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土壤微生物碳利用效率研究进展

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摘要: 土壤微生物碳利用效率(CUE)指微生物生长与碳吸收的比率,反映了受微生物群落影响的土壤有机碳代谢过程,是理解和模拟全球变化下土壤碳储存和碳循环的关键生理生态参数。量化土壤微生物 CUE 有助于理解土壤微生物生物量、土壤潜在碳储量、呼吸碳消耗之间的分异,以及土壤长期碳储存对全球变化的响应。土壤微生物 CUE 及其对环境变化的响应已受到土壤碳循环、全球变化生态学、陆地生态系统模型等研究的广泛关注。我国土壤微生物 CUE 研究是近几年才兴起的。本文分析了碳同位素法、氧同位素法、量热呼吸法、代谢通量分析法、化学计量法五种微生物 CUE 测定方法的优劣及适应性,阐释了土壤微生物 CUE 随生态系统、植被演替、季节的动态变化特征,剖析了微生物群落组成、底物质量和营养可利用性、温度、土壤 pH 值、土壤水分、土壤团聚体与质地、土层深度、人为干扰等生物和非生物因子对土壤微生物 CUE 的影响,并指出了当前土壤微生物 CUE 研究存在的问题,以及今后关注的重点:(1)加强森林生态系统土壤微生物 CUE 研究;(2)综合探讨环境和生物多要素交互影响下土壤微生物 CUE 的响应过程与机制,尤其是全球变化下根系分泌物对土壤微生物 CUE 及长期碳固持的影响;(3)从生态系统视角探讨土壤微生物 CUE;(4)采用不同测定方法估算土壤微生物 CUE;(5)探讨不同土层深度微生物 CUE 及其温度敏感性对长期碳储存影响。

关键词: 碳利用效率;土壤微生物;测定方法;动态变化;影响因子

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土壤微生物碳利用效率(Carbon Use Efficiency, CUE)通常指微生物生长与碳吸收的比率^[1-3],反映了受微生物群落影响的土壤有机碳代谢过程^[1,4-6]。土壤微生物 CUE 影响土壤碳固持、周转、矿化和温室气体排放等生态系统过程及其对气候变化的生物地球化学反馈^[7-11],在调节土壤微生物介导的碳和养分转化中起着重要作用^[11],是土壤微生物生物量周转和土壤碳固持的关键调节因素^[4,12],常作为反映土壤碳同化能力和碳固持潜力的定量指标^[10,13-14]。它适用于种群(CUE_p)、群落(CUE_c)、生态系统(CUE_E)不同尺度,尤其是生态系统尺度

CUE_E 决定了微生物生物量周转率和土壤碳固持^[15],反映了生态系统呼吸、微生物生物量积累和土壤碳固持之间的平衡^[16]。

微生物 CUE 是土壤碳储存和碳循环的关键生理生态参数^[4,17-21],也是反映土壤微生物量碳池分配的重要参数^[54],广泛应用于陆地生态系统模型,尤其是土壤生物地球化学模型^[7,9,22-25],模型通常假设 CUE 为一固定参数,但是这种假设将降低陆地生态系统土壤碳动态模拟的精度和模型的可利用性^[73-74]。通常认为,高的 CUE 表明土壤微生物的生长效率高,有利于土壤中微生物来源碳的积累和

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稳定性^[1,15,55-60];而低的 CUE 有利于呼吸,可能减少土壤碳储存,暗示土壤碳固持潜力的减弱^[1,4,57,61]。也有研究表明,较高的 CUE 加速土壤有机碳(Soil Organic Carbon, SOC)分解,进而导致 SOC 的损失^[62],而较低的 CUE 降低微生物对土壤碳的分解,有利于土壤碳的积累^[63],表明微生物 CUE 与微生物介导的有机碳截获过程并非简单的线性关系^[64]。

由于土壤有机碳转化为微生物生物量及其周转在土壤碳长期稳定中起着重要的作用^[36-38],土壤微生物 CUE 的微小变化可能对土壤碳的储存有重要影响^[7]。量化土壤微生物 CUE,有助于理解土壤微生物生物量、土壤潜在碳储量、呼吸碳消耗之间的分异,以及土壤长期碳储存对全球变化的响应^[11-12,28-35],提高全球气候变化下土壤碳固持和损失的模拟精度^[26-27],对于生态系统可持续管理策略亦至关重要。为此,本文从土壤微生物 CUE 的测定方法、动态变化、影响因子等方面综述了国内外土壤微生物 CUE 研究进展,并分析了当前土壤微生物 CUE 研究存在的问题,展望了未来研究应关注的方向,以为今后的研究提供参考和借鉴。

1 土壤微生物 CUE 测定方法

土壤微生物 CUE 测定主要有直接法和间接法。根据定义($CUE = G / (G + R)$),直接法就是基于微生物生长(G)和呼吸(R)的直接测定估算 CUE。根据生态系统 CUE_E 定义(净微生物生长/(净微生物生长 + 总微生物呼吸 + 微生物死亡))^[15,39], CUE_E 还包括微生物死亡的测定,以捕获随时间推移通过微生物生物量周转和呼吸而损失的碳,以及微生物产物/代谢物的回收效率,即微生物残体(necromass)和分泌物(exudates)^[10,15]。微生物生长可测定为生物量增加的速率、蛋白质合成、DNA 复制、 ^{13}C 标记底物的消耗;呼吸可测定为总 CO_2 释放速率、底物 $^{13}CO_2$ 释放速率、氧消耗量、呼吸电子传递^[16]。通常采用氨基糖含量反映微生物残体积累^[40]。

