 余篇(共约 180 篇, 2007 年最高为 41 篇). 与此同时, 中文菌根论文数量剧增, 由 1991~2000 年均 50 余篇到 2001~2010 年均 130 余篇(2008 年最高为 158 篇). 下面选介 1991~2010 年间中国菌根的主要研究成就.

3 1991~2010 年间中国菌根研究的主要成就

3.1 丛枝菌根研究方面的主要成就

(1) 丛枝菌根真菌的物种丰富度. 在全国共发现 150 科 800 余种植物能够形成丛枝菌根[4,13,56~65], 包括 400 余种野生植物和 150 余种大田栽培植物, 如主要粮食作物、水果、蔬菜和传统中药材. 中国丛枝菌根真菌物种十分丰富多样, 且具有一定地域独特性, 包括属于丛枝菌根真菌 9 属(无梗囊霉属, *Acaulospora*; 原囊霉属, *Archaeospora*; 多胞囊霉属, *Diversispora*; 内养囊霉属, *Entrophospora*; 巨胞囊霉属, *Gigaspora*; 球囊霉属, *Glomus*; 和平囊霉属, *Pacispora*; 类球囊霉属, *Paraglomus* 和盾巨胞囊霉属, *Scutellospora*)之中的 7 个新种和 115 个新记录种[63] (表 2).

表 2 自盖京苹等人后[18,20~22,58,63~65,85,88,373,395~405]新近在中国分离的丛枝菌根真菌 5 属 13 种新种和 6 属 25 种新记录种目录 a)

丛枝菌根真菌种类	分布地点和植被	参考文献
13 new AM species		
Acaulospora taiwania Hu	Taiwan/fir and Taiwania fir	Hu, 1988[22]
Entrophospora kentinensis Wu & Liu	Taiwan/native grasses	Wu et al., 1995[58]
Gigaspora alboaurantiaca	Taiwan/coastal windbreak & other tree plantations	Chou et al., 1991[401]
Glomus chimonobambusae Wu & Liu	Taiwan/bamboo in highlands	Wu et al., 1995[58]
Gl. citricolum Tang & Zang	Chongqing/citrus orchards	Tang & Zang, 1984[18]
Gl. cunnighamia Hu	Taiwan/fir and Taiwania fir	Hu, 1988[22]
Gl. dolichosporum Zhang & Wang	Fujian, Guangxi/mango and eucalypt plantations	Zhang et al., 1997[402]
Gl. formosanum Wu & Chen	Taiwan/bamboo vegetation	Wu & Chen, 1986[20]
Gl. liquidambaris (Wu & Chen) Almeida & Schenck	Taiwan/bamboo vegetation	Wu & Chen, 1987[21]
Gl. spinosum Hu	Taiwan/fir	Hu, 2002[403]
Gl. taiwanensis (Wu & Chen) Almeida & Schenck	Taiwan/bamboo vegetation	Wu & Chen, 1987[20]
Gl. zaozhuangianus Wang & Liu	Shandong/*Digitaria sanguinalis*	Wang & Liu, 2002[395]
Scutellospora trirubiginopa Pan & Zhang	Shanxi/wild plants on Loess Plateau	Pan et al., 1997[404]
25 new records of AM species		
Acaulospora cavernata Blaszkowski	Sichuan, Qinghai/*Rhus chinensis*	Zhang et al., 2007[405]
A. delicate C. Walker, C. M. Pfeiffer & H. E. Bloss	Qinghai, Sichuan, Yunnan/*Trema angustifolia*, *Arachniodes rhomboidea*, *Nouelia insignis*, etc.	Zhao et al., 2006[88] Zhang et al., 2007[405]

续表 2

丛枝菌根真菌种类	分布地点和植被	参考文献
A. gedanensis Blaszkowski	Tibet/Southeastern forests	Gao et al., 2006[397]
A. koskei Blaszkowski	Sichuan/*Lindera communis*, *Camellia oleifera*	Zhang & Guo, 2005[64]
A. nicolsonii C. Walker, L. E. Reed & F. E. Sanders	Tibet, Xinjiang/*Arachis hypogaea* L.	Zhang et al., 2007[405]
A. paulinae Blaszkowski	Tibet/wild *Prunus mume*	Cai et al., 2008[400]
Diversispora spurca C. Walker & A. Schussler	Xinjiang/*Arachis hypogaea*, *Gossypium herbaceum*	Zhang et al., 2007[405]
Gigaspora ramisporophora J. Spain, E. Sieverd. & N. Schenck	Tibet/wild *Prumus mume*	Cai et al., 2007[399]
Glomus aureum F. Oehl, A. Wiemken & E. Sieverding	Tibet/wild *Prumus mume*	Cai et al., 2008[400]
Gl. badium F. Oehl, D. Redecker & E. Sieverding	Sichuan, Inner Mongolia/*Dictycline wilfordii*	Zhang et al., 2007[405]
Gl. brohultii E. Sieverding & R. A. Herrera	Inner Mongolia/various grasslands	Bao and Yan, 2004[65]
Gl. caledonium (T. H.Nicolson & Gerd.) Trappe & Gerd.	Tibet/wild *Prumus mume*	Cai et al., 2007[368]
Gl. coronatum M. Giovannetti & L. Salutini	Beijing, Sichuan/*Triticum aestivum*, *Zay mays*	Zhang et al., 2007[405]
Gl. dominikii Blaszkowski	Xinjiang/*Picea obovata*	Qiao et al., 2005[396]
Gl. eburneum	Shandong/Maize, wheat	Wang et al., 2006[398]
Gl. flavisporum (M. Lange & E. M. Lund) Trappe & Gerd.	Tibet/Southeastern forests	Gao et al., 2006[397]
Gl. hyderabadensis	Shandong/Maize, wheat	Wang et al., 2006[398]
Gl. invermaium Hall	Tibet/Southeastern forests	Gao et al., 2006[397]
Gl. lammellosum Y. Dalpe, R. E. Koske & L. L. Tews	Beijing/*Glycine max*, *Zay mays*	Zhang et al., 2007[405]
Gl. luteum	Sichuan/*Lindera communis*, *Camellia oleifera*	Zhang & Guo, 2005[64]
Gl. multiforum	Yunnan/*Sida szechuensis*, *Urema procumbens*, etc.	Zhao et al., 2006[88]
Pacispora boliviana F. Oehl & E. Sieverding	Tibet/Southeastern forests	Gao et al., 2006[397]
P. robigina F. Oehl & E. Sieverding	Tibet/wild *Prumus mume*	Cai et al., 2008[400]
Scutellospora cerradensis	Shandong/Maize, wheat	Wang et al., 2006[398]
S. dipurpurescens	Yunnan/*Flemingia strobilifera*, *Pteris henryi*, etc.	Zhao et al., 2006[88]

