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全球变化对森林土壤甲烷吸收的影响及其机制研究进展

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摘 要 大气CO_2浓度升高、降水格局改变、全球氮沉降增加和土地覆盖变化等全球变化不仅改变了森林土壤理化性质,而且影响了植物的生长和微生物活性,导致森林土壤碳、氮循环发生改变,进而影响土壤CH_4的吸收.本研究综述了森林土壤CH_4吸收的重要性,森林土壤CH_4吸收对大气CO_2浓度升高、降水格局改变、全球氮沉降增加和土地覆盖变化等全球变化的响应差异及驱动机制.大气CO_2浓度升高抑制土壤CH_4吸收;降水减少倾向于促进土壤CH_4吸收;外源氮输入抑制富氮森林土壤CH_4吸收,而对贫氮森林土壤CH_4吸收则表现为促进或不影响;森林转化为草地、农田或人工林会减少土壤CH_4的吸收量,而植树造林则会增加土壤CH_4的吸收量.今后的研究重点是探讨全球变化对森林土壤CH_4吸收产生长期影响和综合效应,并借助分子生物学方法进一步探究土壤CH_4吸收的微生物学机制.

关键词 全球变化; 森林土壤; CH_4吸收; 响应机制

Effects of global change on methane uptake in forest soils and its mechanisms: A review. HE Shan[1,2], LIU Juan[1,2*], JIANG Pei-kun[1,2], ZHOU Guo-mo[1,2], LI Yong-fu[1,2] ([1]*State Key Laboratory of Subtropical Silviculture, Zhejiang A&F University, Lin'an* 311300, *Zhejiang, China*; [2]*Zhejiang Provincial Key Laboratory of Carbon Cycling in Forest Ecosystems and Carbon Sequestration, Zhejiang A&F University, Lin'an* 311300, *Zhejiang, China*).

Abstract: Elevated atmospheric CO_2 concentration, altered precipitation regime, increased nitrogen deposition, and land cover change have not only changed the physical and chemical properties of forest soils, but also affected plant growth and microbial activity, with concequences on soil carbon and nitrogen cycles, including soil CH_4 uptake. In this study, we summarized the important role of soil CH_4 uptake in forests under global change scenarios. The differences of responses as well as the underlying mechanisms of soil CH_4 uptake in forests to global change were reviewed. Elevated atmospheric CO_2 concentration inhibits soil CH_4 uptake. Reduced precipitation tends to promote soil CH_4 uptake. Increased nitrogen input inhibits soil CH_4 uptake in nitrogen-rich forests, but promotes or has no effects on soil CH_4 uptake in nitrogen-poor forests. Conversion of forests to grassland, farmland, or plantations would reduce soil CH_4 uptake, while afforestation increases soil CH_4 uptake. The future research should explore the long-term and multiple effects of global changes on forest soil CH_4 uptake. In addition, molecular biology methods should be developed to explore the microbial mechanism of soil CH_4 uptake.

Key words: global change; forest soil; CH_4 uptake; responding mechanism.

大气CO_2浓度升高、降水格局改变、全球氮沉降增加和土地覆盖变化是全球变化的重要内容.据统计,全球大气中的CO_2浓度为(403.3±0.1) $\mu L \cdot L^{-1}$,比工业革命前增加了45%[1];全球降水格局的改变使高纬度地区降水增加,亚热带地区降水减少,并且频繁发生干旱和极端降水事件[2];全球N沉降由1950年的41 Tg $N \cdot a^{-1}$增加到了1995年的

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86 Tg N · a^{-1},预计到 2050 年将达到 135 Tg N · a^{-1}[3];而土地覆盖变化则会改变生物地球化学过程.全球森林面积约为 40 亿 hm^2,是全球变化大面积的承受者[4].近几十年来,国内外众多科学家对森林土壤 CH_4 吸收过程极为关注,在全球范围内针对不同地区不同森林类型土壤 CH_4 吸收以及大气 CO_2 浓度升高、降水格局改变、全球氮沉降增加和土地覆盖变化对土壤 CH_4 吸收的影响开展了大量研究.但是,由于气候类型的多样性及森林结构的复杂性,有关森林土壤 CH_4 吸收对全球变化的响应及其机制认识还十分有限,因而,鉴于森林土壤 CH_4 吸收对全球碳循环的重要性,森林土壤 CH_4 吸收对全球变化的响应具有研究价值.本文综述了森林土壤 CH_4 吸收在全球气候变化中的作用和森林土壤 CH_4 吸收对全球变化响应的差异及其机制,并提出未来的研究方向,以期预估森林土壤 CH_4 吸收对未来全球变化的响应,并发展适应全球变化的森林管理体系.

