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土壤有机碳分解对温度响应的研究进展

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摘要 土壤是陆地生态系统中最大的有机碳库, 其有机碳分解速率的微小变化即可显著影响大气二氧化碳浓度, 在调节气候变化进程中发挥重要作用. 近年来, 随着全球变暖持续加剧, 土壤有机碳分解对温度变化的响应及其机制受到广泛关注. 本文系统综述了土壤有机碳分解温度敏感性的研究进展, 重点归纳其生物与非生物调控因子、水平空间分布特征、垂直剖面分异规律以及土壤碳分解对温度变化的动态响应与适应过程. 综合现有证据表明, 土壤有机碳分解温度敏感性在时间和空间上均呈显著异质性, 且由微生物过程、底物特性与物理-化学保护等多重机制耦合调控. 未来研究需进一步量化温度敏感性的时空变异及其驱动机制, 将微生物调控过程纳入陆地碳循环模型, 以提高对土壤碳-气候反馈的预测精度, 为实现“双碳”战略目标提供科学支撑.

关键词 土壤有机碳, 土壤碳分解, 温度敏感性, 全球变暖, 碳中和

全球气候变化已成为当前人类社会面临的突出挑战之一. 土壤作为陆地生态系统中最大的有机碳库, 其碳分解速率的微小变动即可显著改变大气二氧化碳(CO_2)浓度, 进而影响气候变化进程[1]. 在此背景下, 厘清土壤碳-气候反馈效应的空间异质性及其调控机制, 是精准预测土壤碳动态的关键, 也是支撑“碳中和”战略实施的重要科学基础[2]. 温度是调控土壤有机碳(soil organic carbon, SOC)分解速率的核心环境因子之一, 其对分解过程的影响通常用温度敏感性参数Q_{10}表征, 即温度每升高10℃时, 分解速率增加的倍数. 作为刻画土壤碳动态的关键参数, SOC分解的温度敏感性直接关系到陆地碳循环及其对气候变化反馈的定量评估[3].

基于此, 本文在系统梳理国内外相关研究的基础上, 重点分析SOC分解温度敏感性的调控因子及在水平空间和垂直土壤剖面上的分异规律, 并进一步讨论SOC分解对温度变化的时间动态响应与适应特征, 评估现有研究的不足与未来发展方向. 本文围绕以下三个核心科学问题展开: (ⅰ) SOC分解温度敏感性受哪些生物与非生物因子调控? (ⅱ) SOC分解温度敏感性在不同气候带与土壤剖面上的空间分布特征如何? (ⅲ) SOC分解对温度变化的动态响应与适应过程表现出哪些规律? 通过系统整合与比较分析, 旨在揭示SOC分解温度响应的关键控制机制, 为深入理解土壤碳-气候反馈过程和改进陆地碳循环模拟提供理论依据.

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1　土壤有机碳分解温度敏感性的调控因素

SOC分解温度敏感性是衡量土壤碳释放对气候变暖响应强度的关键生态参数[1]. 其动态变化不仅反映土壤碳库对气候变暖的反馈潜力, 也直接影响全球碳循环模型的预测精度. 大量研究表明, Q_{10}并非常数, 而是受多种生物与非生物因子共同调控的动态生态过程[4~6]. 深入解析Q_{10}的形成与调控机制, 对于理解土壤碳-气候反馈、优化碳循环模型参数、提高陆地碳汇预测能力具有重要意义[7]. 本文从生物因子(植被类型、微生物群落与碳利用效率)和非生物因子(温度、水分、养分、底物特性及物理-化学保护)两个维度, 概述影响SOC分解温度敏感性的关键机制及其相互作用(图1).

1.1　生物因子

1.1.1　植被类型

植被类型通过调节有机碳输入的数量与质量, 间接影响SOC分解对温度的响应[8,9]. 有机碳输入数量决定微生物可利用碳源的供给强度, 从而影响SOC分解速率及其温度敏感性. 在初级生产力较高、凋落物输入较大的生态系统中, 底物供给相对充足、微生物代谢活跃, SOC分解速率加快, 但对温度变化的响应通常较弱; 相反, 当碳输入较小时微生物代谢受到抑制, Q_{10}往往较高[10,11].

