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菌根对土壤呼吸影响的研究进展

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摘要: [目的] 菌根作为连接植物与土壤的桥梁,在土壤碳(C)库收支平衡中扮演着关键角色。菌根通过吸收土壤中的矿物营养物质以交换植物光合作用固定的C,同时也通过呼吸作用造成土壤C损失。尽管人们对菌根在土壤碳输入、分解和固持方面的作用已有较深入了解,但关于菌根对土壤呼吸的影响仍相对有限。[方法] 采用网络排除法和比较法综述菌根对土壤呼吸的影响及其调控因子。[结果] 通过网格排除法,有学者成功分离并量化菌根呼吸,发现其平均占土壤呼吸的16.8%。具体而言,丛枝菌根呼吸和外生菌根呼吸对土壤呼吸的贡献分别为18.4%(2.5%~32.0%)和15.1%(3.0%~62.1%)。与无菌根植物相比,接种菌根的植物平均增加26.0%土壤呼吸。菌根呼吸对土壤温度和土壤湿度的响应在不同生态系统中存在差异,菌根呼吸对土壤湿度的变化更加敏感。土壤养分有效性通过影响植物的养分获取策略,从而调控菌根与植物的共生关系,进而调控菌根的呼吸。植物细根生物量、根外菌丝长度密度及植物供应的底物等生物因子也对菌根呼吸有显著影响。[结论] 菌根呼吸是土壤呼吸和自养呼吸的重要组成部分,引起的土壤C损失不容忽视,需要更先进的方法分离和量化菌根呼吸,并将菌根呼吸纳入全球碳模型,以便更准确地评估土壤碳循环动态,为全球碳管理和缓解全球气候变化提供科学依据。

关键词: 菌根呼吸; 土壤呼吸; 土壤温度; 土壤湿度; 生物因子

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Progress in the Study of the Effects of Mycorrhiza on Soil Respiration

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Abstract: [Objective] Mycorrhiza, as a bridge connecting plants and soil, play a crucial role in soil carbon (C) budget. They absorb mineral nutrients from the soil in exchange for C fixed by plant photosynthesis, while simultaneously contributing to soil C loss through respiration. Although the roles of mycorrhiza in soil C input, C stability, and C sequestration are relatively well understood, knowledge of the effects of mycorrhiza on soil respiration remains less explored. [Methods] Using network exclusion and comparison methods, this review synthesizes current knowledge on the influence of mycorrhiza on soil respiration and its regulatory factors. [Results] Using the mesh exclusion method, researchers have successfully isolated and quantified mycorrhizal respiration, and found that it accounted for an average of 16.8% of soil respiration. Specifically, the contributions

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of arbuscular mycorrhizal respiration and ectomycorrhizal respiration to soil respiration are 18.4% (2.5%–32.0%) and 15.1% (3.0%–62.1%), respectively. Compared to mycorrhizal-free plants, mycorrhizal-inoculated plants increased soil respiration by an average of 26.0%. Mycorrhizal respiration responds differently to soil temperature and soil moisture across various ecosystems, with mycorrhizal respiration appearing to be more sensitive to changes in soil moisture. Soil nutrient availability regulates the symbiotic relationship between mycorrhizal fungi and plants by affecting the nutrient acquisition strategies of plants, thereby regulating mycorrhizal respiration. Additionally, biological factors such as fine root biomass, extraradical hyphal length density, and the substrates supplied by plants also have significant effects on mycorrhizal respiration. [Conclusion] As an important component of both soil respiration and autotrophic respiration, mycorrhizal respiration contributes substantially to soil C loss, which cannot be overlooked. More advanced methods are needed to isolate and quantify mycorrhizal respiration, and incorporate it into global C models to more accurately assess soil C cycling dynamics, thus providing a scientific basis for global C management and mitigating climate change.

Keywords: mycorrhizal respiration; soil respiration; soil temperature; soil moisture; biological factors

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二氧化碳(CO₂)作为主要的温室气体之一^[1],其浓度的增加对全球气候变化有着深远的影响。根据IPCC第六次评估报告,2019年大气CO₂浓度已达到(410.5±0.2)μL/L,较工业革命前增加48%^[2]。这些变化不仅反映了人类活动对大气成分的显著影响,也预示着未来气候变化的潜在风险。土壤既是CO₂的重要来源,也是关键的碳汇,在调节大气CO₂浓度中发挥着重要作用。由根系活动和土壤生物代谢驱动的土壤CO₂排放(土壤呼吸)是植物固定的CO₂释放回大气的主要方式^[3]。土壤呼吸代表着陆地生态系统到大气C损失^[4]。因此,控制或减少土壤呼吸速率对于实现“双碳”目标(即碳达峰碳中和)具有重要意义,不仅有助于减少大气CO₂积累,还有效减缓全球变暖进程。

