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## 土壤碳循环微生物作用研究进展

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**摘要** 土壤碳是全球碳循环的重要组成部分, 其碳循环过程在气候调节中发挥着重要作用, 而微生物是土壤碳循环的关键驱动力。土壤微生物能与植物共生间接促进植物光合作用与土壤碳的输入, 可直接参与土壤碳的固定与转化。微生物残体及其分泌物在矿物质结合态有机质和土壤团聚体的形成中发挥关键作用, 有利于土壤有机碳的长期稳定。微生物介导的激发效应对土壤有机质分解具有调控作用, 可影响土壤CO<sub>2</sub>和CH<sub>4</sub>等温室气体的排放。通过微生物作用提升土壤的固碳潜力或碳汇功能, 可助力我国实现“碳达峰、碳中和”的重大战略目标。本文综述了微生物在土壤有机碳输入、有机质形成与稳定、有机质分解矿化等过程中的作用与机制, 以及土壤性质、气候条件、植物因素与人类活动对微生物介导的土壤碳循环的影响, 尤其是相关研究的最新进展与理论更新。未来可加强微生物介导的土壤有机碳稳定化与碳储过程的作用机制研究, 关注土壤微生物群落结构功能与碳循环之间的复杂关系及其对全球变化的响应。

**关键词** 土壤微生物; 土壤碳循环; 微生物固碳; 土壤有机质; 微生物残体

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土壤是陆地上最大的碳储存库, 土壤碳库主要以有机质形式赋存。据统计, 全球土壤有机质(soil organic matter, SOM)的总碳量约为1.5万亿t C<sup>[1]</sup>, 大约是陆地上生物总碳量的2.5倍, 是大气碳库的2倍<sup>[2]</sup>。土壤碳循环作为生态系统中最为关键的生物地球化学循环之一, 不仅影响着土壤肥力质量与生物多样性, 还对全球碳循环与气候变化产生深远影响。全球2 m厚土层储存的有机碳达 $2.4 \times 10^5$ 亿t, 土壤碳库的微小变化也可能引起大气中温室气体浓度的剧烈波动<sup>[2-3]</sup>。为应对气候变化, 中国政府制定了“力争在2030年实现碳达峰、2060年前实现碳中和”的目标。在这一背景下, 调控土壤碳循环过程, 提高土壤的固碳潜力或碳汇功能, 减少碳排放, 可为中国实现“双碳”目标提供重要途径<sup>[4]</sup>。

微生物作为土壤重要组成部分, 既是土壤有机碳转化的驱动者, 又是土壤有机碳的活性库<sup>[5]</sup>。长期以来, 人们对土壤碳循环转化的研究主要集中在动植物残体分解、有机质形成与稳定、有机质矿化分解等方面。在全球变暖的大背景下, 微生物介导的土

壤碳循环及其对大气温室气体的调节作用日益受到研究者的关注。本文综述了微生物在土壤碳循环转化过程中各个环节的作用与机制, 分析了微生物影响土壤碳转化的主要因素(图1), 以期为提升土壤碳汇功能、改善土壤质量提供理论支持, 促进基于全球气候变化下土壤碳库的科学管理。

### 1 微生物驱动的土壤碳循环过程

土壤中存在着地球上种类最丰富的微生物群落, 如细菌、古生菌、真菌、病毒、藻类以及一些原生生物等<sup>[6]</sup>。土壤微生物数量庞大, 群落结构复杂, 各类微生物间存在复杂的相互作用<sup>[7]</sup>, 直接参与碳循环转化的各环节。细菌、真菌、古生菌等微生物通过参与土壤有机碳的腐殖化与矿化分解等过程, 调控土壤碳循环<sup>[8]</sup>(图1)。

#### 1.1 微生物对土壤有机碳输入的作用

1) 微生物对CO<sub>2</sub>的固定。作为土壤有机碳输入重要来源, 自养微生物每年对CO<sub>2</sub>的固定达到700亿t C<sup>[9]</sup>。Jian等<sup>[10]</sup>通过<sup>14</sup>C标记表明, 微生物固定的

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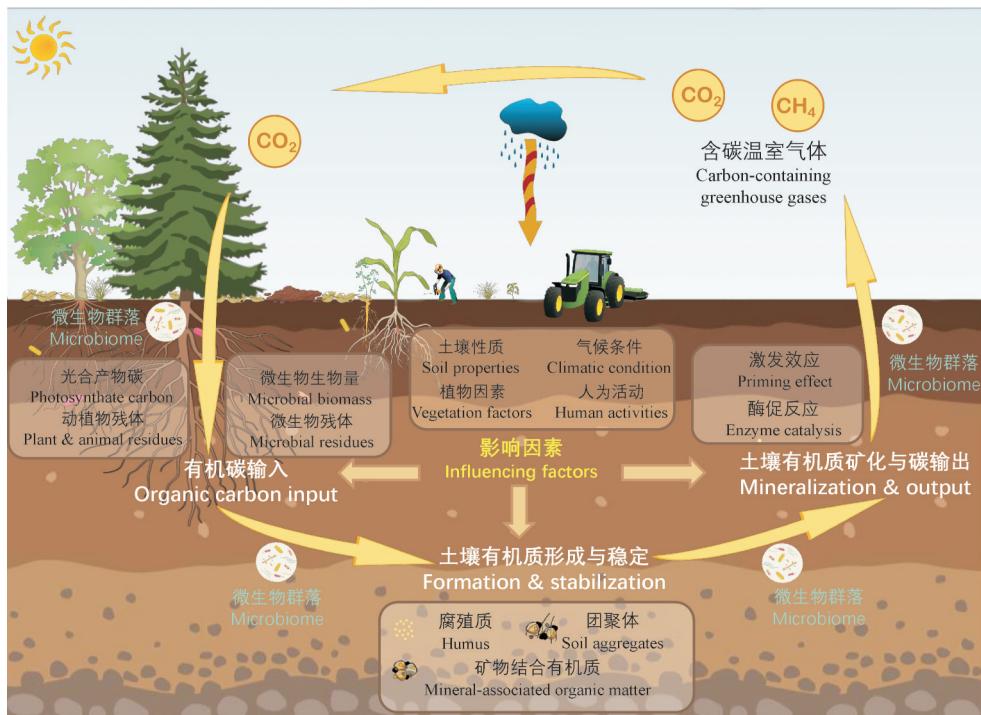


图1 微生物驱动的土壤碳循环过程及其影响因素

Fig.1 Microbial driven soil carbon cycling and its influencing factors

CO<sub>2</sub>占土壤有机碳的0.37%~1.18%。光能自养细菌和藻类的光合作用是土壤碳输入的重要途径。Xiao等<sup>[11]</sup>证实了稻田生态系统中自养微生物组在固定CO<sub>2</sub>提高有机碳库累积中的关键作用。Ge等<sup>[12]</sup>研究表明,土壤光合自养微生物对旱田和稻田土壤有机碳的贡献率分别为0.15%和0.65%。藻类作为土壤中一类自养微生物,全球范围内通过光合作用每年可固定CO<sub>2</sub>约3 600 t,占陆地植被净初级生产力的6%左右<sup>[13]</sup>。微生物不仅可固定CO<sub>2</sub>,其自身生物量还是土壤活性有机碳的重要组成部分,成为土壤有机碳输入不可忽视的一部分。Jian等<sup>[10]</sup>研究表明,土壤有机碳与微生物生物量呈显著正相关。有关德国草原多样性长期试验的研究结果也显示,植物多样性较高土壤的微生物生物量增加促进了土壤有机碳积累<sup>[14]</sup>。参与固定CO<sub>2</sub>的自养微生物包括光能自养和化能自养2大类,它们分别以光和有机物为能源(或底物),分别以光固定与暗固定途径来固定CO<sub>2</sub><sup>[15]</sup>。在农田、草地和森林等土壤中的自养微生物对CO<sub>2</sub>固定较为普遍,而在火山、荒漠等极端生境中也有自养微生物固定CO<sub>2</sub>的报道<sup>[16]</sup>。在干旱地区,自养微生物的暗固定过程有可能成为土壤有机碳的来源<sup>[12]</sup>。生活在岩溶土壤中的自养微生物固碳可通过产生碳酸酐酶诱导碳酸盐岩溶蚀,增加土壤中的微生物可利用无机碳含量,以刺激固碳能力<sup>[17]</sup>。