土壤微生物 CUE 测定的经验方法通常采用同位素标记碳底物添加的微生物短期培养,基于标记底物转化为微生物生物量的数量(代表微生物生长),以及标记底物的呼吸消耗进行估算^[1,4],主要

有碳同位素法、量热呼吸法、代谢通量分析法。碳同位素示踪法基于 ^{13}C 或 ^{14}C 标记底物的实验培养,跟踪碳标记底物的利用,以及微生物呼吸碳消耗和生物量生产估算土壤微生物 CUE^[1],是一种常用测定方法, ^{14}C 标记通常较 ^{13}C 标记具有较高的 CUE^[188],以 ^{13}C 底物标记应用较多;不同底物 CUE 差异较大,葡萄糖是 CUE 测定最常用的底物,CUE 观测应关注底物及微生物产物快速吸收的影响^[188]。该法的基本假设是微生物生物量碳增加仅来源于底物碳,该假设排除了微生物生物量碳的可能循环^[10],不能捕捉投入到胞外酶的碳组分,且难以区分胞外酶碳与未被同化的底物碳或生物量碳^[15],没有考虑微生物生物量的周转。碳同位素法的关键是微生物培养时间,但是由于不同土壤微生物群落组成或生长条件的差异,似乎又不可能统一标准^[2]。量热呼吸法是从热力学角度,基于底物代谢热量和呼吸速率测定,计算能量利用率和合成代谢速率,估算微生物生长和 CUE,理解微生物代谢和生长的相互关系^[2,41]。代谢通量分析法是基于底物代谢质量平衡和能量平衡,采用标记葡萄糖中 $^{13}CO_2$ 的生产,根据培养实验微生物代谢中底物消耗或微生物合成的平衡估算 CUE,该法可定量描述代谢特性,捕获微生物生理信息,但不能反映微生物生物量的周转^[42]。

另外一种不添加碳底物的 CUE 直接测定法是氧同位素示踪法,该法基于微生物生长过程中 $H_2^{18}O$ 同位素掺入 DNA 的测定估算 CUE。该法假设微生物 DNA 合成中的氧 100% 来源于水^[43]。由于基因组 DNA 只在细胞分裂时合成, ^{18}O 同位素掺入 DNA 可以用来计算微生物的生长速率^[44-45];利用微生物 DNA 和微生物生物量碳之间的线性关系^[6,46],基于 ^{18}O -DNA 的增加,估算微生物生物量碳增加动态;结合微生物生长速率和基础呼吸速率,估算微生物 CUE。该法还可评估土壤中微生物生物量周转时间,即微生物生物量除以 ^{18}O 掺入 DNA 后的微生物生长速率。近年来,有学者发展了一种新的基于体内 ^{18}O -水蒸汽平衡的方法,该法允许在不直接加入液态水的情况下对土壤水进行同位素标记,可降低由于直接添加液态 $H_2^{18}O$ 法引起再湿润带来的测定误差^[47]。

近年来, ^{18}O - H_2O 标记法已广泛用于估算微生物 CUE。 ^{18}O 同位素法较 ^{13}C 同位素法更能准确测定原位条件下土壤 CUE。尽管短期碳底物添加可能

贡献于微生物生长,但是难以证实底物诱导的 CUE 是否反映真实的微生物生长,因为它主要反映特定底物利用效率的信息^[4,7,15],而不是微生物生物量生产^[4],更难以捕获土壤环境中可利用复杂底物的原位条件。相比之下,¹⁸O 标记法对原生土壤有机质的质量影响较少,更能反映微生物的实际生长^[7]。碳底物标记估算 CUE 大多接近理论最大值^[7,48],可能高估微生物在自然环境中对碳循环的贡献。基于 H₂¹⁸O 的底物标记法估算 CUE 相对较低^[2,5-6]。

土壤微生物 CUE 主要的间接测定方法是生态化学计量法^[49-50]。该法根据有机质和微生物生物量的元素化学计量比,以及碳与获取营养的生态酶活性之比间接估算 CUE^[16]。CUE 与调节碳和营养获取的生态酶活性的化学计量学相关性最为密切^[16]。土壤微生物群落 CUE 被认为是生长的营养需求和底物营养成分差异的函数,通过细胞外酶活性(Extracellular Enzyme Activity, EEA)、微生物生物量 C/N(C/P)比和可利用有机质估算群落水平微生物 CUE,评估微生物群落对底物化学计量学的响应^[189]。生态化学计量学反映了微生物生物量和碎屑有机质的元素组成之间的平衡,以及营养吸收和生长效率之间的平衡^[51]。该法的优点是利用普通土壤分析进行 CUE 估算,可应用于不同的时空尺度^[16]。最近提出了一种新的多碳循环酶促化学计量 CUE 估算方法(Multi-Carbon Cycling Enzymes Stoichiometry Modeling, MCE-STM),该法能够量化土壤 pH 和植物残体质量对微生物代谢效率的综合影响,是单碳循环酶促化学计量法(Single-Carbon Cycle Enzymatic Stoichiometry, SCE-STM)可行的替代方法,扩大用于 CUE 估算的各种 C-和 N-捕获酶(MCE-STM 酶)的数量,可提高 CUE 间接估算的可靠性^[52]。