1 森林土壤 CH_4 吸收在全球气候变化中的作用

CH_4 是第二大温室气体,其百年尺度上的增温潜势是 CO_2 的 34 倍,对全球变暖的贡献约占 20%[5-6].截止到 2016 年,全球大气中的 CH_4 浓度为 (1.853 ± 0.002) μL · L^{-1},比工业革命前增加了 157%,目前仍以每年 0.9%的速率不断递增[1].大气中 CH_4 的浓度取决于 CH_4 排放与吸收之间的平衡.据估计,全球每年 CH_4 排放量约为(525±125)Tg,主要来源于水稻田、湿地、海洋以及化石燃料的开采和燃烧[7-8].全球每年 CH_4 吸收量约为(560±100) Tg,主要通过对流层中与羟基自由基氧化反应(约占 84%)、向平流层传输(约占 7%)以及在通气条件下被土壤中的甲烷氧化菌氧化所消除(约占 9%)[9-10].土壤中的甲烷氧化菌是氧化大气 CH_4 唯一的生物汇,如果这个生物汇消失,大气 CH_4 浓度的增速将提高约 50%[11-12].水分非饱和土壤每年的 CH_4 吸收量约为 32~36 Tg,与地球大气 CH_4 年均增加量相当[13].其中森林土壤被认为是最有效的大气 CH_4 的陆地生物汇,其贡献约占整个水分非饱和土壤的 80%[14].由此可见,森林土壤 CH_4 吸收在全球气候变化中占据重要地位.

2 森林土壤 CH_4 吸收对 CO_2 浓度升高的响应特征

随着大气 CO_2 浓度的逐渐升高,其对森林土壤 CH_4 吸收的影响逐渐受到重视.研究表明,大气 CO_2 浓度的升高会抑制森林土壤 CH_4 的吸收(表 1).Kim[15]研究发现,高浓度 CO_2(500 μmol · mol^{-1})处理下的温带森林土壤 CH_4 吸收量降低了 59%.Dubbs 等[16]在对温带火炬松(*Pinus taeda*)森林土壤进行 CO_2 熏蒸(580 μmol · mol^{-1})的研究中发现,森林土壤 CH_4 吸收量在 CO_2 熏蒸试验 1、2 和 3 年后,分别比对照减少了 19%、10%和 8%.大气 CO_2 浓度升高抑制森林土壤 CH_4 吸收的原因为(图 1):1)土壤含水量增加,阻碍了土壤 CH_4 扩散.大气 CO_2 浓度升高一方面减少了植物呼吸的气孔导度,抑制了植物的蒸腾作用;另一方面增加了地上部分生物量,凋落物量增加,使土壤表面的水分蒸发减少.双重作用使得土壤含水量增加阻碍了土壤 CH_4 扩散[15];2)凋落物量的增多导致分解过程释放出更多酚类和单萜烯等物质,从而潜在抑制甲烷氧化菌的活性[16];3)大气 CO_2 浓度的升高提高了土壤有机质含量,为微生物提供了充足的碳源,使其与甲烷氧化菌竞争有限的 O_2[20].