土壤中自养微生物固定有机碳的主要途径包括卡尔文循环、还原三羧酸循环<sup>[18]</sup>、还原性乙酰辅酶A途径<sup>[19]</sup>、3-羟基丙酸循环<sup>[20]</sup>、3-羟基丙酸/4-羟基丁酸循环、二羧酸/4-羟基丁酸循环<sup>[21]</sup>等。卡尔文循环是光合自养生物固碳的核心反应,每年可固定的CO<sub>2</sub>约1 000亿t,也是无机碳转变为有机碳的主要途径<sup>[22]</sup>。卡尔文循环的关键酶是核酮糖-1,5-二磷酸羧化/加氧酶,即Rubisco酶<sup>[23]</sup>,藻类在Rubisco酶的帮助下通过卡尔文循环固定CO<sub>2</sub><sup>[24]</sup>。还原乙酰辅酶A途径是碳固定效率最高的途径<sup>[25]</sup>。玉米根际的化能自养菌主要为红假单胞菌属与斯塔普氏菌属,其分泌的一氧化碳脱氢酶通过还原乙酰辅酶A途径固定CO<sub>2</sub><sup>[26]</sup>。年平均降水400~600 mm的条件下,黄土高原草地土壤微生物固定CO<sub>2</sub>的过程以还原三羧酸循环和3-羟基丙酸循环为主导<sup>[27]</sup>。

分子生物学技术是当前研究微生物固碳机制的重要手段,其中应用宏基因组学研究固碳微生物功能基因的报道较多。有研究者<sup>[28]</sup>采用16S rRNA基因扩增子测序和Geo Chip技术测定红树林土壤细菌功能的基因丰度,结果显示土壤中碳循环功能基因丰度超过15%,且碳固定过程中与卡尔文循环相关Rubisco酶基因相对丰度最高,这有利于红树林土壤的固碳作用与碳汇功能提升。Chen等<sup>[29]</sup>利用16S rRNA基因扩增子测序和PICRUSt技术证实了石油

烃污染土壤微生物的代谢途径主要为碳固定,且还原性三羧酸循环过程占比达28.6%~30.6%。稻田土壤微生物碳循环功能基因中,还原三羧酸循环功能基因在深层土壤中发挥了关键作用,增加了土壤有机碳储量<sup>[30]</sup>。内蒙古温带草原土壤的宏基因组数据反映,大型真菌可显著降低自养固碳微生物的相对丰度和微生物生物量,减少草原土壤有机碳储量<sup>[31]</sup>。结合克隆文库测序等分子生物学技术,Yuan等<sup>[32]</sup>识别出参与大气CO<sub>2</sub>同化过程的微生物主要为固氮螺菌(*Azospirillum lipoferum*)、沼泽红假单胞菌(*Rhodopseudomonas palustris*)、慢根瘤菌(*Bradyrhizobium japonicum*)、富养罗尔斯顿菌(*Ralstonia eutrophpha*)及黄绿藻属(*Xanthophyta*)和硅藻门(*Bacillariophyta*)。可见,微生物固定CO<sub>2</sub>是土壤碳输入的有效途径,利用分子生物学技术了解固碳微生物类群与作用机制,有助于开发和增强土壤碳汇能力。

2)微生物介导的植物有机碳输入。植物光合作用是土壤碳输入的起点,微生物可通过直接影响植物生长,或者间接影响植物群落组成,调控植物的光合作用,从而介导植物有机碳输入。有研究表明,植物根际接种植物促生细菌可提高根系对营养物质的吸收效率,刺激植物体内抗氧化酶的活性,增强植物的耐受性<sup>[33]</sup>,从而促进植物生长的作用,增加植物向土壤中输送的有机碳量<sup>[34]</sup>。

土壤真菌与大多数植物能形成共生关系,真菌通过共生体参与植物的光合作用,间接影响土壤碳的输入过程<sup>[35]</sup>。菌根真菌菌丝直径为2~10 μm,远小于植物细根直径,共生关系可极大增强植物获取养分的能力,有效缓解植物的养分限制,进而促进植物光合作用以促进有机碳积累<sup>[36]</sup>。菌根真菌可通过增强植物对其地下部的碳分配,降低植物光合产物积累,而诱导植物提高光合速率进行碳补偿<sup>[37]</sup>;当部分去除与植物共生的丛枝菌根真菌后,光合速率可下降10%~40%<sup>[38]</sup>。丛植菌根和外生菌根对陆地净初级生产力的贡献率分别为63%与24%<sup>[39]</sup>。植物可将一定比例的净初级生产量中的碳通过菌根输入到土壤。据估计,陆生植物每年至少将约1.3×10<sup>3</sup>亿t CO<sub>2</sub>当量分配给菌根真菌的地下菌丝体<sup>[39]</sup>。不同菌根为主的树种养分利用策略以及菌根自身属性对环境变化敏感不同,森林树种菌根类型是调控土壤碳输入的关键要素。如在美国东部森林中,以丛枝菌根为主的森林生态系统根系向土壤的输入量比以外生菌根为主的森林生态系统多54%<sup>[40]</sup>。在氮沉

降与增温条件下,外生菌根树种占主导的森林可显著提升土壤有机碳含量<sup>[41]</sup>。

## 1.2 微生物在土壤有机碳形成与稳定中的作用

1)微生物在腐殖化过程中的作用。动植物残体是SOM的主要初始来源之一,在土壤微生物的介导下,经由复杂的腐殖化过程转化为SOM而稳定存在<sup>[42]</sup>。腐殖质是SOM的主要组成部分,一般占SOM总量的50%~80%<sup>[43]</sup>。腐殖质作为土壤稳定有机质的重要形式,腐殖化过程是SOM稳定化过程中的关键因素<sup>[44]</sup>。微生物在腐殖化过程中的作用尚未形成统一观点,目前存在微生物合成学说、微生物多酚学说、厌氧发酵学说等多种理论假设<sup>[44~45]</sup>。而微生物在腐殖化过程中发挥了核心作用却是各种理论的共识<sup>[45]</sup>。传统的腐殖化理论和有机质连续体模型<sup>[46]</sup>均承认动植物残体在输入土壤后,会先经过物理化学作用而破碎,进而通过微生物胞外酶等分解成相对更小的组分。在后续的过程中,因研究手段的差异,人们提出了腐殖化过程不同的理论模型。Kellehe等<sup>[47]</sup>通过核磁共振光谱分析得到分子混合模型,发现传统意义的土壤腐殖质在很大程度上其实是微生物、植物分子聚合物及其分解产物所组成的复杂混合物。Gerke<sup>[48]</sup>也认为,来自植物和微生物残体的SOM被部分分解成较小的分子,部分在微生物作用下发生聚合、缩聚等反应形成稳定的高分子物质腐殖质;而且不同质量的腐殖质分子之间还可通过超分子键构成腐殖质网络,进一步加强了腐殖质在土壤中的稳定性<sup>[48]</sup>。

2)微生物在土壤有机碳稳定化过程中的作用。微生物通过多种途径影响土壤有机碳的稳定与积累。微生物通过其分泌物与残体分解,参与矿物结合态有机质和土壤团聚体形成等途径来影响SOM的形成和稳定。矿物结合态有机质和土壤团聚体中的有机质约有47.5%和38.6%来源于微生物残体<sup>[49]</sup>。微生物残体通过配位体交换、氢键和分子间作用力等作用与矿物结合,成为矿物结合态有机质的一部分<sup>[50]</sup>。微生物分泌物也可与矿物质表面发生化学键合或被包埋在土壤微孔中,最终形成稳定的矿物结合态有机质<sup>[51]</sup>,如多年生*Panicum virgatum*根际的微生物分泌的多糖可促进土壤矿物结合态有机质的形成<sup>[52]</sup>。相较于氢键等化学反应形成的矿物结合态有机质,吸附作用结合的矿物结合态有机质更易受土壤温度、湿度等条件的影响而变得不稳定<sup>[53~54]</sup>。相比植物源碳有机质,微生物源碳有机质

与土壤矿物的相互作用更强<sup>[55-56]</sup>。但是,植物源碳有机质可能会被微生物吸收,在微生物群落内部循环利用后最终成为微生物源碳有机质而更易被矿物吸附<sup>[57]</sup>。