a) 其他 93 种丛枝菌根真菌新记录种目录请见文献[63]的表 2. 大多数丛枝菌根真菌标样储存在北京市农林科学院植物营养与资源研究所“中国丛枝菌根真菌种质资源库”、中国科学院微生物研究所真菌标本室和台湾台川台湾农业研究所

中国丛枝菌根真菌大部分为 Arum(阿鲁姆)形态型. 如在内蒙古中西部草原 28 科 125 种植物中(图 1 的Ⅱ区), 有 104 种能够形成丛枝菌根, 其中 65%为 Arum 型, 仅 19%为 Paris(帕里斯)型[66]. 在新疆准噶尔盆地的 4 个典型沙漠植物群落中(图 1 的Ⅴ区), 3 种短命植物(囊瓣顶冰花, *Gagea sacculifera*; 小车前, *Plantago minuta* 和弯果胡卢巴, *Trigonella arcuata*)的丛枝菌根真菌也主要是 Arum 型菌[67]. 但海南岛 9 个热带雨林地(图 1 的Ⅳ区)25 种植物的 33 种丛枝菌根真菌(18 种球囊霉、9 种无梗囊霉、1 种内养囊霉、2 种巨胞囊霉和 3 种盾巨胞囊霉)则全部为 Paris 型或中间型, 无一为 Arum 型[68]. 云南草原丛枝菌根真菌的发生与全年降雨量和日照时数显著正相关(图 1 的Ⅳ区)[69,70]. 在云南 24 种马先蒿属寄生植物中, 有 9, 2 和 1 种植物分别同时感染丛枝菌根真菌与暗隔内生真菌(dark septate endophytic fungus, DSEF)、外生菌根真菌与 DSEF 和丛枝菌根真菌、外生菌根真菌与 DSEF 3 种真菌[71], 另有 20 种同时为丛枝菌根和寄生植物 2 种类型[72].

从枝菌根真菌发生的多度或频度因真菌属别而异, 但不论地处东西南北和冷带、温带、亚热带或热带, 球囊霉都为优势菌属. 如在内蒙古草原 30 多种植物中共发现 27 种丛枝菌根真菌, 其中球囊霉 19 种, 无梗囊霉 2 种, 原囊霉、内氧囊霉与巨孢囊霉各 1 种和盾巨胞囊霉 3 种[73,74]. 又如在新疆古尔班通古特沙漠(图 1 的Ⅴ区)11 科 14 种植物中共分离出 14 种丛枝菌根真菌, 其中球囊霉 10 种、无梗囊霉 3 种和原囊霉属 1 种[75]. 另外, 在新疆准噶尔盆地荒漠生态系统中 5 种常见短命植物中共发现有 54 种丛枝菌根真菌, 其中 82.6%属球囊霉, 而其他 4 属(无梗囊霉、原囊霉、内养囊霉和类球囊霉)仅占 17.6%[68,76,77]. 在中国西北的毛乌素沙地(图 1 的Ⅱ和Ⅵ区之间), 球囊霉属真菌是沙鞭(*Psammochloa villosa*)和塔落岩黄芪(*Hedysarum laeve*)的优势菌根真菌[78]. 在长江中上游四川和云南之间金沙江干热河谷(图 1 的Ⅳ和Ⅵ区)67 种植物中, 其中 67%与球囊霉, 22%与无梗囊霉, 低于 5%与植物原囊霉、内养囊霉或巨胞囊霉形成丛枝菌根[79]. 云南元江一个山谷型半稀树草原植被具有类似丛枝菌根真菌分布[80].

在陕西小麦、大麦、玉米、谷子和黄豆农田土壤中(图 1 的Ⅲ和Ⅵ区)分离出 7 种球囊霉真菌(聚丛球囊霉、苏格兰球囊霉、缩球囊霉、地球囊霉、两型球囊霉、摩西球囊霉和地表球囊霉)[81]. 在四川玉米、小麦、水稻和柑桔土壤中分离出 30 种丛枝菌根真菌, 分别

有球囊霉 20 种、无梗囊霉 4 种、盾巨胞囊霉 3 种、双囊霉(Ambispora)和原囊霉与类球囊霉各 1 种[82]. 丛枝菌根真菌在黄壤、红壤和紫壤中的分布基本相似, 但在水稻土中较低且以摩西球囊霉、苏格兰球囊霉和缩球囊霉为主[82]. 跟新垦土地比较, 云南久耕地中的丛枝菌根真菌孢子密度、菌种丰富度和群落组成与未开垦土地中的更为相似[83].

无梗球囊霉属真菌在西北和西南地区, 尤其是在青藏高原及其邻近的横断山脉(图 1 的VI区)的分布仅次于球囊霉属真菌, 但在南部和东部地区的分布与球囊霉属真菌不相上下[84~89]. 无梗球囊霉属真菌在云南西双版纳热带雨林的发生频率为 54%, 球囊霉属真菌为41%[90]; 而盾巨胞囊霉属真菌则主要分布在山东半岛(图 1 的III区)南部和东部沿海的沙丘和盐碱土壤中[91]. 此外, 其他各属真菌菌种在中国的分布特别少. 例如, 类球囊霉属仅一种, 原囊霉属、多胞囊霉属和和平囊霉属各 2 种, 内养囊霉属 3 种, 巨胞囊霉属 6 种[63](表 2). 但从地理分布来看, 多胞囊霉属、内养囊霉属、巨胞囊霉属和类球囊霉属丛枝菌根真菌在全国都有分布, 而原囊霉属和和平囊霉属则仅见于中国台湾.