菌根真菌是一种广泛分布的土壤真菌类群,几乎可与所有陆生植物形成共生关系^[5]。作为连接土壤与植物根系的重要桥梁,菌根在土壤C循环中起着关键作用^[6]。在土壤中,菌根通过庞大的菌丝网络吸收矿物营养物质,并将其传递给宿主植物,以换取植物提供的碳水化合物或脂肪酸^[7-8],可利用多达10%~30%的植物净光合产物^[9]。然而,植物分配给菌根的碳也能以CO₂的形式通过根外菌丝进入大气,即菌根呼吸。JOHNSON等^[10]利用¹³C同位素标记技术,首次在野外条件下证实根外菌丝体是土壤到大气碳通量快速且重要的途径。他们的研究发现,在标记后9~14 h,菌丝释放的¹³CO₂达到顶峰,为理解土壤碳循环和全球碳平衡提供新的视角。

菌根呼吸应被视为自养还是异养一直存在争议。菌根真菌本身是异养生物,但其呼吸的底物直接来源于植物根部,因此,通常被归为自养呼吸的一

部分^[11]。传统意义上,自养呼吸主要指植物根系呼吸,但由于方法限制,在实际操作中自养呼吸还包括根系分泌物、近期死亡细根分解产生的CO₂、根际微生物的异养呼吸及菌根呼吸^[12]。尽管已有研究^[13]探讨不同生态系统中土壤呼吸和/或自养和异养呼吸对生物和/或非生物因子的响应,但菌根呼吸通常作为自养呼吸的一部分。近年来,随着技术手段的发展,自养呼吸进一步分离为根呼吸和菌根呼吸。前人^[14-15]利用不同方法在不同生态系统中研究菌根对土壤呼吸的影响发现,菌根呼吸对土壤呼吸影响的程度和方向存在较大差异,且受多种因子的调控,其背后机制尚不明确。

本文以Web of Science(WOS)核心合集数据库为数据源,采用高级检索方式{TS=[(“arbuscular mycorrhiza” or “ectomycorrhiza”) and (“soil respiration”)]} or (TS=“mycorrhizal respiration”)进行检索,检索时间范围设定为1980—2024年(检索日期为2024年12月20日),文献类型为Article和Review,共检索到已发表文献759篇。VOSviewer对文献的关键词进行聚类共现分析,将以共现网络图进行可视化。共现网络图中圆的大小代表关键词出现的次数,次数越多圆越大;节点之间距离代表关键词共现频率的高低,共现频率越高,则距离越近^[16]。将WOS检索到的759篇文献导出为纯文本文件,使用VOSviewer软件进行关键词聚类分析,设置关键词出现次数阈值为5,并合并关键词中的同义词。最终,筛选出79个关键词,绘制关键词共现网络图(图1),划分为4个主要聚类。聚类1是以arbuscular mycorrhiza、soil respiration、ectomycorrhiza、mycorrhiza、nitrogen、phosphorus、photosynthesis、carbon、temperature、soil

moisture、fine roots、symbiosis、mycelium、nutrient limitation、carbon use efficiency 等为主要关键词,重点探讨菌根对土壤呼吸的影响。聚类 2 是以 microbial biomass、plfa、enzyme activity、microbial activity、root exudation、soil organic matter、carbon sequestration、soil carbon 为主要关键词,主要聚焦于菌根对土壤碳输入、碳分解和碳固持等方面的影响。聚类 3 和聚类 4 是以 fungi、bacteria、soil quality、growth、organic

farming、salinity、glomalin、heavy metals、glomeromycota 为主要关键词,关注菌根在土壤修复中的应用。目前,人们已认识到菌根在土壤碳循环中的重要作用,并对其在土壤碳输入、碳分解和碳固持等方面的影响进行综述^[17-20],然而,关于菌根对土壤呼吸的影响尚缺乏综合性论述。鉴于此,本文重点围绕聚类 1 展开综述,探讨菌根对土壤呼吸的影响及其调控因子,并强调菌根造成的土壤 C 不容忽视。