SOM与矿物颗粒等可在植物根系和微生物的共同作用下形成团聚体,为SOM提供物理保护而不被微生物分解<sup>[58]</sup>。微生物分泌物可以加快团聚体形成进程,如胞外多聚物可作为黏合剂,促进细小的矿物质颗粒与有机质结合<sup>[59]</sup>。一方面,真菌在土壤团聚体形成过程中能提供更强的物理保护,有利于更多的稳定性有机碳存在<sup>[60]</sup>,其原因主要在于真菌菌丝能将土壤颗粒机械地缠绕在一起<sup>[61]</sup>,并且分泌胶结物质,包裹土壤颗粒与微团聚体<sup>[62-63]</sup>,参与形成稳定的大团聚体。另一方面,细菌产生的胞外聚合物,通常作为微米尺度聚集物的黏合剂促进微团聚体的形成<sup>[64]</sup>。不同粒级团聚体是SOM周转的重要调节因子<sup>[65]</sup>。相较于大团聚体,以微生物残体为核形成的微团聚体,结构不易被破坏,其有机质周转周期更长<sup>[66]</sup>,更利于有机质的稳定存在。可见,土壤中矿物结合态有机质和土壤团聚体的形成是维持土壤有机碳长期稳定的主要因素。

### 1.3 微生物介导的土壤有机碳输出

1) 土壤有机质的分解矿化。微生物对SOM的矿化作用主要是改变其官能团或分子结构,将其转变为简单的小分子物质,直至形成CO<sub>2</sub>、H<sub>2</sub>O和能量,以获取有机质中的氮、磷等营养物质供植物生长。在厌氧条件下,微生物利用有机物质作为电子供体,通过胞外电子传递机制将电子传递给硫酸盐等作为电子受体,从而使有机质分解<sup>[67]</sup>。微生物生长过程中分泌水解酶和氧化酶等,能通过共代谢作用转化SOM<sup>[68]</sup>,直接影响SOM的矿化。如碳酸盐矿化细菌可以产生脲酶,分解尿素释放铵离子和碳酸根离子,细菌细胞充当晶体的成核位点,诱导胶结碳酸钙晶体粘结土壤颗粒,在有机质的整个矿化过程中发挥作用<sup>[69]</sup>。在对欧洲云杉森林生态系统的研究中,子囊菌门的大部分真菌可分泌纤维素分解酶来分解SOM<sup>[70]</sup>。虽然外生菌根真菌退化显著减少了其编码的相关分解酶基因,但其仍可分泌过氧化物酶等部分水解酶,参与SOM分解。可见,微生物可通过产生各类酶来促进SOM分解。

新鲜有机物添加到土壤中可影响原有SOM分解速率的激发效应,对SOM分解矿化起着重要调节作用<sup>[71]</sup>。新加入的有机物可改变土壤微生物群落的

组成和多样性,微生物作为激发效应的介导者来调控激发效应的方向与强度<sup>[72]</sup>。外源新鲜有机物的输入可激活微生物增殖和活性,且新鲜有机物分解可能产生特定的酶,这些作用可加速土壤原有有机质分解而产生正激发效应<sup>[73]</sup>。新加入的有机物若不易分解,或引入了如酚类等抑制微生物活性的化合物,会改变微生物对底物的偏好,使得土壤原有有机质的分解速率减缓,产生负激发效应<sup>[68]</sup>。在真菌/细菌高比值的耕作土壤上,正激发效应表现得更为强烈<sup>[72]</sup>。Hamer等<sup>[74]</sup>发现,新鲜有机物质输入能够促进缺氮SOM分解,高C/N值的土壤中产生的正激发效应更显著。Fontaine等<sup>[75]</sup>认为,激发效应的产生受到土壤微生物群落策略变化的影响,微生物对土壤溶解性有机质的亲和力因其生态策略不同而异。r-策略型微生物对易分解物质反应迅速,倾向于利用活性有机碳,K-策略型微生物则偏好利用不易分解的有机碳,对土壤有机碳的利用效率较高<sup>[75]</sup>。我国东北森林SOM分解的温度敏感性与微生物生态策略有关,相较于北部,南部温暖地区土壤中难分解有机质分解对气温升高更为敏感,这可能归因于其土壤中K-策略型微生物群落占优势<sup>[76]</sup>。

2) 土壤含碳温室气体的产生与释放。在微生物的介导下,SOM最终转化为CO<sub>2</sub>和CH<sub>4</sub>等含碳温室气体。其中,土壤呼吸,即通过根系(自养)和微生物(异养)呼吸排放的CO<sub>2</sub>,是土壤碳循环的关键生态过程。土壤呼吸过程产生的CO<sub>2</sub>可导致大气CO<sub>2</sub>增加。有研究表明,土壤呼吸每年释放的CO<sub>2</sub>大约是人为排放CO<sub>2</sub>量的5倍<sup>[77]</sup>。据统计,微生物分解SOM的异养呼吸过程向大气中释放CO<sub>2</sub>的量,可占土壤呼吸总量的50%以上<sup>[78]</sup>。自20世纪80年代以来,微生物的异养呼吸在全球范围内以每10 a约2%的速度增加<sup>[79]</sup>。Nissan等<sup>[79]</sup>利用对未来地表温度和土壤水分的模型预测,认为在气候恶化最极端的情景下,到21世纪末全球土壤微生物异养呼吸将增加约40%,其中北极地区预计将增加2倍以上,主要是由土壤水分下降而非温度上升所驱动的。

CH<sub>4</sub>对气候变暖的潜在影响比CO<sub>2</sub>要强,其全球变暖潜势为CO<sub>2</sub>的34倍<sup>[80]</sup>。厌氧产甲烷菌的微生物CH<sub>4</sub>生成是大气中CH<sub>4</sub>的最大生物来源,而稻田土壤是CH<sub>4</sub>的主要人为来源<sup>[81]</sup>。植物分泌物和根系含有次生代谢产物,影响土壤微生物组成以及CH<sub>4</sub>排放<sup>[82]</sup>。水稻的根系分泌物中黄酮类和异黄酮等次生代谢产物含量高,有利于特定微生物在土壤和植

物根系富集,通过功能基因 $pmoA$ (甲烷单加氧酶基因)的表达,减少CH<sub>4</sub>排放<sup>[83]</sup>。泥炭地土壤是全球大气CH<sub>4</sub>最大的自然来源,泥炭地土壤水分和有机碳含量均高,在室内控温培养下,泥炭地土壤中与产甲烷作用相关的基因数量随温度的上升而增加,35℃时产甲烷古菌的活性受抑制,导致土壤CH<sub>4</sub>释放量下降<sup>[84]</sup>;在不同硫酸盐浓度下,土壤中硫酸盐还原菌与产甲烷菌之间的竞争共存关系,直接影响了土壤CH<sub>4</sub>释放量<sup>[84]</sup>。加拿大北极地区多年冻土的土壤微生物群落结构分析结果也显示,产甲烷古菌在表层土壤和冻土有机质中的丰度较高,SOM易被厌氧分解而以CH<sub>4</sub>形式释放<sup>[85]</sup>。由此可见,微生物介导的SOM分解过程,可影响土壤CO<sub>2</sub>和CH<sub>4</sub>等温室气体的排放。

## 2 微生物介导土壤碳循环的影响因素

### 2.1 土壤性质

土壤理化性质会影响微生物群落结构与代谢活动,进而影响其参与土壤有机碳的转化与积累<sup>[86]</sup>。Patoine等<sup>[87]</sup>通过模型预测发现,土壤pH对微生物的影响具有非线性特征,偏中性土壤的微生物丰度更高;在土壤pH阈值范围,酸度对微生物生长的限制在土壤有机碳积累中具有重要作用。在潮湿和氧气限制的酸性环境中,微生物从生长繁殖转变为呼吸维持,其较低的生产或周转率有利于土壤有机碳积累<sup>[88]</sup>。细菌与真菌的生长比率也受到土壤pH的影响,较高的土壤pH能提高有机碳的细菌可利用性和微生物碳利用效率<sup>[89]</sup>。土壤碳氮比(C/N)影响微生物对有机碳的利用,进而影响SOM的矿化分解,C/N为25:1的SOM通常最利于微生物分解。随有机质C/N增加,微生物代谢受氮的限制作用增强,土壤微生物群落从富营养群落主导转变为寡营养群落主导,这促进了土壤难分解性有机质的分解<sup>[90]</sup>。土壤盐胁迫条件可重塑土壤微生物群落结构与功能。高盐胁迫下土壤中细菌和真菌的 $\alpha$ 多样性显著降低,拟杆菌属(*Bacteroidetes*)等类群受抑制<sup>[91]</sup>,高土壤盐胁迫条件会使微生物失活甚至死亡,导致SOM矿化(分解)速率显著下降<sup>[91-92]</sup>。

土壤质地、水分等物理性质也是影响微生物介导SOM转化的环境因子之一。土壤质地影响SOM聚集,对SOM形成物理保护而不易被微生物分解<sup>[65]</sup>。草地土壤粘粒含量是土壤有机碳变化的重要