(2) 丛枝菌根真菌菌种组成与植物种群关系. 丛枝菌根真菌在热带和亚热带地区的发生比在温带地区要高. 例如, 云南亚热带地区 80%的植物树种与丛枝菌根真菌共生[92,93]. 一般认为, 龙脑香科(Dipterocarpaceae)树种主要与外生菌根共生[5]. 但在海南和云南热带地区 5 属 24 个龙脑香树种根系土壤中却分离到 50 种丛枝菌根真菌, 分别属于无梗囊霉、原囊霉、球囊霉、类球囊霉和盾巨胞囊霉 5 属[94~97], 其中无梗囊霉属和球囊霉属为优势菌种. 云南西双版纳热带次生林 13 科 26 种植物跟 11 种丛枝菌根真菌共生与壳斗科 4 种植物(杯丝锥、红锥、印度锥和截果柯)跟 10 种丛枝菌根真菌共生[98,99], 分属无梗囊霉、球囊霉、巨胞囊霉和盾巨胞囊霉 4 属. 同是羊齿类植物, 在云南热带地区其共生关系较弱, 如 256 种植物中仅有 43 种与丛枝菌根真菌共生[100], 而在四川亚热带地区的 34 种植物中却有 31 种与丛枝菌根真菌共生[101,102]. 在新疆天山草甸干草原、沙漠干草原、干草原沙漠和典型沙漠地区, 20 种常见植物与 28 种丛枝菌根真菌共生(无梗囊霉 5 种、原囊霉 1 种和球囊霉 22 种)[67]. 金沙江干热河谷 91 种植物与 43 种丛枝菌根真菌共生(无梗囊霉 7 种、内养囊霉 2 种、巨胞囊霉 2 种、球囊霉 28 种和盾巨胞囊霉 4 种)[103]. 在云南元江河谷半稀疏草原的 33 科 62 种植物中有 59 种与丛枝菌根真菌共生[79].

云南 34 种湿地植物中有 11 种与 4 属(无梗囊霉、巨胞囊霉、球囊霉和盾巨胞囊霉)16 种丛枝菌根真菌形成共生, 其中摩西球囊霉为优势菌种[104]. 从 7 种水生菌根植物根际沉积物中分离出 10 种丛枝菌根真菌, 隶属于无梗囊霉(2 种)、巨胞囊霉(1 种)、球囊霉(6 种)和盾巨胞囊霉(1 种)4 属, 其中球囊霉孢子/孢子果占 97%[105]. 在西藏高原九种苔草植物中有 7 种与五属(无梗囊霉、巨胞囊霉、球囊霉、和平囊霉和盾巨胞囊霉)26 种丛枝菌根真菌共生, 其中球囊霉和无梗囊霉为优势菌属, 而细凹无梗囊霉为最频繁发生菌种[86]. 全国 24 种(16 科)苔藓植物中有 17 种与 15 种丛枝菌根真菌形成共生(球囊霉 11 种、无梗囊霉 2 种、巨胞囊霉 1 种和类球囊霉 1 种)[64]. 河南和山东两地著名的树牡丹(图 1 的II区)则同 35 种丛枝菌根真菌(无梗囊霉 12 种、原囊霉 1 种、巨胞囊霉 2 种、球囊霉 17 种和盾巨胞囊霉 3 种)共生[106].

(3) 丛枝菌根真菌对养分吸收和植物生长的影响. 就丛枝菌根真菌对 N, P, K, S, Zn, Cl 和 Na 等吸收[106~135], 有机磷[136]、C 和 N 循环[137~140]、P 的双向转运[141]及源于 Al 的土壤酸化[142]等进行了大量研究. 从枝菌根真菌侵染的洋葱(*Allium* spp.)比未侵染者具有更高的硫和丙酮酸含量及辛辣气味[143~145]. 接种摩西球囊霉能增加根系中可溶性糖积累从而提高玉米耐盐性[137]. 接种根内球囊霉显著增加烟草 N, P 和 K 吸收、叶片 P 和绿叶素含量、根超氧化物歧化酶、几丁质酶和硝酸还原酶的活性和植物生物量[146]. 接种摩西球囊霉和地表球囊霉对 P 的吸收与菌丝分泌的酸性、中性、碱性和总磷酸酶含量呈正相关[147]. 此外, 接种根内球囊霉或近明球囊霉能增强羊草(*Leymus chinensis*)对 P 的吸收、气孔导度和光合速率, 但对水分利用和 $\delta^{13}C$ 值则无直接影响[148].

就丛枝菌根真菌对多种植物生长的影响也进行了大量研究[113,129,130,134,149~159]. 聚丛球囊霉和弗兰克氏放线菌(*Frankia*)双重接种显著增强西藏沙棘(*Hippophae tibetana*)生长和固氮[160]及短枝木麻黄(*Casuarina equisetifolia*)结瘤和固氮[161]. 接种摩西球囊霉显著促进澳洲坚果幼苗光合作用[155]. 接种摩西球囊霉和根内球囊霉显著增加两种沙漠植物(天竺葵和车前草属)的光合作用和种子及果实总数[158]. 在 8 mmol Al^{3+}条件下, 接种丛枝菌根真菌显著增加樟树

幼苗绿叶素含量[162]. 应用 13 种丛枝菌根真菌(无梗囊霉、球囊霉、巨胞囊霉和盾巨胞囊霉 4 属)进行中国亚热带退化红壤复垦研究, 发现本地居生的苏格兰球囊霉和木薯球囊霉显著促进绿豆生长, 而苏格兰球囊霉对美丽胡枝子(*Lespedeza Formosa*)的效果最为显著[163]. 丛枝菌根真菌(1 种内养囊霉、3 种无梗囊霉和 5 种球囊霉)显著增加黑麦草(*Rhynchrelyrum repens*)幼苗生物量积累[124]. 以当地农业土壤中分离出来的 14 种丛枝菌根真菌在温室条件下接种红薯, 接种效应因属或属内菌株而异, 其中球囊霉属比无梗囊霉属或盾巨胞囊霉属效果更好, 而幼套球囊霉、摩西球囊霉和 GE6 菌株是球囊霉属真菌中最有效的[156]. 酶联免疫分析(ELISA)显示接种根内球囊霉或珠状巨胞囊霉显著增加荔枝幼苗 IAA(吲哚乙酸)含量[164]. 小麦基因型对丛枝菌根真菌的依赖性取决于菌丝发育及其从无机磷酸盐里摄取磷之效率[111,112,165].