土壤微生物 CUE 的准确估算受到遗传和环境变化的挑战。由于土壤微生物 CUE 影响因素的复杂性和不确定性^[1,53],不同方法估算结果可能不同,且不同方法变异来源不同^[2]。应根据不同的研究目的选择最佳测定方法,整合不同方法可以提高对影响 CUE 变化过程的理解^[52]。未来应尝试比较不同方法估算 CUE,以从不同角度认识和理解微生物代谢规律^[2]。

2 陆地生态系统土壤微生物 CUE 变化

作为生态系统的自然特性,不同生态系统类型和微生物类群 CUE 差异大^[4,65-66]。理论上,热力学估算 CUE 最大值约为 0.6~0.8^[4,7,48]。受环境因素、资源可用性、化学计量学、微生物生理活动和微生物群落组成等影响^[1,4],现有报道的陆地生态系统土壤微生物 CUE 值大多低于理论最大值。基于化学计量模型的全球平均土壤微生物 CUE 为 0.27 ± 0.11 ,相应的微生物量平均周转时间为 67 d^[16]。基于底物独立方法的原位土壤微生物平均 CUE 为 0.20~0.30^[2,5,67-68]。与耕作土壤相比,森林土壤的腐生性真菌丰度较高,从而增加微生物 CUE^[69]。瑞典南部温带和亚北极森林、农用地土壤鲜样微生物 CUE 为 0.03~0.30^[70]。也有报道森林和草地土壤微生物 CUE 没有显著差异(0.24 ± 0.08)^[5]。云南亚热带和温带森林土壤微生物生物量和 CUE 均显著高于热带森林土壤,但微生物呼吸量明显低于热带森林土壤^[71]。加拿大 Mendocino 自然保护区土壤微生物 CUE 随土壤和生态系统发育而显著变化,沿地质时间呈单峰关系,在中间年龄阶段、中等酸性的样地达到最大值^[72]。土壤微生物 CUE 具季节变化特征,夏季土壤具有较高 CUE,与夏季较冬季低的基础呼吸有关^[75];冬季土壤 CUE 大幅度降低反映了生长呼吸向维持呼吸的转移^[8]。*Pinus sylvestris* 林分菌根真菌 CUE 随林龄增加而降低,且生长季节增加,老龄林 CUE 下降与土壤氮利用率下降和菌根真菌群落组成变化有关,而生长季 CUE 增加受光合产物和温度的季节性变化调节^[34]。

微生物 CUE 是植被恢复过程中土壤碳周转的关键指示剂,有助于认识微生物代谢对植被恢复过程中土壤碳动态的影响。黄土高原半干旱区植被自然恢复过程中土壤微生物 CUE 呈下降趋势,以恢复到 100 年左右(森林早期阶段)为最低(0.24~0.41),土壤微生物量碳和磷代谢主要受土壤水分的调控^[190]。废弃农用地植被恢复过程中土壤微生物 CUE(0.66~0.82)呈下降趋势,下降幅度与土壤类型相关,植被恢复可增加微生物活性,提高微生物生长速率和活性微生物比例,以及 C、N、P 循环相关酶的活性,促进微生物介导的碳和养分周转^[191]。热带森林砍伐对土壤微生物群落具有持续影响,热

带次生林需要较长时间才能恢复到与原始森林相似的 CUE, 土壤微生物量碳随林龄增加而增加^[14]。而川西贡嘎山海螺沟冰川退缩区植被原生演替过程中土壤微生物 CUE 呈增加趋势, 平均 CUE 从演替早期草地的 0.54 增加到顶级群落暗针叶林的 0.72, 主要受植被演替过程中不同营养策略的微生物群落聚集影响, 寡营养(oligotroph)控制阶段 CUE 高于共生营养(copiotroph)控制阶段, 土壤微生物 CUE 随土壤寡营养与共生营养微生物群落比率增加而增加, 寡营养微生物群落可能促进土壤碳固持^[193]。植被原生演替和次生恢复过程中土壤微生物 CUE 变化可能有所不同。

3 土壤微生物 CUE 影响因子

陆地生态系统土壤微生物 CUE 受微生物群落组成和结构^[27,76]、环境因子^[7,77]、底物质量和营养可利用率^[1,78-79]等影响。近年来环境条件与 CUE 的关系受到高度关注^[4,15]。

3.1 微生物群落组成

土壤微生物群落组成驱动 CUE 变化^[1,80]。微生物群落组成和多样性是 CUE 最有效的预测因子, 而非生物因子调节多样性与 CUE 的关系^[81]。真菌和细菌群落的相对丰度和活性强烈影响土壤碳转化^[82]和长期碳储存^[53,83]。土壤中真菌和细菌具有不同的 CUE 水平^[53,70,78], 理论上估算细菌最大 CUE 为 0.6 左右^[4,84], 与同位素碳底物标记实验估算结果相似(0.60~0.85)^[15,85], 而代谢模型预测细菌最大 CUE 变异较大(0.22~0.98)^[86]。基于基因组约束的代谢模型预测 200 多种细菌 CUE 发现, 亚门水平和系统发育结构上潜在 CUE 为 0.62 ± 0.17 , 与基因组大小呈负相关, 微生物群落组成的变化可能影响碳储量^[86]。随着森林演替, 与木材腐烂、木质素和其他复杂碳分解等有关的细菌和真菌功能群发生变化, 与土壤总有机碳(TOC)、微生物量碳、CUE 增加密切相关^[29,83,87-94]。菌根真菌的菌丝体在调节北方森林土壤碳循环和碳储存起着十分重要的作用^[34], 至少贡献了北方森林土壤微生物生物量的 1/3^[95]。Costa Rica 北部原始林、次生林较幼龄人工林具有较高的微生物 DNA 序列相对丰度, 以及较高的有机碳、生物量碳和微生物商(microbial quotients)水平, 这些组分可提高 CUE^[96]。生物交