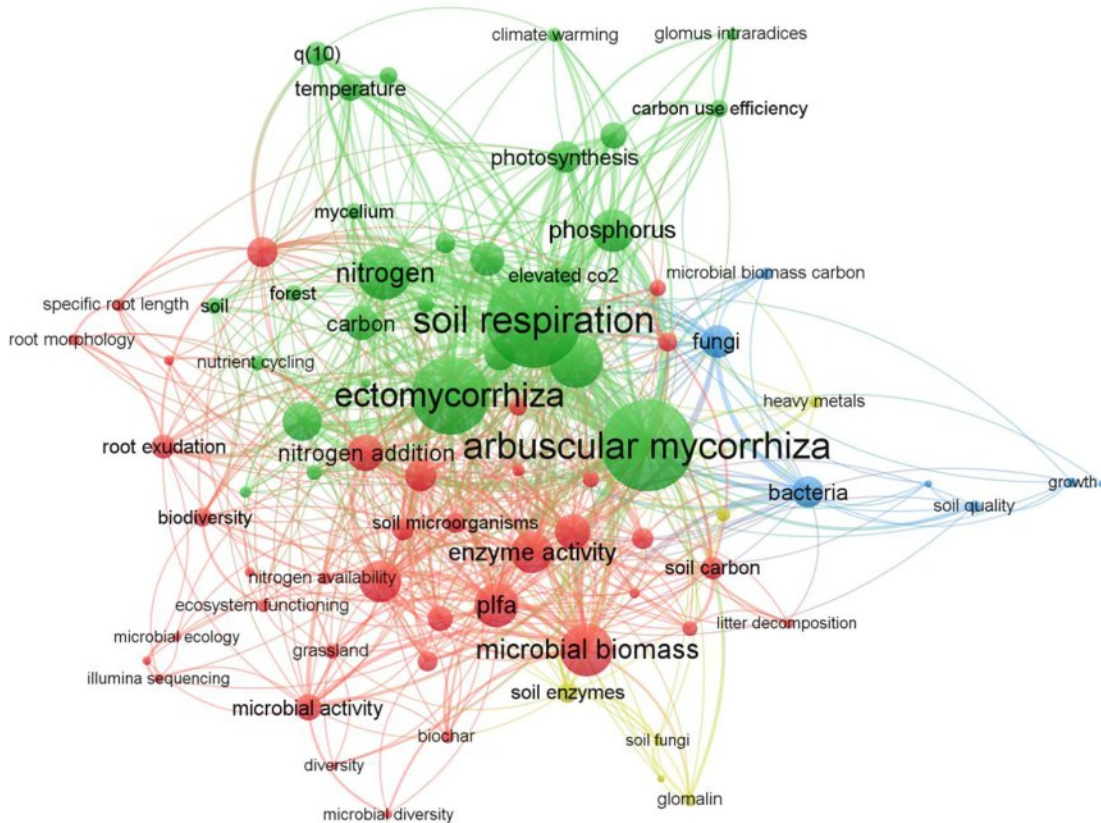


图 1 菌根对土壤呼吸影响的论文关键词共现网络可视化

Fig.1 Co-occurrence network visualization of key words of the impact of mycorrhizal fungi on soil respiration in the literature

1 菌根调控土壤呼吸的研究方法

菌根是绝对的共生体,离开宿主植物则无法独自生存。研究菌根生态功能的一大障碍是必须设法消除植物根系的影响和建立无菌根对照。目前,研究人员主要采用 2 类方法探究菌根对土壤呼吸的影响,分别为网格排除法和灭菌(或抑菌)再接种法。

1.1 网格排除法

网格排除法常用于量化和分离土壤呼吸的不同组分,其原理是利用不同孔径的筛网对根系和菌丝进行物理分离。具体方法为:无筛网覆盖或较大孔径的筛网可允许根系和根外菌丝(RM)进入,从其测量的土壤 CO₂(R_a)认为是由菌根呼吸、根呼吸和土壤微生物呼吸组成的土壤总呼吸;20~40 μm 孔径的筛网可排除根系,但允许根外菌丝(M)进入,从其测量的 CO₂(R_b)认为是由菌根呼吸和土壤微生物呼吸组

成(图 2);0.45~2 μm 孔径的筛网可同时排除根系和根外菌丝(-RM),允许水、细菌、养分通过筛网与外界土壤进行交换,从其测量的 CO₂(R_c)认为是只有土壤微生物呼吸(图 2)。菌根呼吸、根呼吸、土壤微生物呼吸及不同组分对土壤总呼吸的相对贡献计算公式为:

$$\text{土壤总呼吸}(\text{total soil respiration}, R_{\text{total}}) = R_a \quad (1)$$

$$\text{土壤微生物呼吸}(\text{soil microbial respiration}, R_{\text{micro}}) = R_c \quad (2)$$

$$\text{根呼吸}(\text{root respiration}, R_{\text{root}}) = (R_a) - (R_b) \quad (3)$$

$$\text{菌根呼吸}(\text{mycorrhizal fungi respiration}, R_{\text{myc}}) = (R_b) - (R_c) \quad (4)$$

$$R_{\text{myc}} = (R_{\text{myc}}/R_{\text{total}}) \times 100\% \quad (5)$$

$$R_{\text{root}} = (R_{\text{root}}/R_{\text{total}}) \times 100\% \quad (6)$$

$$R_{\text{micro}} = (R_{\text{micro}}/R_{\text{total}}) \times 100\% \quad (7)$$