Liu 等人[166,167]率先提出评价菌根真菌活力(侵染势, Colonization potential, CP)和接种物有效性(接种势, Inoculum potential, IP)的概念. 菌根真菌侵染势定义为接种物中具有活力的真菌繁殖体数量, 而接种势定义为单位数量接种物在侵染初期侵染植物根系的能力. 以巨胞囊霉、根内球囊霉和地表球囊霉分别接种棉花、大豆、红三叶草和玉米, 结果表明侵染势与接种势显著正相关(r=0.92~0.94)[167].

(4) 丛枝菌根真菌在植物修复和/或土地复垦中的作用. 近年来就丛枝菌根真菌对砷、镉、铅、铀、铜、锌、铈和镧等在植物中的积累、植物修复和土地复垦中的作用进行了大量探讨[116,122~124,68~191]. 研究表明, 球囊霉侵染的玉米根际具有更高的有机结合态铜、锌和铅[177]. 丛枝菌根真菌侵染的蜈蚣草枝条中的铅积累比其根系高 24 倍[186,187]. 摩西球囊霉显著减少砷、镉与铜在金鸡菊和蜈蚣草茎干中的积累[122,123]. 丛枝菌根真菌显著增加大麦、蜈蚣草三种豆科植物(长喙田菁、田菁和紫花苜蓿)根系而非茎中铀含量[118,171,173,192]. 根内球囊霉或珠状巨胞囊霉同时减少紫云英茎干和根系镧含量, 从而有效缓解镧毒害[193].

摩西球囊霉和根内球囊霉在低浓度 10 mg/kg 土壤下增加, 但在高浓度 100 和 1000 mg/kg 土壤下降低香根草对铅和锌的吸收[188]. 与单接种蚯蚓或球囊霉真菌相比较, 双接种增加黑麦草对镉的吸收[194]并且降低土壤铅和锌的迁移[195]. 摩西球囊霉降低蚕豆镉、铜、锌或铅诱导的 DNA 损伤[185]. 此外, 暗隔内生真菌(*Exophiala pisciphila*)菌丝可以积累 5%镉和 20%铅[197]. 上述研究表明, 可以应用丛枝菌根真菌筛选当地植物来修复矿山尾矿或废损生态系统[122,124].

目前, 中国亟需应用以植物为寄主的微生物来修复由于致癌多环芳烃(PAHs)等引起的有机物污染[198]. 球囊霉显著降低紫花苜蓿、三叶草和辣椒土壤芘或菲含量[199,200]. 双接种苏格兰球囊霉或地表球囊霉与根瘤菌紫花苜蓿从污染土壤中移除多氯联苯的效果最好[201,202]. 幼套球囊霉降低玉米茎干但增加根系阿特拉津积累[203,204]. 摩西球囊霉和根内球囊霉提高黄麻土壤中蒽的移除[205]. 幼套球囊霉增强紫花苜蓿根际中菲的逸散[206]和根系中 DDT(二氯二苯三氯乙烷, 滴滴涕)的积累[207]. 光壁无梗囊霉显著降低土体中二(2-乙基己基)酯的积累[102,208]并缓解二丁酯邻苯二甲酸对豇豆生长的抑制[209].

(5) 丛枝菌根植物的酶学性质变化. 摩西球囊霉降低旱稻抗坏血酸过氧化物酶、过氧化氢酶和过氧化物酶活性以及百菌清对旱稻生长的不利影响[210]. 苏格兰球囊霉和珠状巨胞囊霉增加海州香薷(*Elsholtzia splendens*)或摩西球囊霉增加玉米或红三叶草根际土壤磷酸酶和脲酶活性[211~213]. 球囊霉降低沙棘和棉花黄萎病菌诱导的枯萎与接种后土壤碱性磷酸酶(ALP)[214]或可溶性致病相关性蛋白的增减相关[215,216]. 地表球囊霉增加根系可溶性酚类和细胞壁束缚的酚类化合物从而减少番茄青枯病病菌[217]. 幼套球囊霉降低黄瓜枯萎病发生与接种后黄瓜具有较高可溶性糖、脯氨酸和多酚氧化酶活性但较低的丙二醛相关[218,219].

组织化学显示, 土壤磷酸酶是由丛枝菌根真菌释放到土壤中[220]. 摩西球囊霉和珠状巨胞囊霉侵染之紫云英的生物量与琥珀酸脱氢酶和碱性磷酸酶活性相关[221]. 珠状巨胞囊霉增强白三叶草菌丝碱性磷酸酶活性[222]. 丛枝菌根真菌提高喜树根系中喜树碱(一种杀癌细胞化合物)含量[88,223]. 此外, 亦有丛枝菌根真菌诱导产生酚类、生物碱与萜类等次生代谢调节化合物方面的报道[224~226].