互作用显著影响微生物功能和 CUE^[97-99], 担子菌类真菌间交互作用降低温带森林枯木微生物 CUE, 且降低幅度接近温度和底物质量的联合效应^[76]。

许多研究表明, 以真菌占优势的土壤较以细菌为主的土壤具有较高的 CUE^[53,82-83,100-103], 真菌群落不仅有助于复杂化合物的分解, 而且有利于活性凋落物分解^[82,104], 因而促进真菌介导的土壤微生物量碳的稳定和有机质的积累^[53,82]。在微生物培养的早期阶段中, 高真菌丰度与 SOC 含量的增加和高 CUE 有关^[105]。而温带云杉和桦木林、亚北极桦木林和温带农用样地土壤微生物 CUE 和真菌-细菌生物量比(F:B)之间的负指数关系^[70], 表明细菌居主导的土壤具有较高 CUE^[128]。也有研究认为不同土壤微生物群落具有相似的 CUE^[53,106], 细菌占优势和真菌占优势的土壤 CUE 无显著差异^[107]。细菌和真菌的优势地位取决于底物的营养可利用性和碳质量^[108-109]。高 C:N 比的土壤通常具有较高的 F:B 比^[101], 增加底物碳与营养元素的比率可能提高真菌群落 CUE, 降低细菌为主的 CUE^[78]。土壤微生物碳分配的变化, 如同化效率、生物量呼吸、胞外酶生产、CUE, 影响土壤碳池平衡, 微生物过程模拟能更好地解释微生物碳分配动态^[110]。

3.2 底物质量和营养可利用性

许多实验研究和模型模拟表明, 土壤底物碳的质量、化学计量比和可利用性影响微生物 CUE^[1,3-4,7,66,70,111-112]。微生物吸收利用的碳底物主要来自土壤有机碳和植被凋落物, 土壤碳底物质量影响土壤微生物 CUE^[1,27,78]。分解结构复杂的碳水化合物(如木质素和酚类等)可能降低的 CUE, 因为其酶促反应需要更多的能量投入^[79]。土壤微生物 CUE 的地理分异主要受土壤底物质量差异的影响^[66]。根际沉积介导氮、磷有效性对微生物 CUE 和周转率的影响, 利用源自根系活性碳的微生物较源自土壤惰性碳的微生物能更有效地积累其生物量, 而利用源自土壤 SOC 的微生物 CUE 和周转率较低^[113]。土壤微生物 CUE 与土壤溶解性有机质 C:N 比(DOC:DN 比)呈负相关^[21]。生物炭老化和与之相联系的土壤 pH 增加通过增加农田土壤微生物 CUE 或降低生物量周转时间促进土壤微生物碳固持^[114]。底物碳还原性程度(γ_s)是影响土壤微生物 CUE 的另一个重要因素, 还原度高的底物通常具有较高的微生物 CUE。微生物利用底物 γ_s 大多为

3~5,与土壤微生物生物量碳还原度相当($\gamma_B \approx 4.2$)^[84]。当底物 $\gamma_S < 4.2$ 时,微生物 CUE 主要受到底物还原度的限制,而当底物 $\gamma_S > 4.2$ 时,微生物 CUE 较高^[1,84]。

不同微生物群落对底物碳质量的响应有所不同。基于不同真菌和细菌种类培养试验表明,真菌 CUE 主要受底物碳影响,而细菌主要受矿质 N 和 P 影响,真菌 CUE 与碳和营养元素的比率呈正相关,而细菌 CUE 与碳和营养元素的比率呈负相关,表明真菌生长较细菌具有较高的碳需求^[53,78]。低质量底物资源(高 C:N 比)有利于真菌生长,高质量底物资源(低 C:N 比)有利于细菌生长^[115]。当资源(如叶凋落物)氮缺乏时,陆地生态系统土壤微生物通常具有较低的 CUE^[116]。东北油松林土壤添加 5 种不同凋落物 3 年后,土壤微生物生物量、基于微生物碳同化与 N 营养消耗的化学计量 $CUE_{C:N}$ 具有显著差异,以木屑添加土壤 $CUE_{C:N}$ 为最高,表明低质量有机质添加促进土壤碳的稳定性^[117]。