碳输入质量同样决定SOC分解速率与温度响应特征. 植物输入既可通过直接提供易降解碳促进SOC分解, 也可通过“激发效应”(priming effect)间接刺激微生物分解相对稳定的碳组分[12,13]. 升温条件下, 根系分泌物(糖类、有机酸、氨基酸等)往往增强激发效应, 进一步提高微生物活性与SOC分解, 被视为影响Q_{10}的重要“热放大因子”[14,15].

此外, 地上部(凋落叶与枝条)与地下部(根系分泌物与根残体)输入在化学组成和周转速率上存在显著差异. 地上部输入多含木质素、纤维素等结构性碳, 分解较慢、对温度更敏感; 地下部输入则以可溶性和低分子有机物为主, 更易被微生物利用, 对温度变化相对不敏感. 不同植被类型在地上-地下输入比例上的差异, 导致SOC底物质量与可利用性呈系统性变化. 一般认为, 森林生态系统以富含结构复杂组分的地上部输入为主, SOC对温度变化较敏感, Q_{10}较高; 草地生态系统根系发达、地下部输入比例高, 以易分解组分为主, 温度响应相对较弱, Q_{10}较低[16]. 这种地上-地下输入格局的差异在很大程度上塑造了不同生态系统间SOC分解温度敏感性的空间差异.

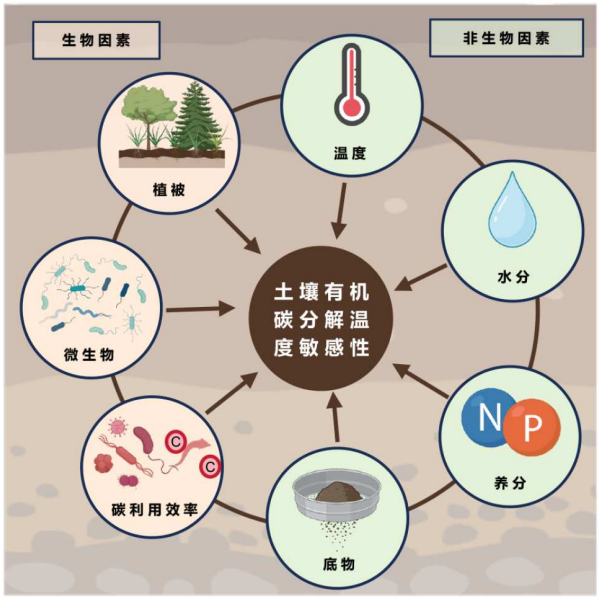


图 1　土壤有机碳分解温度敏感性的调控因子
Figure 1　Regulating factors of the temperature sensitivity of soil organic carbon decomposition

1.1.2　微生物群落组成与活性

微生物是驱动SOC分解的核心生物因子[17~19]. 现有研究普遍认为, 真菌主导的分解体系Q_{10}通常高于细菌主导体系, 这是因为真菌更擅长降解结构复杂、活化能较高的底物, 而细菌偏好简单易分解的底物, 对温度变化的响应较弱[20]. 微生物群落多样性和功能冗余性也会影响Q_{10}: 多样性越高, 群落在应对环境波动时的代谢通路相对较多, 系统整体表现出更高的稳定性与恢复力[21].

胞外酶活性直接反映微生物对有机底物的分解潜力, 其对温度变化的响应可显著影响SOC分解速率和Q_{10}. 研究表明, 酶活性升高往往伴随更高的活化能需求, 从而增强SOC分解对升温的响应[22,23]. 分子生态学研究进一步表明, 与碳代谢相关的功能基因组成与表达水平是解释Q_{10}空间变异的重要生物学基础[24,25]. 其中, β-葡萄糖苷酶、纤维素酶、木质素过氧化物酶和多酚氧化酶等关键酶及其编码基因在不同生态系统中

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的丰度与表达水平差异, 决定了SOC分解活化能与反应速率, 从而在区域尺度上形成Q_{10}的空间异质性.