(6) 分子生物学技术在丛枝菌根研究中的应用. 巢式聚合酶链式反应和特异性分子探针确证类黄酮化合物如芹菜素或异黄酮能够诱导根内球囊霉或摩西球囊霉侵染并与非丛枝菌根芥菜建立共生[227]. 嵌套多重聚合酶链式反应技术检测到 5 种丛枝菌根真菌孢子同时感染紫云英[228]或红薯根系[229]. 巢式聚合酶链式反应技术只鉴定到台湾杉根系中的美丽盾巨胞囊霉而未

检测到蜜色无梗囊霉[230], 但同时检测到黄檗根系中的根内球囊霉、摩西球囊霉和美丽盾巨胞囊霉[231].

磷缺乏下根内球囊霉提高辣椒、茄子或烟草叶片和根系中磷酸盐转运蛋白 Pht1;3 的表达及 Pht1;4 和 Pht1;5 的诱导[232], 而高磷下增强根系中 Pht1;2 的表达. 但丛枝菌根真菌降低辣椒和烟草叶片中 Pht1;2 的表达[232]. 以巢式聚合酶链式反应和变性梯度电泳相结合来检测农业土壤[233,234]或限制性片段长度多态性来检测桤木根际丛枝菌根真菌遗传多样性的方法也正在开发之中[228].

逆转录酶聚合酶链式反应显示苏格兰球囊霉或根内球囊霉降低番茄根系中 LeSUT1(蔗糖转运基因)和 LeHT2(己糖转运基因)的表达, 但前者虽然降低而后者却增加番茄根系和叶片中 LeST3(单糖转运蛋白基因)的表达[235]. 逆转录酶聚合酶链式反应分析表明地表球囊霉能够诱导葡萄对根结线虫的抗性防御涉及到几丁质酶基因 VCH3 在根系中的转录[236]. 大豆抵抗大豆胞囊线虫感染在于聚生球囊霉诱导根系几丁质酶 b1 和苯丙氨酸解氨酶的表达[237]. 无菌培养下质粒 T-DNA 转化的胡萝卜根能与弯丝球囊霉建立共生[238].

(7) 大气 CO_2 和 O_3 浓度升高对丛枝菌根和真菌多样性的影响.　大气 CO_2 浓度倍增显著增加丛枝菌根真菌对玉米、大豆和小麦幼苗根系的侵染[239], 但大气 O_3 浓度倍增却显著降低丛枝菌根真菌对蚕豆幼苗根系的侵染[240]. 虽然大气 CO_2 和 O_3 浓度倍增都显著提高丛枝菌根植物的生产力[239,240], 但大气 CO_2 浓度升高降低稻麦轮作地里丛枝菌根真菌的菌种多样性[241]. 大气 CO_2 倍增下丛枝菌根真菌菌种数量在其独特组群里得到增加, 而在共同组群里却降低[242]. 丛枝菌根真菌物种多样性对大气 CO_2 倍增的响应取决于宿主植物特性, 如在一年生反枝苋、稗草、大豆、黑麦草、水稻和玉米等植物中具有不同程度的降低, 但在两年生野燕麦、牛筋草、鼠麴草、北美车钱草、早熟禾和白三叶草等植物中却有不同程度的增加[242]. 此外, 大气 CO_2 倍增下苏格兰球囊霉显著增加绿豆的根冠比、总碳与总氮含量[243].

(8) 特殊事件下的丛枝菌根.　近 30 年来, 入侵杂草加拿大一枝黄花已导致中国东部 30 多种土生植物灭绝, 并于 2004 年发现其侵入云南西南. 虽然加拿大一枝黄花入侵土壤中球囊霉属真菌的菌种数量得以增加[244], 但根系侵染率却减少[89,245], 而根际中的真菌孢子数、氮与磷的吸收并未受到影响[246]. 在云南常绿落叶混交林紫茎泽兰严重入侵地点其丛枝菌根真菌丰度 1.5 倍高于非入侵地点, 且前者地点的真菌/细菌比值也更高[247]. 1999 年 9 月 21 日地震后, 台湾九九峰地区台湾松演替为优势先锋树种并在其根际中观察到黑色盾巨胞囊霉孢子出现, 且丛枝菌根真菌的物种多样性在山脊线上比在山谷中较高[248,249]. 四川磨溪石油污染土壤 14 种植物中有 13 种与无梗囊霉、原囊霉和球囊霉 3 属 19 种丛枝菌根真菌共生, 且以缩球囊霉和摩西球囊霉为优势菌种[249]. 其中一年生蓬草和艾蒿根系真菌侵染率高达 69%和 47%, 表明它们能忍耐石油污染[249]. 宁夏牧场改种杨树后, 隐子草、羊草、扁蓿豆、蕨麻和大针茅等 5 种优势植物根际丛枝菌根真菌的孢子密度和根系侵染率都显著下降[250]. 此外, Bt176 转基因玉米根系的丛枝菌根真菌侵染率也显著降低[251,252].

(9) 丛枝菌根真菌对植物病原抗性和与其他土壤微生物的相互作用.　摩西球囊霉降低 1 年龄杨树溃疡病发生与树皮中过氧化物酶和多酚氧化酶活性及酚含量正相关[253,254], 且与树皮中可溶性糖和溃疡病致病真菌(*Dathiorella gregaria*)负相关[254]. 地表球囊霉显著增加 6 周龄番茄根系酚类化合物含量[255]. 摩西球囊霉、根内球囊霉或地表球囊霉显著降低 3 月龄银杏叶枯病[256]或 6 月龄君迁子角斑病[257]. 巨孢囊霉属、实果内囊霉属和球囊霉属真菌显著降低棉花黄萎病[215]、西瓜枯萎病[258,259]和玉米纹枯病[260]. 一般说来, 丛枝菌根真菌介导的抗病特性与植物菌根化后具有更高的养分和水分吸收、叶绿素及抗病有机物息息相关[253~262], 而地表球囊霉最能增强植物抗病性[253~260].