生物计量比的差异可能是土壤微生物 CUE 的另一个重要驱动因素,并与异质资源环境下微生物群落结构有关^[113]。生物量化学计量比、资源需求、CUE 间的联系可为自然土壤微生物群落结构和功能提供机制解释。土壤营养可利用性/底物化学计量与 CUE 间的关系较为复杂,碳和营养元素之比与 CUE 的正负相关性取决于土壤是遭受营养限制还是能量限制^[118]。当土壤遭受营养限制(高的碳与养分比率)时,微生物需要消耗更多的能量获取营养,转化为生物量的比率即 CUE 就较低^[6,119-120]。营养限制或引起溢流呼吸(overflow respiration)^[1,4,121-122],或碳分泌增加,或酶生产投入较高^[123],增加碳释放或碳消耗,以维持 C:N 比平衡^[1,66],导致 CUE 下降^[1,124]。微生物 CUE 随着碳底物质量的提高(较低 C:N 比)而增加^[125-127],随营养限制的增加而减少^[1,49],氮磷利用率、有机质质量通过影响土壤微生物生长和呼吸,从而影响 CUE^[1,128]。基于山毛榉和云杉林分土壤微生物培养实验表明,当细菌生长遭受矿物质 N 或低 pH 抑制时,CUE 降低^[128]。微生物 CUE 与土壤有机质含量及凋落物化学计量比(C:N, C:P, N:P)呈正相关^[72]。外源养分和作物残体输入增加微生物生物量和残体碳分解,可能增加微生物 CUE 和稳定 SOC

储存^[39,121,129]。湿地、草地和森林土壤 CUE、微生物量周转时间、 Q_{10} 与可利用 C:N 比、黏土含量和碳质量密切相关,证实了可利用底物的化学计量比和碳质量在预测土壤微生物 CUE 和土壤碳代谢温度敏感性的重要性^[130]。也有研究表明,碳和营养元素化学计量比的增加或提高 CUE^[131],或对微生物 CUE 没有影响^[132]。在营养过剩环境(低的碳与养分比率)中,CUE 与碳和养分比率呈正相关关系^[133]。CUE 也受到磷(P)利用率的影响,CUE 与 N:P 比的关系取决于遭受 N 限制还是 P 限制^[118,134]。当 P 容易获得时,微生物生长速率较快,因为高 P 有利于更多核糖体 RNA,加速蛋白质合成^[135],CUE 与 N:P 间呈正相关关系。在 P 限制环境中,CUE 可能较低。

关于营养输入对土壤微生物 CUE 的影响存在较大争议。大多数研究发现 N 或 N、P、K 添加条件下 CUE 有所增加^[6,60],氮沉降增加氮利用率,影响凋落物质量和数量,二者显著影响 CUE 和激发效应(priming effect)。长期氮添加增加温带草地土壤有机碳浓度,减少微生物呼吸和 F:B 比,增加微生物 CUE,氮沉降下微生物呼吸的减少和碳存储的增加取决于活性碳(labile C)输入而不是惰性碳(recalcitrant C)输入^[59]。N 沉降通过降低底物 C:N 比,提高微生物 CUE^[1,120,136]。长期施肥(N、P、K)减少温带草原土壤微生物呼吸和碳吸收,从而增加 CUE,氮利用率通过影响微生物 CUE 来控制土壤碳循环,而植物群落介导的有机质输入和磷、钾有效性的变化对温带草地微生物碳循环无显著影响^[6]。相对于矿质肥,长期施用有机肥以及有机肥与无机肥的联合施用,可减轻土壤酸化和资源限制,从而提高 CUE 和降低激发效应,促进土壤碳固持^[38,137,192]。长期(5 年)氮添加增加川西亚高山森林植被土壤微生物 CUE,增加幅度与植被类型和氮添加强度有关,暗针叶林较常绿阔叶林增加幅度大,中高氮($20 \sim 40 \text{ kg} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$)添加较低氮($10 \text{ kg} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$)添加增加幅度大,主要与氮添加下土壤化学计量比的不平衡相关^[194]。土壤碳和磷添加的耦合增加澳大利亚东南部 *Paspalum dilatatum* 草地土壤有机碳的损失以及 N_2O 的排放,从而显著影响土壤碳储存^[112],可能原因是当氮利用率较高时,由于获取氮的代谢成本较低,微生物可能会分配更多的碳于生长^[1,6],P 添加可直接减轻微

生物营养的限制^[21]。也有研究发现氮添加对北美草原土壤微生物 CUE 具负影响^[103],施用有机肥土壤具有较低的微生物 CUE 和较高的微生物周转率^[138],而对农田没有影响^[74]。N、P 添加对不同草地土壤中微生物 CUE 和生物量周转时间没有显著影响,验证了地球系统模型中土壤微生物 CUE 恒定参数的假设^[21]。

3.3 温度

温度调节土壤生物因子对微生物生物量、呼吸作用和 CUE 的交互作用^[71]。观测到土壤微生物群落 CUE 对温度升高出现不同的响应,包括增加、降低和无变化^[4,7,77,139]。大多基于微生物短期培养研究认为,土壤微生物 CUE 随温度升高而降低^[8,10,32,48,140];随着温度的升高,农耕地、草地、森林 3 种土地利用类型土壤微生物 CUE 总体上呈增加趋势^[68];我国东部森林带土壤微生物 CUE 与年均温 (Mean Annual Temperature, MAT) 和年均降雨量呈负相关^[141],可能与气候变暖增加现存生物量维持的能量消耗,从而限制微生物生长^[4,7],以及微生物呼吸速率随温度升高的增加幅度大于微生物生长速率等有关^[8,77,142]。随着温度升高 CUE 短期降低或 CUE 季节适应影响土壤呼吸对长期变暖的响应,对于陆地生态系统土壤碳储存具有重要的影响^[8],CUE 下降可能导致高碳存储的森林生态系统土壤损失更多的碳^[143]。