1.1.3 微生物碳利用效率

微生物碳利用效率(carbon use efficiency, CUE)指微生物将底物碳转化为自身生物量的比例, 是连接碳输入、同化与呼吸损失的关键参数[26]. 温度升高通常导致CUE下降, 使更多碳以呼吸形式释放, 从而提高Q_{10}[27]. CUE受微生物群落结构、底物类型与可利用性以及养分供给等多因子影响[27,28], 在环境因子与SOC分解温度响应之间发挥重要“生理桥梁”作用. CUE常通过稳定同位素标记(如^{13}C或^{18}O示踪)或酶化学计量等方法估算, 为定量评估微生物碳分配提供技术支撑[29]. 将CUE及其调控机制纳入碳循环模型, 有望提高对Q_{10}时空变化的预测能力[26].

1.2 非生物因子

1.2.1 温度

虽然Q_{10}的定义源于温度变化, 但长期环境温度背景对其具有重要调节作用. 大量研究表明, Q_{10}随环境温度升高而降低, 即低温条件下Q_{10}较高, 高温条件下Q_{10}较低[30~32]. 在低温环境中, 微生物活性受限, 升温显著提升酶促反应速率和底物扩散效率, SOC分解明显增强; 而在高温环境中, 微生物活动接近适温上限, 酶活性趋于饱和, 易分解底物逐渐耗竭或碳的物理-化学保护增强, 升温效应减弱, Q_{10}相应下降[1,4,33]. 因此, 温度背景既影响微生物对短期升温的响应强度, 也塑造SOC分解对长期气候变暖的敏感性.

1.2.2 水分

水分通过影响微生物生理活性、酶扩散及氧气供应, 对Q_{10}产生重要调节作用[16]. 在干旱或低水分条件下, 微生物受水分胁迫, 细胞功能受损、水膜不连续限制酶扩散, 升温难以显著促进SOC分解, Q_{10}较低. 适中水分(接近田间持水量)有利于通气与供水平衡, 温度与水分协同增强微生物活性, 使Q_{10}达到较高水平; 极高水分(如淹水)下, 缺氧抑制好氧代谢, 碳分解受限, 温度响应减弱、Q_{10}下降[32,34,35]. 此外, 水分波动还通过影响团聚体结构、矿物-有机质结合和溶解性有机碳迁移等间接过程, 进一步调节温度敏感性[36,37].

1.2.3 养分

微生物对温度变化的响应依赖其代谢水平, 而代谢活动往往受到氮(N)、磷(P)等养分的限制[38]. 然而, 养分增加对Q_{10}的影响尚无一致结论. 一些研究认为, N或P添加可增强微生物活性, 提高Q_{10}[39,40]; 另一些研究则发现, 效应不显著甚至呈抑制作用[41~44]. 这种差异可能与气候带、土壤类型及初始养分状况等背景条件有关[45,46]. 例如, 在热带贫养土壤中, N或P添加常显著增强微生物呼吸, 提高Q_{10}; 而在高纬或富养农田中, 则可能因群落结构改变或底物限制而降低Q_{10}[47,48]. Chen等人[38]对来自我国六种典型森林生态系统的36个样点土壤设置N, P及N+P添加处理, 发现Q_{10}平均分别增加约11.3%, 11.5%和23.9%, 且相较于温带和寒带, 热带和亚热带地区Q_{10}对养分添加的响应更敏感, 提示养分供给水平是影响SOC分解温度敏感性的关键非生物因子之一.

除了养分添加量, 土壤C/N/P化学计量比同样重要. 适宜的C/N或C/N/P比有助于维持微生物营养平衡, 提高碳分解效率; 当C/N偏高或P供应不足时, 微生物合成及能量代谢受到限制, SOC分解速率及其温度响应均降低[38,49,50]. 已有研究表明, 在低C/N比条件下, 微生物倾向于快速利用易降解底物, 呼吸活性和温度敏感性均较高; 而在高C/N比或P限制下, CUE下降, 对升温的响应减弱[51,52].