3 森林土壤 CH_4 吸收对降雨变化的响应特征

降雨变化主要包括降雨量、降雨强度和降雨季节等方面的变化,其变化影响了森林土壤的水分、通气状况及可溶性碳、氮等因素,间接影响土壤 CH_4 的吸收.但目前有关降雨变化对森林土壤 CH_4 吸收影响的研究主要集中在降雨量的变化上.一般而言,降水量减少,土壤通气状况得到改善,有助于土壤CH_4的吸收(表2).陈匆琼[28]发现,亚热带杉木

表 1 大气 CO_2 浓度升高对森林土壤 CH_4 吸收的影响
Table 1 Effects of elevated atmospheric CO_2 concentration on soil CH_4 uptake in forests

地点 Site	森林类型 Forest type	CO_2 浓度 CO_2 concentration (μmol · mol^{-1})	CH_4 吸收 CH_4 uptake	参考文献 Reference
日本北海道 Hokkaido, Japan	温带森林 Temperate forest	500	抑制 Inhibition	[15]
美国北卡罗来纳州 North Carolina, USA	火炬松林 *Pinus taeda*	580	抑制 Inhibition	[16]
中国吉林 Jilin, China	蒙古栎林 *Quercus mongolica*	500	抑制 Inhibition	[17]
丹麦哥本哈根 Copenhagen, Denmark	石楠林 *Calluna vulgaris*	510	抑制 Inhibition	[18]
美国北卡罗来纳州 North Carolina, USA	火炬松林 *Pinus taeda*	560	抑制 Inhibition	[19]

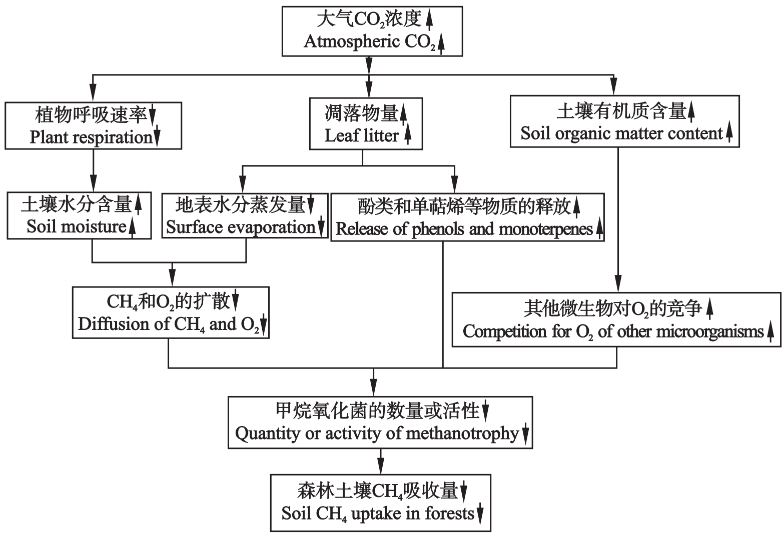

图 1　CO_2 浓度升高抑制森林土壤 CH_4 吸收的机制

Fig.1　Conceptual model of the inhibited soil CH_4 uptake induced by elevated atmospheric CO_2.

表 2　降雨变化对森林土壤 CH_4 吸收的影响

Table 2　Effects of changes of precipitation on soil CH_4 uptake in forests

地点 Site	森林类型 Forest type	降水量变幅 Precipitation variation (%)	CH_4 吸收 CH_4 uptake	参考文献 Reference
中国湖北 Hubei, China	杉木林 *Cunninghamia lanceolata*	−50	促进 Stimulation	[21]
中国河南 Henan, China	温带落叶阔叶林 Temperate deciduous broad-leaved forest	−50	促进 Stimulation	[22]
中国福建 Fujian, China	米槠林 *Castanopsis carlesii*	−30～−60	促进 Stimulation	[23]
澳大利亚墨尔本 Melbourne, Australia	桉树林 *Eucalyptus robusta*	−40	促进 Stimulation	[24]
巴西亚马逊州 Amazonia, Brazil	常绿林 Evergreen forest	−100	促进 Stimulation	[25]
德国萨克森州 Saxony, Germany	云杉林 *Picea abies*	−100	促进 Stimulation	[26]
中国吉林 Jilin, China	温带阔叶红松林 Temperate broad-leaved Korean pine forest	±30	无影响 Negligible effect	[27]
中国湖北 Hubei, China	常绿落叶阔叶混交林、马尾松林 Mixed deciduous and broadleaved evergreen forest, *Pinus massoniana* forest	−50	无影响 Negligible effect	[21]