式中:R_{myc}、R_{root}和 R_{micro} 分别为菌根呼吸、根呼吸和微生物呼吸占土壤总呼吸的百分比,%。

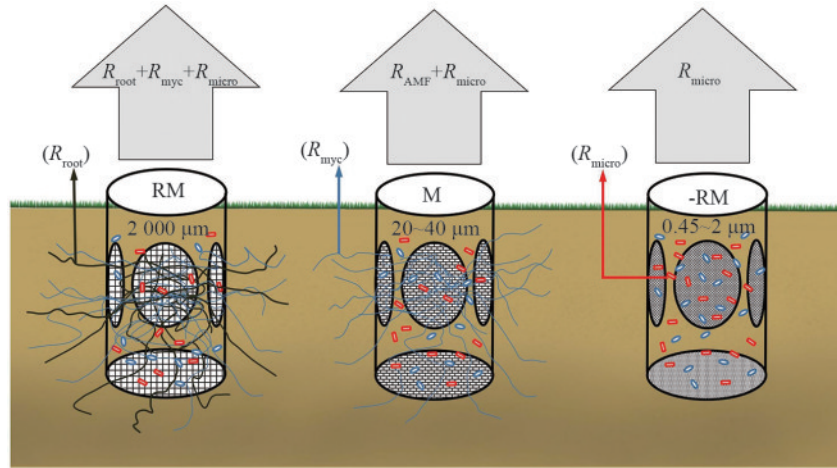


图2 量化菌根呼吸、根呼吸和微生物呼吸设计示意

Fig.2 Schematic diagram showing the experimental design for quantifying mycorrhizal respiration, root respiration, and microbial respiration

使用公式量化菌根呼吸最重要的前提是土壤微生物呼吸在3种不同孔径的筛网中始终保持一致,但实际情况并非如此。一方面,根外菌丝可释放不稳定底物促进微生物生长,并且菌根真菌自身也是土壤微生物的一部分^[21-22],因此,在根外菌丝存在的情况下,M中的土壤微生物呼吸量应大于-RM;另一方面,根外菌丝与其他土壤微生物在竞争性吸收利用土壤养分时,通常占据优势地位^[23-24],从而抑制土壤微生物活动,当根外菌丝被排除时,这种竞争作用被消除,-RM的土壤微生物呼吸率高于M。事实上,已有研究^[25-26]表明,根外菌丝存在时的CO₂通量低于排除根外菌丝时,可能归因于“Gadgil效应”。植物根系和菌根与异养微生物竞争土壤养分,而根系和根外菌丝的去留往往导致土壤微生物活性增加,促进土壤有机质分解,此现象称为Gadgil效应^[27]。根外菌丝吸收水分可引起M与-RM之间的土壤水分差异^[28],而土壤水分会改变异养微生物活性^[26],因此有必要进行培养试验,以探究异养土壤呼吸对水分的依赖性,并进行相应的校正。最后,该法仅量化菌根的根外菌丝体呼吸,但根内的菌根生物量也不可忽视的,特别是嗜根性菌根^[29],理论上菌根对根源性土壤呼吸的全部贡献应高于目前网格排除法量化的菌根对根源性土壤呼吸的占比。尽管网格排除法存在局限性,但由于其试验操作简便,物理分离效果明显,仍被广泛用于研究菌根在土壤碳循环中的作用。

1.2 土壤灭菌后再接种

土壤灭菌(或抑菌)和再接种是菌根研究中常用的方法,分别用于建立无菌根对照组和菌根处理组,通过比较有无菌根真菌侵染的植物根系呼吸速率,间接评估菌根对土壤呼吸的影响。在土壤灭菌过程中,可杀死连同土壤真菌在内的所有

微生物,低估土壤呼吸的异养成分,从而高估菌根对土壤呼吸的贡献。在灭菌土壤中进行菌根真菌接种时,研究人员通常选择特定的、已知的几种菌根真菌以构建菌根处理。由于AMF不具有宿主偏好性和专一性,在自然环境中植物根系通常与多种真菌种类共生,不同种类菌根真菌对土壤呼吸的影响可能存在差异^[30]。因此,即使同时接种多种菌根真菌也未必能够完全模拟自然生态系统中菌根群落的复杂性,从而影响试验结果的生态适用性。还有少量研究^[31-32]采用番茄菌根缺陷突变体(*rmc*)和番茄菌根野生型(76R MYC)来探究菌根对土壤呼吸的影响。此方法操作简单,但受限于特定宿主植物难以探究其他宿主植物与菌根真菌共生时的生态作用。

2 菌根对土壤呼吸的贡献

通过对WOS检索到的759篇文献进行人工筛选,最终获得51篇关于菌根对土壤呼吸影响的文献。在中国知网数据库中进行高级检索并筛选后,补充5篇相关研究,总计56篇。其中,采用网格排除法量化菌根呼吸的研究有41篇,采用菌根接种试验探究菌根对土壤呼吸影响的有15篇。