最近从区域到全球尺度的实证研究表明,CUE 随微生物生长环境 MAT 的增加而增加^[12,16,66]。基于微生物-酶模型,结合哈佛大学森林长期生态研究站碳循环观测表明,野外短期土壤增温降低土壤微生物 CUE,而 20 年的土壤变暖增加 CUE 和微生物量周转时间的温度敏感性,土壤碳通量和土壤碳储存对气候变暖的长期响应更依赖于 CUE 的温度敏感性^[19]。基于全球 110 个旱地土壤和两个大陆-全球尺度跨生物群落数据集的 SOC 模型表明,CUE-MAT 正相关关系能更好地模拟土壤异养呼吸观测结果,较温暖的气候更适宜土壤微生物,且群落具有较高 CUE 的微生物^[61]。CUE-MAT 间正相关关系可能受温暖气候下植物碳输入引起较高资源利用率的间接驱动^[12,16,66]。相对呼吸速率,细菌种群增长率对温度的响应更强,在生物学温度范围内,细菌 CUE 对温度呈正响应或无明显的响应^[144]。也有研究表明 CUE 的温度敏感性较低^[48]。生长和呼吸的

耦合响应导致气候变化下稳定的微生物 CUE^[20]。

3.4 土壤 pH 值

微生物 CUE 受土壤 pH 值调节^[128,132]。基于¹⁴C 标记法的澳大利亚西部农业土壤 CUE 测定表明,CUE 与 pH 和可交换性铝 (Al) 显著相关,CUE 在 pH 值 5.5 以上为最大,低 pH 和高 Al 时微生物 CUE 下降反映 H^+/Al^{3+} 胁迫下高能量碳代谢途径^[132]。较高的碳限制和 β -葡萄糖苷酶与亮氨酸氨肽酶活性比值促进土壤微生物 CUE,因而抵消了土壤酸化下 Al、Mn 等金属胁迫对 CUE 的负影响,证实了化学计量在微生物适应土壤酸化中的重要性^[130]。土壤 pH 对微生物 CUE 的影响有两种机制解释,一是通过影响微生物群落组成影响 CUE。酸性土壤中真菌和耐酸微生物丰度通常较高,随着 F:B 比的增加,微生物 CUE 增加^[82,145]。二是通过细胞胁迫影响微生物活性。酸性环境迫使微生物消耗更多能量维持细胞 pH,较少的能量用于生长^[146]。低土壤 pH 下有毒金属如 Al^{3+} 溶解度增加,细胞遭受胁迫^[132],土壤 CUE 降低。

3.5 土壤水分

土壤水分变化影响微生物生长和维持的平衡,因而影响微生物 CUE 和生物量周转时间^[1,147]。由于富碳溶质积累对水分胁迫的适应,微生物 CUE 随着土壤水分利用率的降低而增加^[65]。也有研究表明,干旱土壤 CUE 随着水分胁迫的加剧而降低^[147]。模拟 Atacama 沙漠不同干旱程度下土壤微生物群落对水分和底物碳有效性的响应表明,微生物 CUE 大小依次为极度干旱、干旱、半干旱,一旦水分条件满足,微生物群落对可利用碳作出快速响应,但在极度干旱土壤中响应较微弱,沙漠土壤极度干旱条件下微生物生物量碳周转较慢^[27]。干旱胁迫导致澳大利亚半干旱草原旱季和雨季 CUE 均略有增加,湿润冬季 CUE 远大于干燥夏季,与水分、温度和底物利用率季节性变化引起的微生物群落组成和胞外酶活性的季节变化有关^[148]。CUE 对土壤水分利用率的响应与微生物培养时土壤条件、生态系统或土壤类型有关。土壤水分控制土壤渗透势和底物扩散,影响微生物生长、休眠和死亡,导致活性微生物群落变化^[149]。有限的底物扩散是土壤水分调节土壤中微生物介导的碳氮转化速率和 CUE 的主要物理机制^[150]。

3.6 土壤团聚体与质地

一般而言,土壤有机碳的可分解性随土壤团聚体的减小而降低^[151-152]。团聚体越小的土壤其有机碳存留时间越长^[153]。与矿物结合有机碳在较小的团聚体中更为丰富,通过有机-矿物配合物的形成得以保护,比其他 SOC 组分稳定性更高^[154]。黄土高原中部造林 42 年后,中团聚体有机碳含量最高,表明大团聚体碳比中团聚体中更不稳定,更容易分解^[155]。有机碳在大团聚体中的平均存留时间显著低于微团聚体^[138]。土壤微团聚体中秸秆残体微生物 CUE 高于大、中团聚体,微生物 CUE 与正激发效应(Positive Effect, PE)呈负相关,免耕土壤中秸秆渣输入和微团聚体高营养水平可增加 CUE,但降低 PE^[156]。在高酸性土壤($\text{pH}_{\text{Ca}} < 4.7$)中,添加碱基阳离子可促进微生物生长,提高酸性土壤微生物 CUE 和生物量,促进农业土壤碳固持^[157]。