(*Cunninghamia lanceolata*)林土壤 CH_4 吸收量随降水量的减少呈增加趋势，隔离 20%、60% 和 100% 的降水量，土壤 CH_4 吸收量分别增加了 19%、54% 和 65%.但由于坡度、土壤保水性的不同，以及采样多在无雨天气进行，无雨天气的植物蒸腾作用，再加上控水试验只是调节穿降雨量而没有改变地表径流[22]，因而有关降雨格局改变对土壤 CH_4 吸收无显著影响的研究也有报道.李伟等[27]研究发现，增减 30%降水对长白山温带阔叶红松(*Pinus koraiensis*)林土壤 CH_4 吸收无明显影响.菊花等[21]研究发现，降水减半对常绿落叶阔叶混交林和马尾松(*Pinus massoniana*)林土壤 CH_4 吸收无明显影响，但显著促进了杉木林土壤 CH_4 吸收.

4　森林土壤 CH_4 吸收对增氮的响应特征

施氮对森林土壤 CH_4 吸收的影响存在促进、抑制和不变 3 种结果，但以抑制森林土壤 CH_4 吸收的结果居多(表 3).Steudler 等[39]最早发现在美国马萨诸塞州的红松林中施加硝酸铵导致土壤 CH_4 的吸收降低了 33%.随后，大量模拟氮输入试验相继开展.总体而言，在非氮限制的热带和亚热带地区，增氮倾向于抑制森林土壤 CH_4 的吸收.Zhang 等[40]研究发现，氮输入导致我国广东鼎湖山大叶相思林(*Acacia auriculiformis*)土壤 CH_4 的吸收降低了

表 3 氮输入对森林土壤 CH_4 吸收的影响
Table 3 Effects of N inputs on soil CH_4 uptake in forests

地点 Site	森林类型 Forest type	氮肥类型 N addition	施氮水平 N level (kg N · hm^{-2} · a^{-1})	CH_4 吸收 CH_4 uptake	参考文献 Reference
中国广东 Guangdong, China	针阔混交林 Mixed pine and broadleaf forest	硝酸铵 NH_4NO_3	100	抑制 Inhibition	[29]
中国广东 Guangdong, China	次生林 Secondary forest	硝酸铵 NH_4NO_3	150	抑制 Inhibition	[30]
中国广西 Guangxi, China	桉树林 *Eucalyptus robusta*	脲甲醛 UF	84.2~333.7	抑制 Inhibition	[31]
中国江西 Jiangxi, China	松树林 Pine plantation	氯化铵 NH_4CL	40~120	抑制 Inhibition	[32]
瑞士阿尔卑斯山 Alps, Switzerland	温带云杉林 Temperate spruce forest	硝酸铵 NH_4NO_3	25	抑制 Inhibition	[33]
日本北海道 Hokkaido, Japan	落叶松林 *Larix gmelinii*	硝酸铵 NH_4NO_3	50	抑制 Inhibition	[34]
加拿大温哥华岛 Vancouver Island, Canada	道格拉斯冷杉 Douglas fir	硝酸铵 NH_4NO_3	200	抑制 Inhibition	[35]
中国内蒙古 Inner Mongolia, China	寒温带针叶林 Cold temperate coniferous forest	氯化铵 NH_4Cl	10~40	不变 Negligible effect	[36]
中国内蒙古 Inner Mongolia, China	寒温带针叶林 Cold temperate coniferous forest	硝酸铵 NH_4NO_3	10~20	促进 Stimulation	[37]
巴拿马巴罗科罗拉多 Barro Colorado, Panama	热带山地雨林 Tropical montane forest	尿素 Urea	125	促进 Stimulation	[38]