2.1 网格排除法量化下的菌根呼吸

已有研究^[33]利用网格排除法分离并量化菌根呼吸发现,菌根呼吸在不同生态系统对土壤呼吸的贡献存在较大差异。丛枝菌根(Arbuscular mycorrhiza, AM)和外生菌根(Ectomycorrhiza, ECM)是2种主要的菌根类型。AM真菌可与超过2/3的陆地植物形成共生关系,广泛分布于中低纬度森林和草原生态系统^[34]。在不同生态系统中,AM呼吸对土壤呼吸的贡献比例有所不同。例如,在潮湿的热带森林中,AM呼吸速率为1.4 t/(hm²·a),约占土壤总呼吸的

14%^[35],在亚马逊干旱雨林中约占24%^[36]。在亚热带中,毛竹林AM呼吸贡献约13%的土壤呼吸和36%的自养呼吸^[37];ZHENG等^[38]研究发现,杉木人工林AM呼吸贡献12%的土壤呼吸和25%的自养呼吸,而XIA等^[39]研究表明,AM呼吸占杉木人工林土壤呼吸的22%,占自养呼吸的50%。即在相同的生态系统中,AM呼吸对土壤呼吸的贡献也不固定。在以AM植物为主的沙漠生态系统中,YUE等^[40]研究发现,24%的土壤呼吸来源于AM呼吸,与李伟晶等^[41]在内蒙古半干旱草原中连续3 a测定的AM呼吸贡献(21%~26%)相近。在农业生态系统中,AM呼吸对苹果园土壤呼吸的贡献(11%)与根的贡献(12%)相近^[42];MOYANO等^[43]研究发现,在整个生长季,大麦土壤呼吸中7.6%的来源于AM呼吸,最高时可达19.1%。整体来看,AM呼吸对土壤呼吸的贡献为2.5%~32.0%,平均值为15.1%±1.1%(表1)。

表1 菌根对土壤呼吸的平均贡献

Table 1 The average contribution of mycorrhizal fungi to soil respiration

寄主植物(AM)	(R_{myc}/R_T)/%	参考文献	寄主植物(ECM)	(R_{myc}/R_T)/%	参考文献
<i>Schima superba</i>	9.0	[25]	<i>Betula pendula</i>	26.2	[14]
Mixed forest	6.8	[35]	<i>Lodgepole</i>	26.0	[14]
Mixed forest	23.2~24.8	[36]	<i>Castanopsis fargesii</i>	12.0	[25]
<i>Cunninghamia lanceolata</i>	9.8~23.0	[38-39]	<i>Larix sibirica</i>	21.3	[26]
<i>Erodium oxycorynchum</i> et al.	24.0	[40]	<i>Pinus sylvestris</i>	4.1	[26]
<i>Stipa grandis</i> et al.	22.5	[41]	<i>Picea abies</i>	52.5~62.1	[45]
<i>Malus domestica</i>	10.7	[42]	<i>Pinus contorta</i>	13.4~15.1	[46]
<i>Hordeum vulgare</i>	7.6	[43]	<i>Larix kaempferi</i>	6.5	[47]
<i>Acer pseudoplatanu</i> , <i>Fraxinus excelsior</i>	8.0	[52]	<i>Pinus sylvestris</i>	4.9~48.0	[48, 50, 56-57, 59, 63, 70]
<i>Rubiaceae</i> et al.	2.5~30.2	[54]	<i>Fagus sylvatica</i> , <i>Fraxinus excelsior</i>	3.0	[51]
<i>Festuca pseudovina</i> et al.	13.7~15.8	[60, 62] [66, 72]	<i>Picea abies</i>	8.0	[51]
C ₃ grasses	32.0	[64]	<i>Quercus robur</i>	17.7	[53]
C ₄ grasses	23.0	[64]	<i>Tsuga heterophylla</i>	15.4	[55]
Forbs	9.0	[64]	<i>Quercus acutidentata</i>	10.3~15.3	[58]
Diverse plant communities	9.0	[64]	<i>Pinus contorta</i> , <i>Pinus sylvestris</i>	12.9	[61]
<i>Rusa unicolor</i> et al.	7.3~20.3	[67]	Broad-leaved Korean pine mixed forest	13.2~14.4	[65]
<i>Phyllostachys pubescens</i>	11.5~18.5	[68]	Mixed forest	12.1	[71]
Mixed forest	6.8~10.6	[69]	Moso bamboo	13.3~22.6	[37, 71]
Broadleaved forest	10.2	[71]			

在不同生态系统中,菌根呼吸在土壤呼吸组分中的占比存在较大差异。菌根呼吸平均贡献16.8%的土壤呼吸(表1)。表明菌根呼吸是土壤呼吸和自养呼吸的重要组成部分,对土壤碳循环的影响不容忽视。考虑到菌根独特的碳来源和微生物作用,不应简单地将其归类为自养呼吸,需要将其从自养呼