因素,粘粒含量最高的土壤,其总有机碳含量最高,原因在于粘粒吸附的有机质较为稳定,难以被微生物分解<sup>[93]</sup>。土壤水分可影响微生物活性而间接影响土壤有机碳的转化与积累,土壤含水量过低不利于微生物生长增殖,而淹水易因氧气不足制约微生物生长<sup>[94]</sup>。土壤团聚体之间及其内部的孔隙大小制约着水分在土壤中的运输,也会间接影响微生物对土壤有机碳的利用程度<sup>[95]</sup>。

### 2.2 气候条件

温度、降水等气候变化可改变土壤微生物群落的丰度及其残体碳比例而影响SOM的稳定性。比较2种土壤在输入玉米叶时的激发效应,相对稳定SOM的激发效应较活性SOM对升温更为敏感,这是因为不同类型土壤微生物生长对升温的响应存在差异<sup>[96]</sup>。对稻田土壤进行原位土柱室内培养试验,研究结果显示15~30 cm底层SOM矿化的温度敏感性更高,这是由于升温可提高底层土壤寡营养菌的相对丰度,驱动难分解有机质分解,最终导致底层土壤碳的损失<sup>[97]</sup>。增温还提高农田土壤表层真菌与细菌微生物残留碳的比例,增强土壤有机碳的持久性<sup>[98]</sup>。降水异常可显著改变土壤微生物群落的多样性,进而影响土壤碳的损失与储量。降水减少可降低草原土壤细菌和真菌的多样性及其相互作用<sup>[99]</sup>,而降水增加可提升土壤微生物耐胁迫基因相对丰度<sup>[100]</sup>;土壤真菌群落比例表现出对降水的选择性,SOM矿化速率与对降水增加具有积极响应的真菌丰度呈正相关<sup>[100]</sup>。气候条件胁迫下,微生物优先考虑资源获取或胁迫耐受,而非提高其生物量,这会导致SOM分解或碳损失<sup>[99-100]</sup>。

### 2.3 植物因素

地上植被类型种类和多样性影响有机碳在土壤各层的分配<sup>[101]</sup>,且间接影响土壤结构和土壤特性<sup>[102]</sup>,进而影响土壤微生物的群落组成和多样性特征<sup>[101-102]</sup>。草原生物多样性的长期试验结果表明,植物多样性通过微生物生长和周转的加快,促进了微生物生物量及其残体的增加,从而提升了土壤有机碳含量<sup>[14]</sup>。微生物残体对土壤有机碳的贡献因不同生态系统类型而异。如农田、草地和森林0~20 cm表层土壤的微生物残体对有机碳的平均贡献率分别为51%、47%和35%<sup>[103]</sup>。

不同植物的根系分泌物与凋落物的组成与分解速率均存在差异,可影响或调控土壤的微生物群落结构和功能<sup>[104-105]</sup>。对亚热带森林土壤而言,毛竹林

土壤的根系分泌物丰富,细菌和固碳细菌基因丰度显著高于其他林分<sup>[106]</sup>。凋落物中丹宁和多酚类化合物易形成难分解的腐殖物质,有助于SOM的稳定<sup>[107]</sup>。不同菌根类型的宿主植物的凋落物在化学组成上的差异导致其分解速率不同,从而影响土壤碳循环过程<sup>[108]</sup>。例如,外生菌根宿主植物的凋落物碳氮比高,分解速率慢,导致土壤表层有更多的有机碳积累<sup>[109]</sup>。可见,科学种植和管理植被类型,可增强土壤固碳潜力<sup>[110]</sup>。

#### 2.4 人为活动

施肥、耕作、种植等人为活动深刻影响着土壤碳循环过程。长期施肥影响土壤碳储量及不同形态碳在各粒径土壤中的分布<sup>[111]</sup>,施肥可提升土壤有机碳含量<sup>[112]</sup>,通常更利于土壤微生物残体碳的增加<sup>[113]</sup>。Wang等<sup>[114]</sup>的研究结果显示,长期施用农家肥可减少突发升温时土壤有机碳损失,原因在于突发升温时受温度刺激的异养细菌与真菌相对丰度降低,土壤微生物网络联系更为密切,且古菌具有较高CO<sub>2</sub>截获能力。

耕作扰动也是土壤有机碳损失的主要因素之一。据统计,平均每年约有30万~100万t土壤有机碳因耕作而损失<sup>[115]</sup>。与传统耕作相比,免耕促进有机质积累的微生物类群增多<sup>[116]</sup>。长期增温田间试验的研究表明,增温与保护性农业措施交互作用可加快真菌群落演替,真菌残体对土壤有机碳的贡献率从28%提高到53%<sup>[117]</sup>。在美国东南部,与连续放牧相比,采用适应性多围场放牧管理的草原土壤有机碳含量更高<sup>[118]</sup>;适应性多围场放牧管理措施可改善土壤结构,有利于微生物活动与SOM积累<sup>[118]</sup>。黄土高原草地土壤细菌与真菌的相对丰度随恢复进程而提高,微生物残体在土壤中的积累由真菌和细菌共同残留转变为以细菌残留为主,草地微生物群落适应营养富集环境而提高了土壤碳储量<sup>[119]</sup>。

轮作模式可通过根系分泌物数量和组成的差异影响土壤理化性质<sup>[120]</sup>,还可改变归于土壤中的作物根系或残体的组成与数量,从而影响SOM矿化和有机碳含量。轮作中豆科植物对土壤有机碳含量的影响规律并不一致,如Yang等<sup>[121]</sup>在我国北方平原开展田间试验,其结果显示引入豆科作物的轮作体系能刺激土壤微生物活性,使土壤有机碳储量增加8%;而Cui等<sup>[122]</sup>进行田间试验的结果表明,与玉米单作相比,长期玉米-大豆轮作土壤中子囊菌门微生物丰度要高,SOM分解加剧,其土壤有机碳含量低,

但玉米-大豆轮作土壤中真菌残体碳所占比例更高,这有利于碳的长期固定。

### 3 结语

随着全球变化进程的加剧,如何通过管理措施增强土壤的碳汇功能,缓解气候变化的生态效应,已成为当前环境土壤学研究的重要任务<sup>[110]</sup>。土壤微生物作为陆地生态系统的关键组成,广泛参与了土壤有机碳的输入与稳定化、土壤有机质分解矿化等过程,对土壤碳循环的驱动机制与影响效应起着至关重要的作用,且在提升土壤碳汇方面具有巨大应用潜力。纵观土壤碳循环的微生物作用研究历史和前沿进展,可发现微生物通过其分泌物和残体、群落结构与功能的变化,以及与植物的相互作用等多方面,显示了其在土壤碳循环中的重要地位。微生物介导的土壤碳循环过程,尤其是土壤微生物在土壤含碳温室气体排放中的调控作用,对土壤固碳减排潜力的提升具有重要的理论意义,可为实现区域可持续发展提供科学指导。

考虑到土壤环境、植物因素和人为活动对微生物介导的土壤碳循环过程的影响,未来的研究,须进一步探索微生物群落结构功能与土壤碳循环之间的复杂关系,量化各类微生物在土壤碳循环中的作用;加强微生物对土壤碳循环影响及其对全球变化的响应研究;深入挖掘土壤固碳微生物资源,最终构建以微生物为核心的土壤生态调控技术体系。这将有助于我们更准确地预测和管理土壤碳库,助力我国“碳达峰、碳中和”重大战略目标的实现。

### 参考文献 References

- [1] CROWTHER T W, VAN DEN HOOGEN J, WAN J, et al. The global soil community and its influence on biogeochemistry [J/OL]. Science, 2019, 365 (6455) : eaav0550 [2024-06-01]. <https://doi.org/10.1126/science.aav0550>.
- [2] COOPER R N, HOUGHTON J T, MCCARTHY J J, et al. Climate change 2001: the scientific basis [J/OL]. Foreign affairs, 2002, 81 (1) : 208 [2024-06-01]. <https://doi.org/10.2307/20033020>.
- [3] BEILLOUIN D, CORBEELS M, DEMENOIS J, et al. A global meta-analysis of soil organic carbon in the Anthropocene [J/OL] Nature communications, 2023, 14 (1) : 3700 [2024-06-01]. <https://doi.org/10.1038/s41467-023-39338-z>.
- [4] 于贵瑞,朱剑兴,徐丽,等.中国生态系统碳汇功能提升的技术途径:基于自然解决方案[J].中国科学院院刊,2022,37