21%~35%.陈朝琪等[41]在亚热带森林的模拟氮沉降试验中发现,氮输入使 CH_4 吸收速率下降了7%~31%.究其原因为:1)外源氮输入改变了土壤物理扩散性能,间接影响了森林土壤 CH_4 吸收.氮输入增加了凋落物层的厚度和植被根系生物量,加大了大气 CH_4 向土壤剖面扩散的难度[42-43];2)通过竞争抑制、毒性抑制[如 NH_3 和 CH_4 在分子水平上竞争甲烷单加氧酶(MMO)、代谢产物(羟胺和 NO_2^-)的影响、土壤酸化以及溶出 Al^{3+} 的毒害作用和盐基渗透压等]等直接影响森林土壤 CH_4 的吸收[44-45].而在氮限制的森林中,外源氮输入引起的生态系统碳截留会提高氮限制森林土壤 CH_4 的氧化潜力[46],氮沉降减轻了氮对细胞生长的限制作用,甲烷氧化菌的活性增强[47],另外,氮输入会增加氨氧化菌活性和数量,在一定条件下氨氧化菌也能氧化 CH_4[48],因而增氮对森林土壤 CH_4 吸收的影响多为促进或不变.Maljanen 等[47]在试验中发现,添加草木灰和硝酸铵增强了甲烷氧化菌的活性,使得北方云杉(*Picea asperata*)林土壤 CH_4 的吸收速率提高了16%.

外源氮输入对森林土壤 CH_4 吸收的影响还与施氮量和施氮类型相关.Aronson 等[49]通过 Meta 分析发现,低剂量的氮添加会增强土壤 CH_4 的吸收能力,高剂量的氮添加则会减弱土壤 CH_4 的吸收能力,并表示氮输入对非湿地土壤 CH_4 吸收速率转变的临界值是 100 kg N · hm^{-2} · a^{-1}.Zhang 等[50]研究发现,低氮(50 kg N · hm^{-2})、中氮(100 kg N · hm^{-2})和高氮(150 kg N · hm^{-2})处理导致亚热带常绿阔叶林土壤 CH_4 平均吸收速率分别下降了6%、14%和32%.另外,森林土壤 CH_4 吸收速率通常与 NH_4^+浓度呈负相关,而与 NO_3^-浓度呈负相关或正相关[36,51].王汝南[52]在温带森林开展的不同形态的氮素输入试验发现,铵态氮的输入抑制了土壤 CH_4 的吸收,而因甲烷氧化菌从土壤中同化无机氮时比较偏好硝态氮,硝态氮的输入有利于增强甲烷氧化菌活性,因而硝态氮的输入促进了土壤 CH_4 的吸收.张丹丹等[53]的研究表明,长期添加铵态氮肥抑制了温带森林土壤甲烷氧化菌的生长并导致其群落结构发生改变,而硝态氮的添加对土壤甲烷氧化菌的群落组成和丰度无显著影响.

5 森林土壤 CH_4 吸收对土地覆盖变化的响应特征

土地覆盖变化通过影响凋落物的质量与数量、土壤的理化性质等,间接影响土壤 CH_4 吸收能力.一般而言,森林转变为草地或农田时,土壤孔隙度降低,限制了 CH_4 和 O_2 的扩散,再加上后续的一些人为经营措施,其转换会抑制土壤 CH_4 的吸收(表 4).Carmo 等[54]研究表明,大西洋森林转化为草地导致土壤 CH_4 吸收能力下降了 67%.还有研究指出,森林转变为草地或农田时,土壤 CH_4 吸收能力的恢复需要百年之久[8].天然林转化为人工林也抑制土壤CH_4的吸收.据估计,在中国,人工林土壤CH_4的

表 4　土地覆盖变化对森林土壤 CH_4 吸收的影响
Table 4　Effects of land cover change on soil CH_4 uptake in forests

地点 Site	土地利用类型 1 Land use 1	土地利用类型 2 Land use 2	CH_4 吸收 CH_4 uptake	参考文献 Reference
巴西圣埃斯皮里图州 Espírito Santo, Brazil	大西洋森林 Coastal Atlantic forest	草地 Pasture	抑制 Inhibition	[54]
中国浙江 Zhejiang, China	天然阔叶林 Natural broad-leaved forest	马尾松林 *Pinus massoniana*	抑制 Inhibition	[55]
美国密歇根州 Michigan, USA	温带落叶阔叶林 Temperate deciduous broad-leaved forest	农田 Cropland	抑制 Inhibition	[56]
中国福建 Fujian, China	天然阔叶林 Natural broad-leaved forest	杉木林 *Cunninghamia lanceolata*	抑制 Inhibition	[57]
丹麦哥本哈根 Copenhagen, Denmark	农田 Cropland	挪威云杉林 Norway spruce forest	促进 Stimulation	[58]
英国苏格兰 Scotland, UK	草地 Pasture	松树林 Pine forest	促进 Stimulation	[59]
爱尔兰洛伊斯 Laois, Irish	草地 Pasture	锡卡云杉林 Sitka spruce forest	促进 Stimulation	[60]
瑞士弗里堡州 Fribour, Switzerland	草地 Pasture	挪威云杉林 Norway spruce forest	促进 Stimulation	[61]