1.2.4 底物

SOC分解过程高度依赖底物质量与可利用性. “碳质量-温度”假说(carbon quality-temperature hypothesis)认为, 有机质化学稳定性与其对温度变化的敏感性呈正相关: 结构复杂、难降解有机质因活化能高, 对温度变化更敏感, Q_{10}较高; 易降解底物(糖类、有机酸等)反应活化能低, 对温度变化的响应相对有限[27,28,32,53]. 该假说基于酶促反应动力学与Arrhenius方程, 强调“碳质量”通过影响反应活化能, 从而决定SOC分解对温度变化的响应强度.

该假说的适用前提包括: (ⅰ) 分解过程主要受酶促反应控制; (ⅱ) 底物供应相对充足, 未被强烈矿物保护或物理包埋; (ⅲ) 微生物群落处于稳态代谢条件. 在此条件下, 温度变化可直接通过酶动力学调控分解速率, 不同“碳质量”组分的温度响应明显分化[32]. 在碳受限、底物耗竭或矿物保护显著的环境中, 该假说的

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解释力明显下降. 此时, 微生物代谢受限, 升温对SOC分解的促进作用减弱[54]. 部分研究也表明, “碳质量-温度”假说在不同气候带和生态系统中的适用性存在差异[1,4,55]. 总体看, 该假说更适用于底物充足且生化动力学占主导的系统, 而在碳受限或强理化保护条件下需与底物可获取性、微生物代谢策略等因素综合考虑.

1.2.5 物理化学保护作用

土壤物理-化学保护是维持SOC稳定性并调节其温度响应的重要非生物机制[56]. SOC主要通过两条途径受到保护: 一是物理包裹, 即有机质被团聚体或土壤孔隙结构包裹, 限制微生物与酶的接触; 二是矿物结合, 即有机碳与铁、铝氧化物或黏土矿物形成稳定复合体, 从而增强其化学惰性并降低微生物可获取性[57]. 物理-化学保护程度越高, 底物可接近性越低, SOC分解对温度变化的响应越弱, Q_{10}相对较小; 在扰动或保护减弱的土壤中, 底物可利用性提高, Q_{10}随之上升[58,59].

综上所述, 生物因子(植被类型、微生物群落、CUE)与非生物因子(温度、水分、养分、底物特性及物理-化学保护)并非独立作用, 而是在改变碳分解活化能、底物可利用性及代谢途径的过程中耦合调控SOC分解温度敏感性. 生物因子主要通过调节底物输入质量和微生物代谢特征影响反应活化能; 非生物因子则通过环境胁迫或理化保护调节底物可获取性及酶促反应速率. 二者交互作用构成了Q_{10}变化的核心机制框架, 为理解SOC分解温度敏感性的空间异质性奠定基础.

2 土壤有机碳分解温度敏感性的水平空间分布特征

近年来, Q_{10}的空间变异性逐渐成为碳循环研究的前沿问题. 全球尺度模拟表明, 若忽视Q_{10}的空间异质性, 可能低估约25%的土壤碳-气候反馈强度[60]. 不同地理格局塑造了多样的气候条件和土壤性质, 从而影响SOC分解对温度变化的响应. 大量实验证据表明, 温度、水分、有机碳质量和微生物特征是驱动Q_{10}空间变异的关键因子.

非生物因子方面, 温度、水分、有机碳质量及土壤理化性质共同决定碳底物的可利用性与有机碳分解. Li等人[61]对我国203个森林样地土壤进行变温培养, 发现Q_{10}介于2.7~6.2之间, 整体呈由低纬向高纬逐渐升高的趋势, 年均温被认为是主导Q_{10}地理格局的首要因子. Chen等人[62]在湿地生态系统中发现, 不同地点和水分条件下Q_{10}在1.6~6.1之间变化, 强调了水分对Q_{10}调控的重要性. Fierer等人[63]通过对美国77个样点土壤的培养研究发现, Q_{10}平均为3.0(2.2~4.6), 且与采样时大气温度呈正相关、与土壤碳质量呈负相关, 说明气候条件与碳底物特征共同驱动Q_{10}的水平空间变异. 然而, 当前多数土壤碳循环模型仍将Q_{10}视作固定常数[64], 难以准确反映未来气候情景下的土壤碳动态, 这凸显在地球系统模型中纳入Q_{10}空间变异的必要性.