- (4):490-501.YU G R,ZHU J X,XU L,et al.Tecnological approaches to enhance ecosystem carbon sink in China:nature-based solutions[J].Bulletin of Chinese Academy of Sciences,2022,37(4):490-501(in Chinese with English abstract).
- [5] HUANG Q,WANG B R,SHEN J K,et al.Shifts in C-degradation genes and microbial metabolic activity with vegetation types affected the surface soil organic carbon pool[J/OL].Soil biology and biochemistry,2024,192: 109371 [2024-06-01].<https://doi.org/10.1016/j.soilbio.2024.109371>.
- [6] 朱永官,沈仁芳,贺纪正,等.中国土壤微生物组:进展与展望[J].中国科学院院刊,2017,32(6):554-565.ZHU Y G, SHEN R F, HE J Z, et al.China soil microbiome initiative: progress and perspective[J].Bulletin of Chinese Academy of Sciences,2017,32(6):554-565(in Chinese with English abstract).
- [7] 朱永官,陈保冬,付伟.土壤生态学研究前沿[J].科技导报,2022,40(3):25-31.ZHU Y G,CHEN B D,FU W.Research frontiers in soil ecology [J].Science & technology review,2022,40(3):25-31(in Chinese with English abstract).
- [8] FIERER N. Embracing the unknown: disentangling the complexities of the soil microbiome[J].Nature reviews microbiology,2017,15(10):579-590.
- [9] BERG I A.Ecological aspects of the distribution of different autotrophic CO<sub>2</sub> fixation pathways [J].Applied and environmental microbiology,2011,77(6):1925-1936.
- [10] JIAN Y,ZHU Z K,XIAO M L,et al.Microbial assimilation of atmospheric CO<sub>2</sub> into soil organic matter revealed by the incubation of paddy soils under <sup>14</sup>C-CO<sub>2</sub> atmosphere [J].Archives of agronomy and soil science,2016,62(12):1678-1685.
- [11] XIAO K Q,GE T D,WU X H,et al.Metagenomic and <sup>14</sup>C tracing evidence for autotrophic microbial CO<sub>2</sub> fixation in paddy soils [J].Environmental microbiology,2021,23 (2) : 924-933.
- [12] GE T D,WU X H,CHEN X J,et al.Microbial phototrophic fixation of atmospheric CO<sub>2</sub> in China subtropical upland and paddy soils [J].Geochimica et cosmochimica acta,2013,113: 70-78.
- [13] JASSEY V E J,WALCKER R,KARDOL P,et al.Contribution of soil algae to the global carbon cycle[J].New phytologist,2022,234(1):64-76.
- [14] PROMMER J,WALKER T W N,WANEK W,et al.Increased microbial growth,biomass, and turnover drive soil organic carbon accumulation at higher plant diversity [J].Global change biology,2020,26(2):669-681.
- [15] HUANG J R,YANG J,HAN M X,et al.Microbial carbon fixation and its influencing factors in saline lake water [J/OL].Science of the total environment,2023,877:162922 [2024-06-01].<https://doi.org/10.1016/j.scitotenv.2023.162922>.
- [16] LI Z W,TONG D,NIE X D,et al.New insight into soil carbon fixation rate: the intensive co-occurrence network of auto-trophic bacteria increases the carbon fixation rate in deposition-sites[J/OL].Agriculture,ecosystems &. environment,2021,320: 107579 [2024-06-01]. <https://doi.org/10.1016/j.agee.2021.107579>.
- [17] 程澳琪,康卫华,李为,等.岩溶区土壤微生物驱动的自养固碳过程与机制研究进展[J].微生物学报,2021,61(6):1525-1535.CHENG A Q,KANG W H,LI W,et al.Research progress in the process and mechanisms of autotrophic carbon sequestration driven by soil microorganisms in Karst areas [J].Acta microbiologica sinica,2021,61 (6) : 1525-1535 (in Chinese with English abstract).
- [18] MANGIPIA M,SCOTT K.From CO<sub>2</sub> to cell:energetic expense of creating biomass using the Calvin-Benson-Bassham and reductive citric acid cycles based on genome data[J/OL].FEMS microbiology letters,2016,363(7):fnw054 [2024-06-01].<https://doi.org/10.1093/femsle/fnw054>.
- [19] BECERRA A,RIVAS M.A phylogenetic approach to the early evolution of autotrophy: the case[J].International microbiology,2014(17):91-97.
- [20] SHIH P M,WARD L M,FISCHER W W.Evolution of the 3-hydroxypropionate bicycle and recent transfer of anoxygenic photosynthesis into the Chloroflexi[J].PNAS,2017,114(40): 10749-10754.
- [21] HU G P,LI Y,YE C,et al.Engineering microorganisms for enhanced CO<sub>2</sub> sequestration [J].Trends in biotechnology,2019,37(5):532-547.
- [22] SARMIENTO J L.Atmospheric CO<sub>2</sub> stalled [J].Nature,1993,365:697-698.
- [23] SCHULZ L,GUO Z J,ZARZYCKI J,et al.Evolution of increased complexity and specificity at the dawn of form I Rubisco[J].Science,2022,378(6616):155-160.
- [24] MISTRY A N,GANTA U,CHAKRABARTY J,et al.A review on biological systems for CO<sub>2</sub> sequestration: organisms and their pathways[J].Environmental progress &. sustainable energy,2019,38(1):127-136.
- [25] SONG Y,LEE J S,SHIN J,et al.Functional cooperation of the glycine synthase-reductase and Wood-Ljungdahl pathways for autotrophic growth of *Clostridium drakei*[J].PNAS,2020,117(13):7516-7523.
- [26] LI X Z,RUI J P,XIONG J B,et al.Functional potential of soil microbial communities in the maize rhizosphere[J/OL].PLoS One,2014,9 (11) : e112609 [2024-06-01].<https://doi.org/10.1371/journal.pone.0112609>.
- [27] HUANG Q,HUANG Y M,WANG B R,et al.Metabolic pathways of CO<sub>2</sub> fixing microorganisms determined C-fixation rates in grassland soils along the precipitation gradient[J/OL].Soil biology and biochemistry,2022,172: 108764 [2024-06-01].<https://doi.org/10.1016/j.soilbio.2022.108764>.
- [28] MENG S S,PENG T,LIU X B,et al.Ecological role of bacteria involved in the biogeochemical cycles of mangroves based