土壤质地影响微生物对养分的获取。黏土含量高的土壤能束缚更多有机质,但不易于微生物利用,因此周转率较慢^[158]。高黏土土壤具有较高的持水能力,土壤含水量过高将降低分解率^[159-160],黏土含量与 CUE 呈负相关^[72]。

3.7 土层深度

CUE 随土壤深度而不同^[5,66]。CUE 是随着土层深度是增加还是减少存在较大的争议^[5]。土壤碳底物可利用性和质量通常随土壤深度的增加而降低,因此 CUE 可能随深度而降低^[5,66]。除少数例外,C:N 比随土壤深度的增加而降低^[161],因此化学计量比的调节可能导致深层土壤高的 CUE。土壤深度的变化导致真菌与细菌比的变化,进而影响 CUE^[70]。沿湿地—草原—森林水文梯度,CUE、微生物生物量存留时间(Microbial Residue Time, MRT)、 Q_{10} 均随土壤深度的增加而增加,低质量底物在较深土层中分解导致了较高的 CUE^[162]。长期施肥后,随着土壤深度水稻土 CUE 逐渐增加,以 20 ~ 30 cm 土层最高,深层水稻土碳吸收的减少可能被 CUE 增加所补偿,微生物功能策略的变化可解释大量施肥水稻土中 SOC 的积累^[38]。在针叶林和针阔叶混交林土壤中,微生物 CUE 并未随土壤深度呈现出适应性变化,表土层微生物 CUE 与心土层相似,而在牧草地土壤中,心土层微生物 CUE 较表土层低;森林土壤微生物生物量周转时间(turnover time)随土壤深度的增加而增加,深层土壤较低的微生物

碳摄取速率,可能得到较长的微生物生物量碳周转时间的部分补偿^[5]。心土层在全球碳循环中起着至关重要的作用,因为大约一半的全球土壤 SOC 储存在心土层^[163]。与表土层相比,心土层具有更大的碳固持潜力,尤其是黏土含量高的土壤^[161,164]。心土层碳固持潜力取决于 CUE 和 MRT 与温度敏感性的竞争效应,高的 CUE 和长的 MRT 导致碳作为微生物副产物的存留较高,而高的温度敏感性将导致未来 CO_2 分解损失较大^[162]。

3.8 干扰

干扰影响陆地生态系统土壤微生物 CUE。森林干扰长期影响土壤微生物群落结构^[165-166],包括增加细菌优势度和共生营养类群丰度^[167],进而影响微生物介导的森林土壤碳循环^[168]。未遭受干扰的森林土壤通常具有较高的微生物 CUE,主要与微生物平衡生长相关^[169]。森林干扰通过影响土壤 pH、凋落物化学计量比,促进土壤微生物分解代谢活性^[170],增加添加碳底物分解代谢与呼吸碳消耗^[171],受干扰土壤微生物群落 CUE 降低^[172],导致土壤长期碳储存的减少。较强的分解代谢可能是导致森林干扰后土壤可溶性有机碳(DOC)池减少的主要原因^[167]。秸秆还田^[173]、减少土壤耕作^[174]可增加土壤微生物 CUE,增加表层土有机质积累,促进对土壤碳稳定功能的正反馈。

4 问题与展望

国外土壤微生物 CUE 研究大约始于二十世纪八十年代,尤其是近二十年来受到越来越多的关注,主要集中在北美和欧洲^[16,175]。近年来,微生物转化和调控 SOC 形成已成为土壤 SOC 形成和稳定机制关注的前沿^[176],土壤微生物 CUE 及其对环境变化的响应已受到土壤碳循环、全球变化生态学、陆地生态系统模型等研究的广泛关注。土壤微生物碳泵(Microbial Carbon Pump, MCP)机制概念强调土壤微生物同化合成以及 CUE 在土壤有机碳库稳定的作用^[64]。我国土壤微生物 CUE 是近几年才兴起的,主要集中在农田生态系统^[68, 114, 137-138, 156, 177-182],以及少量森林^[117, 71, 141]和草地生态系统^[59, 180]。纵观当前土壤微生物 CUE 研究,主要有以下几个特点:

(1)从土壤微生物 CUE 研究关注的生态系统类型来看,国外研究几乎涵盖所有陆地生态系统类

型^[16],以农田和草地较多^[16,175],并注重农田、草地、灌丛、森林等不同生态系统间的比较与分析。森林以热带森林、温带阔叶林、北方森林、次生林等为主。我国森林土壤微生物 CUE 研究仅见东部森林样带^[71],云南热带、亚热带、温带天然林^[141],华北油松人工林^[117],川西亚高山森林^[193-194]等几例报道。今后应加强森林生态系统尤其是不同森林植被类型及其不同生长发育阶段土壤微生物 CUE 研究。

(2)从土壤微生物 CUE 研究关注的重点来看,大多是单站点、单因素的影响研究,关注重点主要包括真菌和细菌功能群变化、碳底物质量、营养限制、碳氮磷添加和有机肥施用、温度升高、土壤 pH 值、水分、团聚体大小、森林干扰、土地利用变化等对土壤微生物 CUE 的影响。由于复杂的土壤-植物-微生物交互作用,全球变化背景下土壤微生物 CUE 响应与反馈存在较大的不确定性^[183],受众多生物和非生物因素的影响,未来研究应综合探讨环境和生物多要素交互影响下土壤微生物 CUE 的响应过程与机制^[183],深入关注全球变化下根系分泌物对土壤微生物 CUE 以及土壤长期碳固持的影响,根际作为土壤中的微生物热点区,调控着土壤碳循环诸多关键过程,根源活性碳的持续输入可能诱发较高的微生物 CUE,从而导致较高的微生物源碳(微生物生物量和残体)累积,影响土壤有机碳形成与稳定。