生物因子方面, 微生物群落被认为是调控SOC分解温度敏感性的核心驱动. Pei等人[18]沿我国约5000 km的纬度梯度设置7个土壤采样点, 结合微生物接种实验发现, Q_{10}由低纬向高纬递增, 微生物群落结构是解释其水平空间变异的直接因子. 微生物组成及其功能特征决定酶促反应效率与底物利用途径, 不同生态系统中群落适应性差异可导致SOC分解速率及Q_{10}显著变化.

数据整合研究从更大尺度上进一步揭示了Q_{10}的水平空间格局及其驱动因子. Feng等人[65]整合171个中国草地样点数据, 发现Q_{10}范围为1.0~8.1, 不同草地类型间差异显著, 且Q_{10}与土壤温度呈显著负相关, 与SOC含量及植被生物量呈正相关. Li等人[30]基于全球480个样点构建结构方程模型, 指出年均温是解释Q_{10}水平空间变异的最重要因子, 而降水和土壤属性作用相对较弱. Zhang等人[32]整合21979个培养实验数据发现, 高纬或冻土区等寒冷地区Q_{10}普遍较高. 进一步分析表明, 在碳不受限制时, Q_{10}主要受碳质量调控, 难分解组分对温度变化更敏感; 在碳受限时, Q_{10}主要受碳可利用性约束.

总体而言, SOC分解温度敏感性的水平空间异质性反映了气候因子、土壤理化性质、底物特征与微生物群落在不同环境背景下的耦合调控. 气候因子决定温度与水分的宏观格局, 土壤理化特征与碳质量调控底物可利用性, 微生物群落结构与功能多样性塑造具体的温度响应轨迹. 水平空间尺度上的Q_{10}分布可视为生物-非生物耦合机制在区域乃至全球尺度上的综合表现, 也为后续从剖面视角解析Q_{10}垂直异质性提供了宏观背景.

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3 土壤有机碳分解温度敏感性的垂直剖面分布特征

全球约68%的SOC储存在30~200 cm的深层土壤中[66], 深层土壤在全球碳循环中具有不可忽视的地位. 尽管其碳密度与周转速率低于表层土壤, 研究表明深层SOC并非惰性碳库[67]. 然而, 对四本主流土壤学期刊中1000余篇论文的统计显示, 现有SOC研究的平均采样深度仅约23 cm[68]. 受限于取样和实验技术, 深层土壤对气候变化的响应仍被严重低估. 与此同时, CMIP5模型预测表明, 在未来一个世纪内, 表层与1 m深层土壤的升温幅度大致相当[69], 因此在评估全球变暖背景下陆地碳库变化时必须纳入深层SOC的响应.

SOC含量、化学结构和微生物特征沿剖面发生显著变化. 随深度增加, 持久性有机碳比例升高[70,71], 矿物结合态碳占比增加, SOC稳定性增强、周转速率下降[72,73]. 相较于表层, 深层SOC稳定性更依赖于矿物类型、电荷特性和比表面积等理化因素[74]. 同时, 深层土壤碳输入有限, 微生物生物量与活性降低[17,75], 胞外酶活性普遍下降[76], 呼吸作用减弱[77]. 但单位微生物生物量的酶合成能力未必降低, 部分生态系统中甚至随深度增加[76]; 微生物CUE沿剖面的变化趋势则在不同生态系统间存在差异[78,79]. 植物输入同样在不同土层中发挥重要调节作用: 表层土壤直接接受凋落物和根系分泌物, 底物丰富且周转快, SOC分解更依赖活性有机质和微生物代谢; 深层土壤主要接受根残体和溶解性有机碳输入, 其数量有限、迁移路径长, 更易与矿物结合形成稳定复合体, 从而增强SOC持久性并削弱温度响应[80].