- on functional genes detected through GeoChip 5.0 [J/OL]. mSphere, 2022, 7 (1) : e0093621 [2024-06-01]. <https://doi.org/10.1128/msphere.00936-21>.
- [29] CHEN K J, HE R, WANG L A, et al. The dominant microbial metabolic pathway of the petroleum hydrocarbons in the soil of shale gas field: carbon fixation instead of CO<sub>2</sub> emissions[J/OL]. Science of the total environment, 2022, 807: 151074 [2024-06-01]. <https://doi.org/10.1016/j.scitotenv.2021.151074>.
- [30] HUANG X W, LIN J J, LI D J, et al. Bacterial functions are main driving factors on paddy soil organic carbon in both surface soil and subsoil [J/OL]. Agriculture, ecosystems & environment, 2024, 373: 109123 [2024-06-01]. <https://doi.org/10.1016/j.agee.2024.109123>.
- [31] LIU M H, WEI Y Q, LIAN L, et al. Macrofungi promote SOC decomposition and weaken sequestration by modulating soil microbial function in temperate steppe [J/OL]. Science of the total environment, 2023, 899: 165556 [2024-06-01]. <https://doi.org/10.1016/j.scitotenv.2023.165556>.
- [32] YUAN H Z, GE T D, CHEN C Y, et al. Significant role for microbial autotrophy in the sequestration of soil carbon[J]. Applied and environmental microbiology, 2012, 78 (7) : 2328-2336.
- [33] JU W L, JIN X L, LIU L, et al. Rhizobacteria inoculation benefits nutrient availability for phytostabilization in copper contaminated soil: drivers from bacterial community structures in rhizosphere [J/OL]. Applied soil ecology, 2020, 150: 103450 [2024-06-01]. <https://doi.org/10.1016/j.apsoil.2019.103450>.
- [34] BAI X H, BOL R, CHEN H S, et al. A meta-analysis on crop growth and heavy metals accumulation with PGPB inoculation in contaminated soils [J/OL]. Journal of hazardous materials, 2024, 471: 134370 [2024-06-01]. <https://doi.org/10.1016/j.jhazmat.2024.134370>.
- [35] NETHERWAY T, BENGTSSON J, BUEGGER F, et al. Pervasive associations between dark septate endophytic fungi with tree root and soil microbiomes across Europe[J/OL]. Nature communications, 2024, 15(1): 159 [2024-06-01]. <https://doi.org/10.1038/s41467-023-44172-4>.
- [36] SMITH S E, FACELLI E, POPE S, et al. Plant performance in stressful environments: interpreting new and established knowledge of the roles of arbuscular mycorrhizas [J]. Plant soil, 2010, 326(1):3-20.
- [37] SCHWEIGERT M, HERRMANN S, MILTNER A, et al. Fate of ectomycorrhizal fungal biomass in a soil bioreactor system and its contribution to soil organic matter formation [J]. Soil biology and biochemistry, 2015, 88:120-127.
- [38] GAVITO M E, JAKOBSEN I, MIKKELSEN T N, et al. Direct evidence for modulation of photosynthesis by an arbuscular mycorrhiza-induced carbon sink strength [J]. New phytologist, 2019, 223(2):896-907.
- [39] HAWKINS H J, CARGILL R I M, VAN NULAND M E, et al. Mycorrhizal mycelium as a global carbon pool [J]. Current biology, 2023, 33(11):R560-R573.
- [40] KELLER A B, BRZOSTEK E R, CRAIG M E, et al. Root-derived inputs are major contributors to soil carbon in temperate forests, but vary by mycorrhizal type [J]. Ecology letters, 2021, 24(4):626-635.
- [41] YANG K, ZHANG Q, ZHU J J, et al. Mycorrhizal type regulates trade-offs between plant and soil carbon in forests[J]. Nature climate change, 2024, 14:91-97.
- [42] HEDGES J I, OADES J M. Comparative organic geochemistries of soils and marine sediments [J]. Organic geochemistry, 1997, 27(7/8):319-361.
- [43] TREVISAN S, FRANCIOSO O, QUAGGIOTTI S, et al. Humic substances biological activity at the plant-soil interface: from environmental aspects to molecular factors [J]. Plant signaling & behavior, 2010, 5(6):635-643.
- [44] FERNANDEZ I, CABANEIRO A, GONZÁLEZ-PRIETO S J. Partitioning CO<sub>2</sub> effluxes from an Atlantic pine forest soil between endogenous soil organic matter and recently incorporated <sup>13</sup>C-enriched plant material [J]. Environmental science & technology, 2006, 40(8):2552-2558.
- [45] DOU S, SHAN J, SONG X Y, et al. Are humic substances soil microbial residues or unique synthesized compounds? a perspective on their distinctiveness [J]. Pedosphere, 2020, 30 (2):159-167.
- [46] LEHMANN J, KLEBER M. The contentious nature of soil organic matter[J]. Nature, 2015, 528(7580):60-68.
- [47] KELLEHER B P, SIMPSON A J. Humic substances in soils: are they really chemically distinct? [J]. Environmental science & technology, 2006, 40(15):4605-4611.
- [48] GERKE J. Concepts and misconceptions of humic substances as the stable part of soil organic matter: a review [J/OL]. Agronomy, 2018, 8 (5) : 76 [2024-06-01]. <https://doi.org/10.3390/agronomy8050076>.
- [49] ANGST G, MUELLER K E, NIEROP K G J, et al. Plant- or microbial-derived? a review on the molecular composition of stabilized soil organic matter[J/OL]. Soil biology and biochemistry, 2021, 156: 108189 [2024-06-01]. <https://doi.org/10.1016/j.soilbio.2021.108189>.
- [50] WU H W, CUI H L, FU C X, et al. Unveiling the crucial role of soil microorganisms in carbon cycling: a review[J/OL]. The science of the total environment, 2024, 909: 168627 [2024-06-01]. <https://doi.org/10.1016/j.scitotenv.2023.168627>.
- [51] LAVALLEE J M, SOONG J L, COTRUFO M F. Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century[J]. Global change biology, 2020, 26(1):261-273.
- [52] SOKOL N W, SLESSAREV E, MARSCHMANN G L, et al. Life and death in the soil microbiome: how ecological processes influence biogeochemistry[J]. Nature reviews.microbiol-

- ogy, 2022, 20(7):415-430.
- [53] KLEBER M, BOURG I C, COWARD E K, et al. Dynamic interactions at the mineral - organic matter interface [J]. *Nature reviews earth & environment*, 2021, 2: 402-421.
- [54] BUCKERIDGE K M, CREAMER C, WHITAKER J. Deconstructing the microbial necromass continuum to inform soil carbon sequestration [J]. *Functional ecology*, 2022, 36 (6) : 1396-1410.
- [55] COTRUFO M F, SOONG J L, HORTON A J, et al. Formation of soil organic matter via biochemical and physical pathways of litter mass loss [J]. *Nature geoscience*, 2015, 8: 776-779.
- [56] FAN X L, GAO D C, ZHAO C H, et al. Improved model simulation of soil carbon cycling by representing the microbially derived organic carbon pool [J]. *The ISME journal*, 2021, 15 (8):2248-2263.
- [57] LIANG C, SCHIMEL J P, JASTROW J D. The importance of anabolism in microbial control over soil carbon storage [J/OL]. *Nature microbiology*, 2017, 2: 17105 [2024-06-01]. <https://doi.org/10.1038/nmicrobiol.2017.105>.
- [58] 徐英德, 汪景宽, 王思引, 等. 玉米残体分解对不同肥力棕壤团聚体组成及有机碳分布的影响[J]. *中国生态农业学报*, 2018, 26(7): 1029-1037. XU Y D, WANG J K, WANG S Y, et al. Effects of maize residue decomposition on aggregate composition and organic carbon distribution of different fertilities brown soils [J]. *Chinese journal of eco-agriculture*, 2018, 26 (7):1029-1037(in Chinese with English abstract).
- [59] JIAO Y Q, CODY G D, HARDING A K, et al. Characterization of extracellular polymeric substances from acidophilic microbial biofilms [J]. *Applied and environmental microbiology*, 2010, 76(9):2916-2922.
- [60] SOKOL N W, BRADFORD M A. Microbial formation of stable soil carbon is more efficient from belowground than aboveground input[J]. *Nature geoscience*, 2019, 12:46-53.
- [61] COBAN O, DE DEYN G B, VAN DER PLOEG M. Soil microbiota as game-changers in restoration of degraded lands [J/OL]. *Science*, 2022, 375 (6584) : abe0725 [2024-06-01]. <https://doi.org/10.1126/science.abe0725>.
- [62] XIAO K Q, ZHAO Y, LIANG C, et al. Introducing the soil mineral carbon pump[J]. *Nature reviews earth & environment*, 2023, 4:135-136.
- [63] YANG Y, DOU Y X, WANG B R, et al. Increasing contribution of microbial residues to soil organic carbon in grassland restoration chronosequence [J/OL]. *Soil biology and biochemistry*, 2022, 170: 108688 [2024-06-01]. <https://doi.org/10.1016/j.soilbio.2022.108688>.
- [64] DENG J Z, ORNER E P, CHAU J F, et al. Synergistic effects of soil microstructure and bacterial EPS on drying rate in emulated soil micromodels [J]. *Soil biology and biochemistry*, 2015, 83:116-124.
- [65] KING A E, CONGREVES K A, DEEN B, et al. Quantifying the relationships between soil fraction mass, fraction carbon, and total soil carbon to assess mechanisms of physical protection [J]. *Soil biology and biochemistry*, 2019, 135:95-107.
- [66] HAN L F, SUN K, JIN J, et al. Some concepts of soil organic carbon characteristics and mineral interaction from a review of literature [J]. *Soil biology and biochemistry*, 2016, 94:107-121.
- [67] SI D F, WU S, WU H T, et al. Activated carbon application simultaneously alleviates paddy soil arsenic mobilization and carbon emission by decreasing porewater dissolved organic matter [J]. *Environmental science & technology*, 2024, 58(18):7880-7890.
- [68] BLAGODATSKAYA E, KUZYAKOV Y. Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review [J]. *Biology and fertility of soils*, 2008, 45(2):115-131.
- [69] CUI M J, ZHENG J J, ZHANG R J, et al. Soil bio-cementation using an improved 2-step injection method [J/OL]. *Arabian journal of geosciences*, 2020, 13(23) : 1270 [2024-06-01]. <https://doi.org/10.1007/s12517-020-06168-y>.
- [70] ŠTURSOVÁ M, ŽIFČÁKOVÁ L, LEIGH M B, et al. Cellulose utilization in forest litter and soil: identification of bacterial and fungal decomposers [J]. *FEMS microbiology ecology*, 2012, 80(3):735-746.
- [71] KUZYAKOV Y, FRIEDEL J K, STAHR K. Review of mechanisms and quantification of priming effects [J]. *Soil biology and biochemistry*, 2000, 32(11/12):1485-1498.
- [72] BELL J M, SMITH J L, BAILEY V L, et al. Priming effect and C storage in semi-arid no-till spring crop rotations [J]. *Biology and fertility of soils*, 2003, 37(4):237-244.
- [73] ROUSK K, MICHELSEN A, ROUSK J. Microbial control of soil organic matter mineralization responses to labile carbon in subarctic climate change treatments [J]. *Global change biology*, 2016, 22(12):4150-4161.
- [74] HAMER U, MARSCHNER B. Priming effects in soils after combined and repeated substrate additions [J]. *Geoderma*, 2005, 128(1/2):38-51.
- [75] FONTAINE S, MARIOTTI A, ABBADIE L. The priming effect of organic matter: a question of microbial competition? [J]. *Soil biology and biochemistry*, 2003, 35(6):837-843.
- [76] LI H, YANG S, SEMENOV M V, et al. Temperature sensitivity of SOM decomposition is linked with a K-selected microbial community [J]. *Global change biology*, 2021, 27 (12) : 2763-2779.
- [77] SÁEZ-SANDINO T, GARCÍA-PALACIOS P, MAESTRE F T, et al. The soil microbiome governs the response of microbial respiration to warming across the globe [J]. *Nature climate change*, 2023, 13:1382-1387.
- [78] HE L Y, XU X F. Mapping soil microbial residence time at the global scale [J]. *Global change biology*, 2021, 27 (24) : 6484-