丛枝菌根真菌与某些细菌双接种更能促进植物生长, 如地表球囊霉与拮抗细菌双接种 6 周龄番茄酚类化合物含量比单接种幼苗较高[255]. 根内球囊霉和根瘤菌双接种 4, 7 和 10 周龄紫云英根瘤形成与固氮、菌根侵染和菌丝生长与琥珀酸脱氢酶和碱性磷酸酶活性等都比单接种幼苗较高[263]. 双接种根内球囊霉和慢生根瘤菌紫花苜蓿[264]、摩西球囊霉和解磷细菌红三叶草[265]或摩西球囊霉和重氮营养醋酸杆菌超甜玉米[266]的磷素营养和植株生长都显著增加.

3.2　外生菌根方面的主要成就

(1) 外生菌根真菌的物种丰富度.　在全国共发现 40 科 80 属 500 余种外生菌根真菌, 包括网盖金牛肝菌、甘肃牛肝菌、黑牛肝菌、贵州华牛肝菌、广

东大团囊菌、突癌大团囊菌、粗壮蜡伞、屑状块菌、井冈块菌、会东块菌、阔孢块菌、刘氏块菌、脐凹块菌、西藏块菌、中甸块菌等新菌种[267~295], 而优势菌属为鹅膏属、牛肝菌属、丝膜菌属、乳菇属、红菇属和口蘑属等[4,274,275,279,280,286,293,295]. 它们中 3/4 与不同针叶树木共生(其中 1/3 与松树共生)而其他与桦树、栲树、木麻黄、桉树、栎树、杨树等共生.

(2) 外生菌根真菌菌种的遗传结构. 二元逻辑回归分析表明, 非外生菌根植物能对四川都江堰亚热带森林中外生菌根真菌子实体的发生产生负影响, 并且真菌类群的无性生长不是鹅膏菌科、牛肝菌科和红菇科等外生菌根真菌空间分布格局的唯一决定性因素[296~299]. 随机扩增多态性 DNA 检测出酒色红菇共有 121 条 DNA 带, 其中 94.2%即 114 条具有多态性[297]. 简单序列间重复扩增分析表明遗传变异主要发生在当年生长的隐花青鹅膏菌单个子实体之间且在年份间具有显著差异[298]. 二阶空间格局分析表明, 栲树、马尾松、栓皮栎 3 种林木的林份分布与 17 种外生菌根真菌子实体(3 种鹅膏菌、9 种牛肝菌、1 种乳菇和 4 种红菇)的林中发生率相关[299].

随机扩增多态性分析表明北京人工华北落叶松林下棕灰口蘑性孢子繁殖在其生活史方面具有重要作用[300]. 以单核苷酸多态性构建了中国西南相距 350 公里的两株松茸菌株基因组文库[301], 系统发育分析显示在 178 个单核苷酸多态性单体型中具有三种单倍体型, 包括一些在菌株内和菌株间共享的单倍体型. 以这两株菌株开发出的 14 种限制性片段长度多态性分子标记, 对云南 16 个和四川 1 个地理区域的 154 株松茸菌株进行基因型归类表明松茸地理种群以有性繁殖和遗传重组为主且具显著遗传分化[302].

(3) 外生菌根真菌对养分吸收和植物生长的影响. 外生菌根真菌显著影响氮、磷、钾等养分吸收和植物生长[303~311], 且其菌丝能分泌脱落酸、生长素、赤霉素、吲哚乙酸和玉米素[312]. 11 种外生菌根真菌电子能谱分析表明彩色豆马勃 Tb1665 菌株对氮和磷的吸收能力最强[313]. 电子显微镜检显示菌根化 23 年龄火炬松和 34 年龄湿地松根际粘胶层厚度为 50 μm×55 μm 和 70 μm×90 μm, 而非菌根化植株根际间的粘胶层厚度分别为 20 μm×20 μm 和 40 μm×50 μm[314]. 此外, 接种粘盖牛肝菌后樟子松光合系统 I 和 II 氧气释放在 25 mg/L 铜处理下才受抑制[176].

引进非本地或本地外生菌根真菌促进中国热带和亚热带地区的植树造林(多为松树和桉树)[315~317]. 对澳大利亚和中国两国的桉树接种 23 属 90 种菌株孢子和菌丝, 其苗床幼苗真菌侵染率总体达到 38%[318~322]. 中国南方 155 处人工桉林接种硬皮马勃与彩色豆马勃孢子和菌丝后真菌侵染率却普遍偏低[311,312], 但人工银杉林真菌感染率较天然林为高[323,324]. 此外, 银杉愈伤组织无菌接种土生空团菌, 5 周后便可形成菌根[323,324].

对同一宿主植物内生和外生菌根真菌之间的相互作用也进行了研究. 与英弗梅球囊霉和美丽盾巨孢囊霉相较, 光壁无梗囊霉促进尾叶桉植株生长最佳[325]. 光壁无梗囊霉、英弗梅球囊霉、美丽盾巨孢囊霉或红色蜡蘑单接种对蓝桉生长影响较弱, 而内外生真菌双接种效果更好[325]. 室内外试验都表明苏格兰球囊霉、黏滑菇或根瘤菌三接种刺槐幼苗的生长和固氮最高[326].

(4) 金属元素对外生菌根生长和酶学活性的影响. 在 5~25 mg/L 铜浓度下, pH 3.0~4.0 而非 4.5~6.0 显著抑制毒蝇菌菌丝生长[327]. 层腹菌、彩色豆马勃和硬皮马勃菌株因能耐受高浓度铝、铜、铁与锌而具有在金属污染土壤上进行植被重建的潜力[328]. 葡萄糖-6-磷酸脱氢酶和甘露醇脱氢酶活性与铜或锰处理后的真菌生长显著相关[327]. 接种彩色豆马勃或滑锈伞菇马尾松对人工酸雨和铝毒害的抗性得以增强[329,330], 在 pH 4.0 和 150 μmol/L 铝浓度下彩色豆马勃马尾松葡萄糖和果糖含量得以增加[331].