尽管关于表层土壤CO_2通量对温度高度敏感的认识较为一致, 深层SOC的温度响应特征仍缺乏统一结论. 目前研究表明, 控制Q_{10}的主导机制在剖面上存在明显差异(图2). 部分研究指出, 随着深度增加, 矿物结合态和物理保护态SOC比例升高, 从而削弱SOC分解对温度变化的响应[81]. 而根据“碳质量-温度”假说, 深层土壤中富集结构复杂、活化能高的有机碳, 理论上更易表现出较高的Q_{10}[1]. 胞外酶活性温度敏感性在不同研究中也呈现不一致的结果, 有研究认为其与深度无关[82], 也有研究发现随深度增加而下降[83].

当前用于评估剖面Q_{10}的主要方法包括实验室培养、原位增温与模型模拟. 单一实验室研究结果差异较大[84~86], 但荟萃分析表明, 土壤深度与生态系统类型之间存在显著交互: 在森林和永久冻土区, Q_{10}随深度增加而升高[87,88], 而在农田、草地和湿地中这一趋势则不明显[74].

原位增温实验进一步揭示了土壤类型与生态系统特征对Q_{10}垂直变化的调控. 在温带森林中, 不同深度土壤Q_{10}相近或无一致趋势[69,77]; 亚热带森林增温实验则显示, 升温显著加快亚表层碳周转[89]; 在热带火山灰土壤中, 40 cm以下深层土壤对增温响应较弱[90]. 在SPRUCE泥炭地实验中, 增温诱发2 m泥炭剖面大量CO_2和CH_4释放, 但主要来源于表层过程而非深层泥炭分解[91]. Wang等人[92]结合时空替代与元分析发现, 随深度增加, 增温引起的土壤碳损失比例降低, 进一步支持深层SOC对升温相对不敏感的观点. 这些差异主要与不同生态系统中碳底物性质、氧气可得性及微生物活性变化有关. 表层土壤底物充足、根系输入强、好氧环境占主导, 升温直接促进酶促反应与呼吸; 深层土壤中有机质多为矿物结合态或难降解组分, 氧扩散受限、微生物代谢减弱, 对升温响应受限[74]. 在湿地和泥炭地等还原环境中, 增温往往更多促进表层好氧分解或CH_4产生, 而非深层碳矿化. 然而, Li等人[87]基于我国90个典型森林生态系统1 m深度土壤的室内培养实验发现, SOC分解的温度敏感性随土壤深度显著升高, 表明深层土壤碳分解对气候变暖具有更高的敏感性.

总体来看, SOC分解温度敏感性沿剖面的垂直分异, 体现了同一调控机制在不同深度的尺度延伸. 在表层, 活跃的微生物活动与底物周转主导SOC分解, 表现为典型的生物驱动响应; 在深根植物主导、颗粒有机碳丰富或根系输入较多的深层土壤中, 矿物保护与底物限制逐渐成为主要约束, Q_{10}更多受碳质量和理化保护程度共同影响; 而在根系较浅、生物输入有限且矿物保护作用强或长期水饱和的土壤中, 深层SOC对温度变化的响应则更具缓冲性. 这种从生物控制向理化限制的垂直过渡, 为理解SOC分解温度响应的深层机制提供了重要视角.

4 土壤有机碳分解对温度变化的动态响应与适应

SOC分解对温度的响应具有显著时间动态特征.