吸中分离,以更准确地评估其在土壤碳损失和碳循环中的作用。

外生菌根真菌虽然仅与约2%的陆地植物形成共生关系,但其分布广泛,尤其是在中高纬度和高山森林生态系统中,覆盖全球陆地植被面积的1/4以上^[44]。ECM呼吸对土壤呼吸的贡献因生态系统类型而异,表现出较大的区域性差异。例如,NEUMANN等^[45]研究表明,挪威云杉幼林ECM呼吸占土壤呼吸50%以上,占自养呼吸70%以上。在火炬松林中,ECM呼吸对土壤呼吸的贡献(25%)高于根系呼吸(15%)^[14]。在落叶松林中,YAN等^[46]研究表明,ECM呼吸贡献14%的土壤呼吸,而MAKITA等^[47]研究发现,ECM呼吸贡献仅为6%。在温带樟子松人工林中,ECM呼吸约占土壤总呼吸的20%^[48],而在油松林中贡献率为12%^[49],在苏格兰松林约为5%^[50],在欧洲山毛榉林为3%^[51]。总体来看,ECM呼吸对土壤呼吸的贡献范围较广,为3.0%~62.1%,平均值为18.4%±1.6%(表1),略高于AM呼吸的平均值(15.1%)。

2.2 菌根接种对土壤呼吸的影响

接种菌根可显著提高土壤呼吸速率,相较于未接种菌根的土壤,其土壤呼吸速率最高可增加104%,说明菌根对土壤呼吸具有促进作用。接种菌根可降低土

壤呼吸,最高可减少49%。整体来看,与无菌根对照相比,接种菌根平均可增加26%的土壤呼吸(表2)。可能的原因:1)接种菌根增加植物的养分吸收^[73],促进植物生长和新陈代谢的能量需求来影响自养呼吸^[74]; 2)菌根通过菌丝分泌物和菌丝的快速周转向土壤释放

不稳定碳源^[75],可刺激土壤微生物生长和繁殖^[76],并为微生物酶生产和土壤有机质分解提供能量^[77],进而增加微生物异养呼吸;3)菌根真菌的菌丝在营养转运、生长和维持过程中需要消耗能量,导致额外的呼吸成本,其自身的呼吸活动也直接增加土壤呼吸成本^[78]。

表2 菌根真菌定殖对土壤呼吸的影响

Table 2 The impact of mycorrhizal fungi colonization on soil respiration

寄主植物	菌根真菌物种	增加率/%	参考文献
<i>Allium porrum</i>	<i>Glomus mosse</i>	57.1	[79]
<i>Trifolium subterraneum</i>	<i>Glomus mossese</i>	-5.4	[80]
<i>P. major ssp. pleiosperma</i>	<i>Glomus fasciculatum</i>	13.0~20.0	[81]
<i>Pisum sativum</i>	<i>Glomus intraradices</i>	3.7	[82]
<i>Capsicum annuum</i>	<i>Glomus intraradices</i>	38.3~94.3	[83]
<i>Capsicum annuum</i>	<i>Glomus AZ112</i>	14.9~62.9	[83]
<i>Helianthus annuus</i>	<i>Glomus intraradices</i>	30.0	[30]
<i>Helianthus annuus</i>	<i>Gigaspora gigantea</i>	19.0	[30]
<i>Trifolium alexandrinum</i>	<i>Glomus intraradices</i>	-29.0~-23.0	[84]
<i>Lycopersicon esculentum</i>	<i>Glomus mosseae</i>	40.4	[85]
<i>Phaseolus vulgaris</i>	<i>Glomus etunicatum</i>	-15.9~41.9	[86]
<i>Plantago lanceolata</i>	<i>Glomus hoi</i>	33.1	[74]
<i>Lolium multiflorum</i>	Mixture AMF species	5.0	[87]
Rice	<i>Glomus mosseae</i>	23.8	[88]
<i>Prunus discadenia</i>	<i>Funneliformis mosseae</i> BGCXJ01	29.6	[89]
<i>Prunus dictyneura</i>	<i>Funneliformis mosseae</i> BGCXJ02	46.0	[89]
<i>Xanthoceras sorbifolium</i>	<i>Funneliformis mosseae</i> BGCXJ03	32.2	[89]
<i>Armeniaca sibirica</i>	<i>Funneliformis mosseae</i> BGCXJ04	34.5	[89]
Tomato(中杂9号)	<i>Glomus intraradices</i>	19.8	[90]
<i>Sabina chinensis</i>	<i>Funneliformis mosseae</i>	-49.0~86.2	[91]
<i>Sabina chinensis</i>	<i>Rhizophagus intraradices</i>	-42.4~104.4	[91]