0.5%~2.0%橄榄油促进松口蘑菌丝生长[176]. 双向电泳和质谱分析显示, 美味牛肝菌在 4%氯化钠盐胁迫下 22 个蛋白位点发生改变, 其中 14 个为上调, 8 个为下调[332]. 电雾极化时飞质谱确定其中 16 种蛋白改变涉及到蛋氨酸合成、糖酵解和 DNA 修复[332]. 外源铜降低黏盖牛肝菌菌丝体己糖激酶、磷酸果糖激酶和谷氨酰胺合成酶活性但提高其谷氨酸脱氢酶活性[175,176]. 彩色豆马勃和土生空团菌在 0.28~0.45 mol/L 极低汞浓度下仍然吸收汞, 而后者可能对汞具有更强适应性[333]. 松乳菇和二色蜡蘑菌株酸性磷酸酶分泌随外源磷酸二氢钠的增加(0.23>1.15>5.74 g/L)而增加, 表明外源磷影响外生菌根真菌活化土壤磷[334].

室内实验表明, 土生空团菌、层腹菌、彩色豆马勃、干巴菌和硬皮马勃菌株等能够利用栲树、石栎和栎树根系分泌物中的多酚化合物如单宁等[335]. 15 天纯培养美味牛肝菌、褐疣柄牛肝菌、铆钉菇和双色蜡蘑菌丝积累 40%~50%外源滴滴涕(5 mg/L), 其余滴滴涕

则降解为二氯苯乙烷和二氯二苯甲酮[336]. 红绒盖牛肝菌漆酶和过氧化物酶活性显著增强且 36 天培养液中(80.0 mg DDT/L)的滴滴涕残留率仅为初始添加量的 3.5%[337]. 10 mg 五氯酚/L 下虽然影响美味牛肝菌、红绒盖牛肝菌、大毒黏滑菇和长柄黏滑菇菌丝生长, 但对铆钉菇、双色蜡蘑和褐疣柄牛肝菌则无影响, 且铆钉菇的多酚氧化酶、漆酶和过氧化物酶活性最高[338]. 接种铆钉菇后白皮松幼苗在 85%煤矸石与 15%黄土之混合基质中生长良好[339], 显示出铆钉菇在矿区土壤生物修复和植树造林中的应用潜力[338,339].

3.3　兰花菌根研究方面的主要成就

在全国共分离到大约 100 种兰花菌根真菌新类群或新种如开唇兰小菇、石斛小菇、兰小菇和兰镰刀菌菇等, 其中多为担子菌和半知菌[340~351]. 如从香港黄花美冠兰、叶兰、鹭兰和香港绶草根系分离到 21 株丝核菌状菌株, rDNA 片段分析为角菌根菌属和瘤菌根菌属[352]. 最近开发出一种能进行死活菌丝团鉴别和能从含有多个兰花菌根真菌类群之同一菌丝团里分离出单一类群且避免真菌与细菌污染的实验方法[351].

接种角菌根菌、瘤菌根菌、兰花菇、石斛小菇、兰小菇、紫萁小菇、或胶膜菌等都促进兰花种子萌发和生长, 如金线莲、独花兰、杜鹃兰、建兰、莲瓣兰、墨兰、大花蕙兰、长苏石斛、白花石斛、鼓槌石斛、密花石斛、美花石斛、罗河石斛、环草石斛、报春石斛、双叶厚唇兰、天麻、长茎羊耳蒜、杏黄兜兰、独蒜兰和万代兰等[342,343,348,350,353~355]. 组织培养表明接种兰花菌根真菌并加入 0.12 mol 果糖或 0. 25 mol 磷酸二氢钾, 兰花植株叶绿素 *a* 和 *b*、幼苗生长和养分吸收都得到促进[119,340,356~361]. 丝核菌和其他兰花菌根真菌对兰花种子萌发与移栽成活率、营养与生殖生长以及抗病毒能力等都产生积极影响[362].

光学和扫描电子显微镜镜检显示老嫩变色彩叶兰根系菌丝团都有典型的兰花菌根结构(tolypophagy), 但接种 7 株丝核菌菌株后只有 R01 和 R022 株能促进兰花种子发芽[363]. 进一步研究表明真菌菌丝侵入所有接种过的兰花杂交亲本或F1杂交后代原球茎(台湾金线莲×变色彩叶兰或变色彩叶兰×台湾金线莲)且与丝核菌株 R01, R02 和 R04 分别形成菌丝团[364]. 丝核菌株 R02 和 R04 还能促进金线莲叶片超氧化物歧化酶与根系酸性和碱性磷酸酶活性以及抗坏血酸、多酚、类黄酮和多糖化合物含量[364]. 最近中国内地开发出扩增片段长度多态性与 rDNA 内转录间隔区段等分子技术来进行兰花菌根研究[365~367]. 此外, 应用兰花菌根真菌大规模生产金线莲、白芨枫香、紫晶舌石斛、金钗石斛、黄花石斛、变色彩叶兰、南茜文心兰以及朵丽蝶兰属、兜兰属和蝴蝶兰属等兰花品种也提上了议事日程[362].

4　菌根研究之中国学术团体和国际合作简介

中国大陆菌根研究学者散布在中国菌物学会、中国植物学会、中国土壤学会、中国林学会、中国生态学会、中国食用菌协会和中国植物营养与肥料学会等专业学术团体. 在台湾也有类似的学术团体, 这些学术团体负责组织专业学术活动如同行评审出版物和召开研讨会等. 中国菌根研究除少许发表在英文期刊外(表 1), 绝大部分发表在中国大陆出版的期刊上, 如云南植物研究、生态学报、土壤学报, 生物多样性、植物学通报(现植物学报)、Chinese Forestry Science and Technology、应用生态学报、生态学杂志、菌物研究、Journal of Integrative Plant Biology(英文, 原植物学报)、Journal of Plant Ecology(英文, 原中国植物生态学报)、菌物学报(原真菌学报)、Pedosphere(土壤圈)、植物营养与肥料学报、林业科学、土壤等等, 最近 10 年中国大陆也有菌根书籍出版[4,13,14,59,60,315~317,349]. 与此同时, 汪洪钢先生等“VA 菌根主要生物学特性及应用”荣获 1995 年国家科技进步三等奖, 花晓梅先生等“截根菌根化应用及其机理的研究”荣获 1997 年度国家科技进步二等奖和“林木菌根化生物技术的研究”荣获 2001 年国家科技进步一等奖以及刘润进先生等“中国丛枝菌根研究”荣获 2005 年山东省自然科学奖一等奖. 此外, 菌根研究也发表在中国台湾出版的期刊上, 如 Botanical Studies(英文, 原中央研究院植物学汇刊)、中华农业研究、中华真菌学会会刊、中华农学会报、中国林业季刊、土壤与环境、台湾林业科学等等. 同时, “Dr. Root”, “Mycovam”和“Ai-gen-how”等丛枝菌根真菌接种物已在台湾商品化.