(3)从土壤微生物 CUE 研究关注的尺度来看,早期大量研究主要关注种群和群落尺度的微生物 CUE,近期生态系统尺度 CUE_E 变化及其对环境的响应受到更多的关注。种群和群落尺度微生物 CUE 大多不包括微生物残体(necromass)和分泌物(exudates)的再循环,而 CUE_E 整合了 CUE 的所有内部和胞外限制,可反映生态系统视角微生物生物量合成和分解的所有驱动因素,能捕获随时间推移通过微生物生物量周转和呼吸而损失的碳,以及微生物产物/代谢物的回收效率,即微生物残体和分泌物。微生物残体在土壤碳循环和固持潜力中具有重要的作用^[105,184]。从生态系统视角探讨土壤微生物 CUE_E,是今后的发展方向。

(4)从土壤微生物 CUE 的研究方法来看,现有研究大多采用单一的碳同位素标记法或氧同位素示踪法,少数采用化学计量模型法,尚缺乏多种方法的结合与应用。由于土壤微生物 CUE 的不确定性^[1,4],未来应尝试比较不同方法估算 CUE,以从不

同角度认识和理解土壤微生物代谢^[2,16]。

(5)从土壤微生物 CUE 观测土层来看,绝大多数研究关注 0~15(20)cm 表土层,对不同土层深度微生物 CUE 研究较少^[162]。深层土壤在全球碳循环中起着至关重要的作用,全球大约一半土壤 SOC 储存在深层土壤^[163],深层土壤碳固持潜力取决于微生物 CUE 和生物量存留时间与温度敏感性的竞争效应^[162]。现有土壤微生物呼吸(Q_{10R})及 CUE 的温度敏感性研究大多集中在表土层^[185-186]。深层土壤 Q_{10R} 在碳循环模型中至关重要,并受到越来越多的关注^[139,186-187]。今后应加强不同土层 CUE 及其温度敏感性对长期碳储存影响的研究。

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Research Advances in Soil Microbial Carbon Use Efficiency

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Abstract: Soil microbial carbon use efficiency (CUE) is a critical physiological and ecological parameter in measuring soil C cycle and stock under the global change scenarios. It is defined usually as the ratio between carbon (C) allocated to growth and C taken up by microorganisms. It expresses the processes of C retention, turnover, soil mineralization, and greenhouse gas emission. CUE serves as a key regulator of microbial biomass turnover and soil C sequestration. Understanding the variation of soil microbial CUE and its influence mechanism in the context of global environmental change is critical for a better understanding of the partitioning of C between microbial biomass, and soil stock potential, and respiration, and the response of long-term C stock in soil to global changes. Soil microbial CUE and its response to environmental changes have received increasing attention from studies on soil carbon cycle, global change ecology, and terrestrial ecosystem models. In this review, it evaluated the advantages and adaptability of five microbial CUE measurement methods including ¹³C (or ¹⁴C) and ¹⁸O isotope tracing approaches, calorimetry, metabolic flux analysis, and stoichiometric modeling; it summarized the dynamic characteristics of soil microbial CUE with ecosystems, vegetation succession and different seasons; it analyzed the effects of the biological and abiotic factors including microbial community composition, substrate quality and nutrient availability, temperature, soil pH, soil moisture, soil aggregates and texture, soil layer depth, and anthropogenic disturbances on soil microbial CUE. According to the overview of CUE, the research prospect should be extended to: (1) Strengthen the soil microbial CUE research of forest ecosystems; (2) Explore the response process and mechanism of soil microbial CUE under the interaction of environmental and biological factors, especially for the effects of root exudates on soil microbial CUE and long-term carbon sequestration under the global changes; (3) Explore the dynamic of soil microbial CUE from microorganism's ecosystem perspective;

(4) Cross-compare CUE estimates by integrating different methods to capture different aspects of microbial metabolism and improve our understanding of processes controlling CUE variability; (5) Analyze dynamics of microbial CUE at the different soil layers and the influence of the CUE temperature sensitivity on long-term carbon stock in soil.

Key words: carbon use efficiency; soil microorganism; dynamic variation; measurement approach; influencing factor

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黄河流域面积 79.5 万 km²,干流全长 5464 m,流经九省区,是中华民族的“母亲河”,在我国经济社会发展和生态安全方面具有举足轻重的战略地位。依据《黄河流域生态保护和高质量发展规划纲要》划定的黄河水源涵养区以流域 38% 的面积贡献了 84% 的河川径流量,是黄河流域主要水量来源区,但其生态环境脆弱,对气候变化敏感,受人类活动影响显著。强化水源涵养功能是其生态保护中一项关键内容。如何解析水源涵养区水源涵养能力调控阈值,提出提升水源涵养能力的路径和措施成为迫切需要解决的问题。探究水循环要素演变特征及其对水源涵养的影响,或可为水源涵养区水源涵养能力的提升提供依据。

详见本期《黄河水源涵养区近 60a 降水、气温和径流演变及其对水源涵养的影响》一文。