3 菌根影响土壤呼吸的驱动因子

根据菌根影响土壤呼吸的驱动因子将聚类1中的关键词分为3类,第1类归为土壤环境因子(temperature、soil moisture);第2类是土壤养分(nitrogen、phosphorus、nutrient limitation);第3类属于生物因子(fine roots、symbiosis、mycelium、photosynthesis、carbon use efficiency)。

3.1 土壤温湿度

菌根呼吸对土壤环境(温度和湿度)变化的响应不同。MAKITA等^[47]研究发现,在落叶松林中ECM呼吸速率随温度升高呈指数增加,尽管ECM呼吸的总排放量较小,但对温度变化极为敏感;YAN等^[46]在不同林龄(幼苗、幼林和成熟林)的落叶松林中发现,ECM呼吸与土壤温度呈正相关,当土壤水分高于0.055 cm³/cm³时ECM呼吸与土壤水分呈负相关,而林龄对ECM呼吸无显著影响;HAGENBO等^[70]研究表明,无论林分年龄如何变化,菌丝体对土壤呼吸的

贡献比例相对恒定;HEINMEYER等^[14]研究发现,菌根呼吸对土壤温度变化无明显响应,但对土壤水分的减少响应强烈,当土壤水分降至15%以下时,真菌活性受到显著抑制,是由于真菌在土壤表面附近最为丰富,较容易受到干旱影响。在土壤湿度较高的亚热带杉木林中,ZHENG等^[38]研究发现,土壤湿度对AM呼吸的驱动力似乎比土壤温度更为重要;ZENG等^[63]研究表明,温带针叶松林ECM呼吸年度变化主要受土壤水分体积分数调控,而土壤温度的变化对其无显著影响。菌根呼吸在不同生态系统中对土壤温度和湿度的响应存在差异,其对土壤湿度的变化似乎更为敏感,而对土壤温度的响应则较为复杂且不一致。部分研究结果中菌根呼吸对土壤温度变化不敏感,与传统观点认为土壤呼吸与土壤温度显著正相关相悖,表明菌根呼吸可能具有独立的环境响应机制,在不同生态系统和环境条件下表现出不同的适应策略。

3.2 土壤养分有效性

资源配置理论^[73]认为,菌根与植物的共生关系受土壤养分有效性调控,菌根与植物共生状态的改变会影响菌根的呼吸。植物主要通过根系和菌根2种途径获取土壤养分^[92],其对不同途径的依赖程度取决于土壤养分的可利用性。有研究^[93]表明,在土壤养分相对匮乏的条件下,植物可能更依赖与菌根真菌共生,并为菌根提供更多的光合产物进行养分交换。随着土壤养分的增加,寄主植物可能改变养分获取策略,减少对菌根的依赖,从而减少菌根真菌定殖或由共生转变为寄生关系^[94-95]。例如,在北方樟子松林中,N添加会减少植物对ECM的C分配,从而减少北方森林ECM呼吸^[57]。HASSELQUIST等^[56]研究表明,低N[20 kg/(hm²·a)]添加下真菌子实体产量略高于对照,增加北方樟子松林ECM呼吸和自养呼吸,而高N[100 kg/(hm²·a)]添加几乎完全抑制ECM真菌的子实体形成,导致ECM呼吸显著降低。ZENG等^[48]在N限制的温带樟子松林中发现,不同N处理中根系呼吸和ECM呼吸对自养呼吸贡献的比例不同,是由于植物在不同土壤氮有效性状态下的投资策略不同;在对照处理中,ECM呼吸的占比是根呼吸的2倍,表明在氮有限的森林生态系统中,植物可能更依赖ECM获得氮,而不是根系;当低N[20 kg/(hm²·a)]和中N[50 kg/(hm²·a)]处理解除N限制时,植物将倾向于通过根系而不是ECM吸收氮,从而增加根呼吸的占比。随着氮有效性的持续增加[100 kg/(hm²·a)],生态系统达到氮饱和,富氮缺磷,植物将再次投资于ECM以获取磷,导致ECM呼吸的占比增加。在N限制的温带针叶松林中4 a的磷添加对ECM呼吸无影响,但增加根呼吸^[63],与XIA等^[39]的研究结果不一致;VALENTINE等^[85]研究表明,在土壤P浓度突然增加72 h后,活丛枝的比例下降75%,菌根真菌定殖受到抑制,土壤呼吸下降50%。综上所述,土壤养分有效性的改变会影响植物的养分获取策略,从而调控菌根-植物的共生关系,影响菌根呼吸和土壤呼吸。