迄今中国大陆已举行了 11 届全国菌根学术研讨会, 参加者由几十人到数百人逐届增加. 大陆菌根学者近年来也积极参与和举办或协办国际学术会议与讲习班, 如由澳大利亚国际农业研究中心赞助 1994 年在广东开平(约 100 名澳大利亚和南亚代表)和 1998 年在

广州(约60名澳大利亚、巴西和亚洲国家代表)召开的菌根讲习班. 第五届国际菌根性食用菌国际会议也于2007年8月在云南楚雄举行. 澳大利亚国际农业研究中心1996年出版在世界上广泛使用的菌根研究方法手册便是1994年研讨会的成果. 这些学术活动已对世界菌根生物学研究产生了深远的影响.

5 中国菌根共生研究的未来和前景

菌根真菌为生态系统碳素与其他养分循环过程中的核心成分, 菌根共生在土壤结构、植物营养吸收、植物多样性和生产力等方面具有十分重要的作用[4,5,368~372]. 近30年来, 中国学者在丛枝、外生和兰花菌根的生态分布和组成、对植物生长与林木种植及重金属或有机污染物的植物修复等方面取得了重大进展[4,13,14,59,60,63,315,316,373], 虽然大都为描述性研究且以中文形式发表, 但越来越多在国际英文刊物上发表. 鉴于中国生态系统的多样性和独特的真菌、植物和土壤资源, 我们在此展望中国菌根研究的一些未来方向与前景[369,374~393]:

(ⅰ) 传统分类与现代分子生物技术相结合鉴定丛枝、外生与兰花菌根在中国尤其在青藏高原和中国的两个全球生物多样性热点地区(图1的Ⅳ和Ⅵ区[1])的生物地理分布和分类;

(ⅱ) 系统探索中国境内826种(全球约1000种)杜鹃花科植物(524种中国特有种)和571种杜鹃属树种(409种中国特有种)的浆果鹃类菌根(arbutoid)共生生物学;

(ⅲ) 兰花菌根真菌新菌种分离及其对兰花萌发生芽的作用, 探索室内兰花菌根植物种植以遏制对珍稀野生兰花(如单株价值高达175000美元[394])的过度采集;

(ⅳ) 菌根共生对植物病原体抗性影响、菌根真菌与其它土壤微生物, 特别是固氮根瘤菌和放线菌及根际植物生长促进细菌之间的相互作用;

(ⅴ) 丛枝与外生菌根真菌双接种对本土和引进植物(如相思、桉树、橡胶和紫檀等)根系形态、养分与水分和植物生长的影响;

(ⅵ) 大规模种植麻疯树(生物燃料)、橡胶树(橡胶)、桉树(造纸)、紫檀(经济)、转基因作物与树木及外来紫茎泽兰和加拿大一枝黄花入侵等对菌根真菌群落的组成和丰富度的影响;

(ⅶ) 菌根真菌遗传结构与功能多样性、信号传递与植物生长调节物质对菌根真菌与植物共生在不同生态系统中的关联机制;

(ⅷ) 菌根真菌在早期幼苗与树冠建立及在因人类活动或自然灾害如2008年5月四川地震山体滑坡等引起的荒废土地复垦中的作用;

(ⅸ) 菌根植物在重金属和无机与有机物污染的土壤修复及在抗盐与抗旱中的应用;

(ⅹ) 宿主植物、菌根真菌和土壤资源在营养元素与水分移动或通过菌根网络相连接之植物群落资源竞争与共享中的互动作用;

(ⅺ) 应用^{2}H, ^{18}O, ^{13}C和^{15}N研究与菌根真菌相关的植物生理与生理生态机制和在陆地生态系统生物地球化学养分循环中的作用;

(ⅻ) 菌根植物对土壤水分从深层向表层抬升和再分布在全球环境变化下尤其是在半干旱和干旱地区对维持生态系统持续性的作用;

(xiii) 丛枝菌根真菌在土地利用变化和现代农耕特别是在干旱和半干旱生境下之土壤球囊蛋白(球囊霉素)形成、土壤团聚体和土壤结构间的互动作用;

(xiv) 现代农耕如长期施用有机肥料或无机氮磷肥、有机农业、机耕和免耕对丛枝菌根真菌群落生态分布和组成的影响;

(xv) 通过适宜农耕管理并结合生物强化(http://www.harvestplus~china.org/)来探索菌根真菌在生物强化农产品品质及减缓人类营养元素隐性不良中的作用;

(xvi) 植物地上生长和地下菌根相互作用对全球环境变化特别是二氧化碳、氮素沉积和温度增加的响应;

(xvii) 菌根真菌群落与多样性影响植物群落与多样性, 抑或植物群落与多样性影响菌根真菌群落与多样性进程中的植物和菌根相互调控;

(xviii) 海南、西藏、云南热带地区和中国的两个全球生物多样性热点地区(图1第Ⅳ区和第Ⅵ区[1])中的真菌混合营养和菌生异养相互作用;

(xix) 筛选新型食用性外生菌根真菌并探索它们在人工或天然林下的食用菌持续生产的作用和从菌根性珍稀食用蘑菇中进行药物化合物的分离;

(xx) 菌根真菌资源与接种物的互换和共享, 林业、园艺、农业及食用菌产业中效优价廉菌根接种物的开发、应用和管理.

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