- 6497.
- [79] NISSAN A, ALCOLOMBRI U, PELEG N, et al. Global warming accelerates soil heterotrophic respiration [J/OL]. *Nature communications*, 2023, 14 (1) : 3452 [2024-06-01]. <https://doi.org/10.1038/s41467-023-38981-w>.
- [80] CHEN H Y, XU X, FANG C M, et al. Differences in the temperature dependence of wetland CO<sub>2</sub> and CH<sub>4</sub> emissions vary with water table depth [J]. *Nature climate change*, 2021, 11: 766-771.
- [81] LI X, BEI Q C, RABIEI NEMATABAD M, et al. Time-shifted expression of acetoclastic and methylotrophic methanogenesis by a single *Methanosarcina* genomospecies predominates the methanogen dynamics in Philippine rice field soil [J/OL]. *Microbiome*, 2024, 12(1) : 39 [2024-06-01]. <https://doi.org/10.1186/s40168-023-01739-z>.
- [82] PANG Z Q, CHEN J, WANG T H, et al. Linking plant secondary metabolites and plant microbiomes: a review [J/OL]. *Frontiers in plant science*, 2021, 12: 621276 [2024-06-01]. <https://doi.org/10.3389/fpls.2021.621276>.
- [83] DING H N, LIU T Q, HU Q Y, et al. Effect of microbial community structures and metabolite profile on greenhouse gas emissions in rice varieties [J/OL]. *Environmental pollution*, 2022, 306: 119365 [2024-06-01]. <https://doi.org/10.1016/j.envpol.2022.119365>.
- [84] AMINITABRIZI R, GRAF-GRACHET N, CHU R K, et al. Microbial sensitivity to temperature and sulfate deposition modulates greenhouse gas emissions from peat soils [J]. *Global change biology*, 2023, 29(7):1951-1970.
- [85] VARSADIYA M, URICH T, HUGELIUS G, et al. Microbiome structure and functional potential in permafrost soils of the Western Canadian Arctic [J/OL]. *FEMS microbiology ecology*, 2021, 97(3) : fiab008 [2024-06-01]. <https://doi.org/10.1093/femsec/fiab008>.
- [86] HE P, ZHANG Y T, SHEN Q R, et al. Microbial carbon use efficiency in different ecosystems: a Meta-analysis based on a biogeochemical equilibrium model [J]. *Global change biology*, 2023, 29(17):4758-4774.
- [87] PATOINE G, EISENHAUER N, CESARZ S, et al. Drivers and trends of global soil microbial carbon over two decades [J/OL]. *Nature communications*, 2022, 13 (1) : 4195 [2024-06-01]. <https://doi.org/10.1038/s41467-022-31833-z>.
- [88] MALIK A A, PUSSANT J, BUCKERIDGE K M, et al. Land use driven change in soil pH affects microbial carbon cycling processes [J/OL]. *Nature communications*, 2018, 9 (1) : 3591 [2024-06-01]. <https://doi.org/10.1038/s41467-018-05980-1>.
- [89] SILVA-SÁNCHEZ A, SOARES M, ROUSK J. Testing the dependence of microbial growth and carbon use efficiency on nitrogen availability, pH, and organic matter quality [J]. *Soil biology and biochemistry*, 2019, 134:25-35.
- [90] CUI J W, ZHU R L, WANG X Y, et al. Effect of high soil C/N ratio and nitrogen limitation caused by the long-term combined organic-inorganic fertilization on the soil microbial community structure and its dominated SOC decomposition [J/OL]. *Journal of environmental management*, 2022, 303: 114155 [2024-06-01]. <https://doi.org/10.1016/j.jenvman.2021.114155>.
- [91] ZHANG G L, BAI J H, JIA J, et al. Soil microbial communities regulate the threshold effect of salinity stress on SOM decomposition in coastal salt marshes [J]. *Fundamental research*, 2023, 3(6):868-879.
- [92] RATH K M, FIERER N, MURPHY D V, et al. Linking bacterial community composition to soil salinity along environmental gradients [J]. *The ISME journal*, 2019, 13(3):836-846.
- [93] BICHARANLOO B, BAGHERI SHIRVAN M, DIJKSTRA F A. Decoupled cycling of carbon, nitrogen, and phosphorus in a grassland soil along a hillslope mediated by clay and soil moisture [J/OL]. *Catena*, 2022, 219: 106648 [2024-06-01]. <https://doi.org/10.1016/j.catena.2022.106648>.
- [94] LI Y H, SHAHBAZ M, ZHU Z K, et al. Oxygen availability determines key regulators in soil organic carbon mineralisation in paddy soils [J/OL]. *Soil biology and biochemistry*, 2021, 153: 108106 [2024-06-01]. <https://doi.org/10.1016/j.soilbio.2020.108106>.
- [95] ZHANG W J, MUNKHOLM L J, LIU X, et al. Soil aggregate microstructure and microbial community structure mediate soil organic carbon accumulation: evidence from one-year field experiment [J/OL]. *Geoderma*, 2023, 430: 116324 [2024-06-01]. <https://doi.org/10.1016/j.geoderma.2023.116324>.
- [96] ZHANG X W, ZHU B, YU F H, et al. Long-term bare fallow soil reveals the temperature sensitivity of priming effect of the relatively stabilized soil organic matter [J]. *Plant and soil*, 2023, 488(1):57-70.
- [97] SU R L, WU X, HU J L, et al. Warming promotes the decomposition of oligotrophic bacterial-driven organic matter in paddy soil [J/OL]. *Soil biology and biochemistry*, 2023, 186: 109156 [2024-06-01]. <https://doi.org/10.1016/j.soilbio.2023.109156>.
- [98] MA L X, JU Z Q, FANG Y Y, et al. Soil warming and nitrogen addition facilitates lignin and microbial residues accrual in temperate agroecosystems [J/OL]. *Soil biology and biochemistry*, 2022, 170: 108693 [2024-06-01]. <https://doi.org/10.1016/j.soilbio.2022.108693>.
- [99] ZHAI C C, HAN L L, XIONG C, et al. Soil microbial diversity and network complexity drive the ecosystem multifunctionality of temperate grasslands under changing precipitation [J/OL]. *Science of the total environment*, 2024, 906: 167217 [2024-06-01]. <https://doi.org/10.1016/j.scitotenv.2023.167217>.
- [100] WANG M M, SUN X, CAO B C, et al. Long-term elevated precipitation induces grassland soil carbon loss via microbe-plant-soil interplay [J]. *Global change biology*, 2023, 29 (18) :