3.3 生物因子

菌根呼吸还受到多种生物因素(细根生物量、菌丝长度密度和植物供应的底物)的调节。在落叶松人工林中细根生长量对ECM呼吸有促进作用,较高的细根生物量可能导致更多的ECM真菌定殖,从而增加ECM真菌的活性和呼吸^[96]。菌根根外菌丝长度与菌根呼吸密切相关。例如,GUI等^[64]研究发现,温带草原AM根外菌丝长度与限制根系进入但允许根外菌丝进入的微环境土壤CO₂排放速率呈正相关。

植物作为菌根的碳源,其光合产物的供应也影响菌根呼吸。森林环剥可作为消除树木同化物从树冠到根部运输的一种手段,从而去除自养呼吸底物^[97]。SUBKE等^[55]通过环剥试验结合网格排除法发现,根系C供应的减少显著影响ECM呼吸。在云杉林中的研究^[51]表明,菌根呼吸与光合作用显著相关,与土壤温度不相关,是由于菌根呼吸在很大程度上依赖根系基质的可用性,与其在大麦田中的前期研究^[43]结果一致。植物吸收的C通过呼吸作用返回大气需要几个小时甚至几天,取决于C是分配给根系还是分配给菌根^[98]。在匈牙利干旱草原的研究^[72]表明,AM呼吸的日变化主要由总初级生产力导致的地下C分配调控,而非土壤温度;在植物光合活性最低的时期滞后时间最长,而在光合活性活跃期滞后时间最短;总初级生产力是AM呼吸的主要驱动因素,平均滞后时间为18 h(10~36 h)。

4 研究展望

菌根呼吸在土壤碳循环中的作用不容忽视,其影响机制仍需深入研究。然而,目前国内外研究仍存在一些不足。未来的研究可以在多个方面深入推进,以进一步揭示菌根对土壤碳损失的潜在机制。

1)菌根呼吸的量化主要依赖网格排除法和菌根接种试验,此2种方法仍存在一定局限性。例如,网格排除法无法完全排除菌根与土壤微生物的相互作用,而菌根接种试验的菌根群落组成与自然生态系统可能存在差异。未来研究应结合稳定同位素标记技术、发展同步测定技术,如呼吸室结合光学碳分析技术,更精确地量化菌根呼吸和实时监测其动态变化。

2)关于菌根呼吸的研究主要集中于森林和草原等生态系统,而对于湿地、农田等生态系统的研究较少。由于不同生态系统的土壤养分状况、气候条件及植被类型存在显著差异,菌根对土壤呼吸的贡献及其影响机制可能存在较大差异。因此,未来应在不同气候带和生态系统中,充分比较菌根呼吸的特征及其驱动因素。

3)全球气候变化正在显著影响陆地生态系统的碳循环过程。温度升高、降水模式变化、极端气候事件、大气CO₂浓度升高及氮沉降等环境变化可能对菌根呼吸产生重要影响。但目前关于菌根呼吸对全球变化的响应机制仍不明确。未来研究可通过长期野外监测、控制试验等手段,评估菌根呼吸在不同区域变化情景下的变化规律及其对土壤碳循环的潜在影响。

4)菌根呼吸在全球C循环中的作用尚未被充分纳入碳模型中,导致对土壤碳通量的估算存在较大不确定性。未来研究应基于实测数据,构建更加完善的

菌根呼吸动力学模型,并将其整合至全球碳循环模型中,以提高对未来C循环变化趋势的预测能力。

5 结论

菌根呼吸是土壤呼吸的重要组成部分,不容忽视。其中,AM呼吸平均贡献18.4%(2.5%~32.0%)的土壤呼吸,ECM呼吸平均贡献15.1%(3.0%~62.1%)的土壤呼吸。植物接种菌根可显著增加土壤呼吸,增幅达26.0%。表明传统的土壤呼吸组分划分方法(根移走法、壕沟法和林隙法等)在量化根际呼吸时,可能在很大程度上来源于菌根呼吸。菌根可促进土壤呼吸,但菌根的存在也可降低土壤呼吸,可能归因于“Gadgil效应”。在不同生态系统中,菌根呼吸对土壤温度和土壤湿度的变化表现出独立的响应。由于菌根与宿主植物的共生关系受土壤养分有效性调控,其变化可能进一步影响菌根的呼吸。菌根呼吸还受到细根生物量、根外菌丝长度密度及植物对菌根的C供应等生物因子的调控。在高度依赖菌根共生的植物群落中,菌根呼吸对土壤呼吸的影响可能更加显著。目前菌根对土壤呼吸的影响及造成的土壤C损失尚未受到足够重视,且受到试验方法的制约。鉴于菌根在土壤C循环中的关键作用,未来研究应在不同生态系统和宿主植物中采用更先进的方法分离并量化菌根呼吸,解析环境调控机制,并深入研究全球变化及菌根真菌群落组成对菌根呼吸的调控机制,将菌根呼吸纳入全球碳模型,以更准确地评估菌根在碳平衡和气候变化中的作用。

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(下转第32页)