吸收速率为(22.64±26.83) μg $CH_4 \cdot m^{-2} \cdot h^{-1}$,仅为天然林土壤 CH_4 吸收速率的 40%[62].张睿[55]发现,天然林转化为马尾松林后,土壤 CH_4 吸收速率下降了 22%.天然林转化为人工林后土壤 CH_4 吸收速率下降的原因为:1)土壤孔隙度下降,限制 CH_4 和 O_2 的扩散[63]; 2)有机质含量减少.Tate[8]的研究表明,土壤有机质通过限制维持微生物活性的总可矿化碳来影响土壤 CH_4 的吸收,同时有机质还会影响土壤保水性和土壤肥力等因素,间接影响土壤 CH_4 的吸收;3)土壤养分的减少.Nikiema 等[64]研究表明,土壤 CH_4 的吸收对磷非常敏感.Zhang 等[65]的研究表明,磷肥的添加促进了磷限制森林土壤 CH_4 的吸收.

然而,草地或农田转化为人工林后一方面疏松了土质,增加了土壤孔隙度,另一方面改变了甲烷氧化菌的数量与群落组成,从而促进了土壤 CH_4 的吸收.Livesley 等[66]发现,草地恢复成桉树(*Eucalyptus robusta*)林后,土壤由 CH_4 排放源(60 μg $CH_4 \cdot m^{-2} \cdot h^{-1}$)转变为 CH_4 吸收汇(−36 μg $CH_4 \cdot m^{-2} \cdot h^{-1}$).Bárcena 等[58]研究发现,农田转变为挪威云杉林后土壤甲烷氧化菌的数量增加,从而提高了土壤 CH_4 的吸收速率.Nazaries 等[59]发现,从草地转化为松树林后,土壤中的优势甲烷氧化菌由低亲和力的利用磷酸核酮糖途径(RuMP pathway)氧化 CH_4 的Ⅰ型甲烷氧化菌(MOB Ⅰ)向高亲和力的利用丝氨酸途径(serine pathway)氧化 CH_4 的Ⅱ型甲烷氧化菌(MOBⅡ)转化,土壤 CH_4 的吸收能力增强.

6 展　望

森林土壤 CH_4 吸收是 CH_4 产生、传输和氧化过程综合作用的结果.大气 CO_2 浓度升高、降水格局改变、外源氮输入以及土地覆盖变化改变了森林土壤 CH_4 吸收的环境条件和微生物群落组成与结构,影响了土壤 CH_4 吸收.目前森林土壤 CH_4 吸收对单一全球变化因子的短期响应特征已开展了丰富的研究,并对其物理、化学及微生物学机制进行了探讨.然而,森林土壤 CH_4 吸收对全球变化的长期响应特征及多个变化因子之间的交互影响机制还缺乏深入系统的研究.温度是影响 CH_4 吸收的重要因素,目前气候变暖对土壤 CH_4 吸收的影响研究多集中在农田生态系统,对森林土壤 CH_4 吸收影响的研究还鲜有报道.因此,在未来研究中,可重点加强以下几方面的研究:1)利用人工模拟试验及建模分析等方法研究森林土壤 CH_4 吸收对全球变化的长期响应特征以及气候变化因子间的交互影响机制;2)结合磷脂脂肪酸技术(PLFA)、变性梯度凝胶电泳(DGGE)和末端限制性片段长度多态性分析(T-RFLP)等分子生物学研究方法,揭示全球变化对森林土壤 CH_4 吸收影响的微生物学机制;3)通过模拟增温试验,探讨气候变暖对森林土壤 CH_4 吸收的影响及机制.

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