- 5429-5444.
- [101] NOTTINGHAM A T, FIERER N, TURNER B L, et al. Microbes follow Humboldt: temperature drives plant and soil microbial diversity patterns from the Amazon to the Andes [J]. *Ecology*, 2018, 99(11): 2455-2466.
- [102] 张瀚曰,包维楷,胡斌,等.植被类型变化对土壤微生物碳利用效率的影响研究进展[J].*生态学报*,2023,43(16):6878-6888.ZHANG H Y, BAO W K, HU B, et al. Effect of vegetation type change on soil microbial carbon use efficiency: a review [J]. *Acta ecologica sinica*, 2023, 43 (16) : 6878-6888 (in Chinese with English abstract).
- [103] WANG B R, AN S S, LIANG C, et al. Microbial necromass as the source of soil organic carbon in global ecosystems [J/OL]. *Soil biology and biochemistry*, 2021, 162: 108422 [2024-06-01]. <https://doi.org/10.1016/j.soilbio.2021.108422>.
- [104] BACH L H, GRYTNES J A, HALVORSEN R, et al. Tree influence on soil microbial community structure [J]. *Soil biology and biochemistry*, 2010, 42(11): 1934-1943.
- [105] 刘泽琴,刘宁,李淑娟,等.紫云英与油菜间作模式下根系分泌物对土壤微生物的影响[J].*华中农业大学学报*,2023,42(4):177-184.LIU Z Q, LIU N, LI S J, et al. Effects of root exudates on soil microorganisms under intercropping pattern of Chinese milkvetch and rapeseed [J]. *Journal of Huazhong Agricultural University*, 2023, 42 (4) : 177-184 (in Chinese with English abstract).
- [106] 刘茗,曹林桦,刘彩霞,等.亚热带4种典型森林植被土壤固碳细菌群落结构及数量特征[J].*土壤学报*,2021,58(4):1028-1039.LIU M, CAO L H, LIU C X, et al. Characterization of population and community structure of carbon-sequstration bacteria in soils under four types of forest vegetations typical of subtropical zone [J]. *Acta pedologica sinica*, 2021, 58 (4): 1028-1039 (in Chinese with English abstract).
- [107] FERNÁNDEZ-ALONSO M J, CURIEL YUSTE J, KITZLER B, et al. Changes in litter chemistry associated with global change-driven forest succession resulted in time-decoupled responses of soil carbon and nitrogen cycles [J]. *Soil biology and biochemistry*, 2018, 120: 200-211.
- [108] SEYFRIED G S, DALLING J W, YANG W H. Mycorrhizal type effects on leaf litter decomposition depend on litter quality and environmental context [J]. *Biogeochemistry*, 2021, 155 (1): 21-38.
- [109] 金文豪,邵帅,陈俊辉,等.不同类型菌根对土壤碳循环的影响差异研究进展[J].*浙江农林大学学报*,2021,38(5):953-962.JIN W H, SHAO S, CHEN J H, et al. Research progress in the impact of different mycorrhizal types on soil carbon cycling [J]. *Journal of Zhejiang A & F University*, 2021, 38(5): 953-962 (in Chinese with English abstract).
- [110] 方精云.碳中和的生态学透视[J].*植物生态学报*,2021,45(11):1173-1176.FANG J Y. Ecological perspectives of carbon neutrality [J]. *Chinese journal of plant ecology*, 2021, 45 (11): 1173-1176 (in Chinese with English abstract).
- [111] DONG X L, HAO Q Y, LI G T, et al. Contrast effect of long-term fertilization on SOC and SIC stocks and distribution in different soil particle-size fractions [J]. *Journal of soils and sediments*, 2017, 17(4): 1054-1063.
- [112] 胡启良,杨滨娟,刘宁,等.绿肥混播下不同施氮量对水稻产量、土壤碳氮和微生物群落的影响[J].*华中农业大学学报*,2022,41(6):16-26.HU Q L, YANG B J, LIU N et al. Effects of application rates of nitrogen on rice yield, carbon and nitrogen, microbial community in soil under mixed sowing of green manure [J]. *Journal of Huazhong Agricultural University*, 2022, 41(6): 16-26 (in Chinese with English abstract).
- [113] LI Z, WEI X M, ZHU Z K, et al. Organic fertilizers incorporation increased microbial necromass accumulation more than mineral fertilization in paddy soil via altering microbial traits [J/OL]. *Applied soil ecology*, 2024, 193: 105137 [2024-06-01]. <https://doi.org/10.1016/j.apsoil.2023.105137>.
- [114] WANG E Z, YU B, ZHANG J Y, et al. Low carbon loss from long-term manure-applied soil during abrupt warming is realized through soil and microbiome interplay [J]. *Environmental science & technology*, 2024, 58(22): 9658-9668.
- [115] CHAPPELL A, BALDOCK J, SANDERMAN J. The global significance of omitting soil erosion from soil organic carbon cycling schemes [J]. *Nature climate change*, 2016, 6: 187-191.
- [116] SOUZA R C, CANTÃO M E, VASCONCELOS A T R, et al. Soil metagenomics reveals differences under conventional and no-tillage with crop rotation or succession [J]. *Applied soil ecology*, 2013, 72: 49-61.
- [117] TIAN J, DUNGAIT J A J, HOU R X, et al. Microbially mediated mechanisms underlie soil carbon accrual by conservation agriculture under decade-long warming [J/OL]. *Nature communications*, 2024, 15(1): 377 [2024-06-01]. <https://doi.org/10.1038/s41467-023-44647-4>.
- [118] MOSIER S, APFELBAUM S, BYCK P, et al. Adaptive multi-paddock grazing enhances soil carbon and nitrogen stocks and stabilization through mineral association in southeastern U. S. grazing lands [J/OL]. *Journal of environmental management*, 2021, 288: 112409 [2024-06-01]. <https://doi.org/10.1016/j.jenvman.2021.112409>.
- [119] YANG Y, DOU Y X, WANG B R, et al. Deciphering factors driving soil microbial life-history strategies in restored grasslands [J/OL]. *iMeta*, 2023, 2(1): e66 [2024-06-01]. <https://doi.org/10.1002/imt.266>.
- [120] 周信雁,杨尚东.番茄连作土壤中微生物群落的变化特征及其重塑研究进展[J].*华中农业大学学报*,2024,43(1):1-8.ZHOU X Y, YANG X D. Progress on changing characteristics and reconstruction of microbial communities in soil under tomato continuous cropping [J]. *Journal of Huazhong Agricultural University*, 2024, 43(1) : 1-8 (in Chinese with English abstract).

- [121] YANG X L, XIONG J R, DU T S, et al. Diversifying crop rotation increases food production, reduces net greenhouse gas emissions and improves soil health [J/OL]. *Nature communications*, 2024, 15 (1) : 198 [2024-06-01]. <https://doi.org/10.1038/s41467-023-44464-9>.
- [122] CUI J W, YANG B G, XU X P, et al. Long-term maize-soybean rotation in Northeast China: impact on soil organic matter stability and microbial decomposition [J/OL]. *Plant soil*, 2024; 1-18 [2024-06-01]. <https://doi.org/10.1007/s11104-024-06592-z>.

## Roles of microorganisms in carbon cycling in soil

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**Abstract** Carbon in soil is an important component of the global carbon cycle, and the processes of carbon cycling play a crucial role in regulating climate, with microorganisms being the key driving force behind carbon cycling in soil. This article reviewed the roles and mechanisms of microorganisms in the input of organic carbon in soil, formation and stabilization of organic matter in soil, the processes of decomposing and mineralizing organic matter in soil, and the effects of soil properties, climate conditions, plant factors, and human activities on microorganisms mediated carbon cycling in soil, especially the progress and theoretical updates in related studies. Microorganisms in soil can indirectly promote the photosynthesis in plant and the input of carbon in soil through its symbiosis with plants, and can directly participate in the fixation and transformation of carbon in soil. Microbial residues and their secretions play a crucial role in the formation of mineral-associated organic matter and aggregates in soil, which is beneficial for the long-term stability of organic carbon in soil. The microorganisms mediated effect of priming has a regulatory effect on the decomposition of organic matter in soil, which can affect the emissions of greenhouse gases such as CO<sub>2</sub> and CH<sub>4</sub> from the soil. Studies on the mechanism of microorganisms mediated processes of stabilizing the organic carbon and storing carbon in soil in the future should be strengthened and focus on the complex relationship between the structure and function of microbial community and the carbon cycling in soil, as well as their response to global changes. It will provide new insights for China to achieve its major strategic goals of “carbon peak” and “carbon neutrality” through enhancing the potential of carbon sequestration or the function of carbon sink with microbial activity.

**Keywords** soil microorganism; carbon cycling in soil; microbial carbon sequestration; soil organic matter; microbial residues

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