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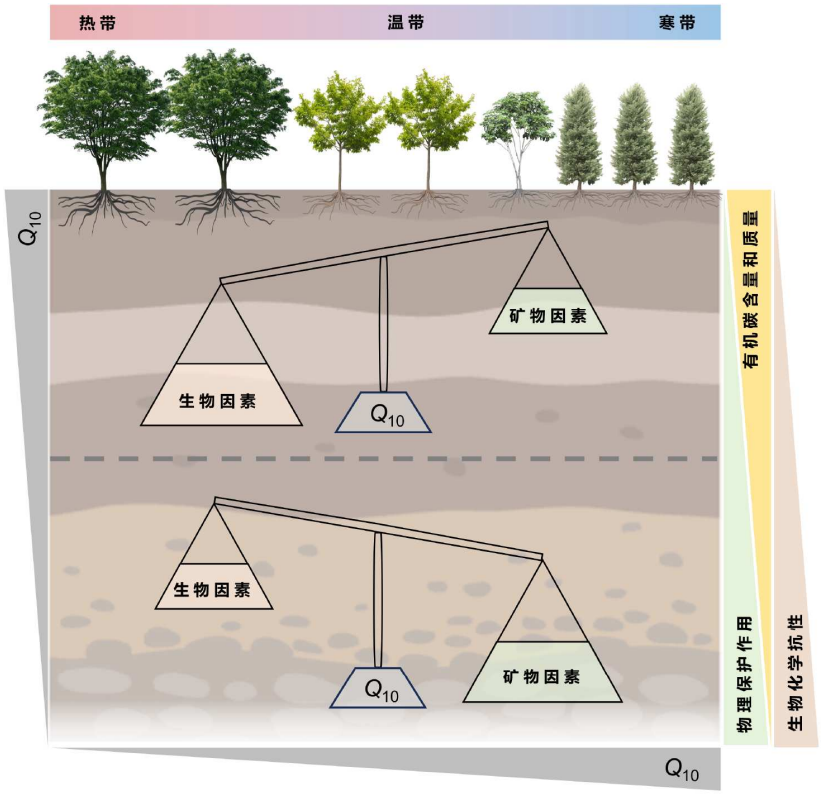


图 2　土壤有机碳性质和碳分解温度敏感性(Q_{10})沿水平空间和土壤剖面的分布特征
Figure 2　The horizontal and vertical patterns of SOC properties and the temperature sensitivity of SOC decomposition (Q_{10})

根据动力学理论，在底物充足且环境无明显胁迫的条件下，SOC分解温度敏感性随背景温度升高而降低[1] (图3)．大量实验室研究也验证了这一趋势，如Leifeld和Fuhrer[93]发现，培养温度从15~25℃升至25~35℃时，Q_{10}由5.2降至2.8．Hamdi等人[94]通过荟萃分析亦表明，Q_{10}与活化能(E_a)均随温度升高而下降．全球增温实验整合分析显示，模拟增温可使土壤呼吸Q_{10}平均降低13%[95]．但也有研究认为，增温对Q_{10}影响不显著，如Carey等人[96]对全球26个增温实验数据分析发现, 增温并未显著改变土壤呼吸温度敏感性，提示实际生态系统中温度响应远比理论模型更复杂．

在不同时间尺度上，SOC分解对温度的响应可大致区分为“调节(regulation)”和“适应(adaptation)”两个层次：前者主要指短期温度波动下微生物和生态系统的即时响应，如酶促反应速率、底物可利用性及水分反馈等；后者则反映长期增温背景下群落结构和功能的调整与优化，包括代谢通路重组、膜脂修饰和热激蛋白表达等生理适应过程．调节过程多具有可逆、快速的特征，而适应过程则相对缓慢且持久．二者共同塑造SOC分解对温度变化的时间动态，也有助于理解“表观热适应”现象的形成：短期调节更多由环境因子驱动，而长期适应则依赖微生物群落的功能重构与演化．

4.1　长期增温下的“表观热适应”

长期气候变暖引起一系列物理、化学与生物过程联动，驱动SOC分解对温度响应发生时间上的“再调节”．大量田间增温实验表明，虽然短期增温显著提高SOC分解(平均提升约7%~15%)，但其促进效应往往随时间递减[95,97~100]，即所谓“表观热适应”．在俄克拉荷马草原增温实验中, Luo等人[101]发现, 增温对土壤呼吸的促进效应有限，且增温处理的Q_{10}低于对照．哈佛森林长期增温实验中，Melillo等人[102,103]将土壤呼吸响应划分为“初期促进且逐年减弱-相对平稳-再次增强-最终下降”四个阶段[104]，展示了长期增温下SOC分解的复杂动态．

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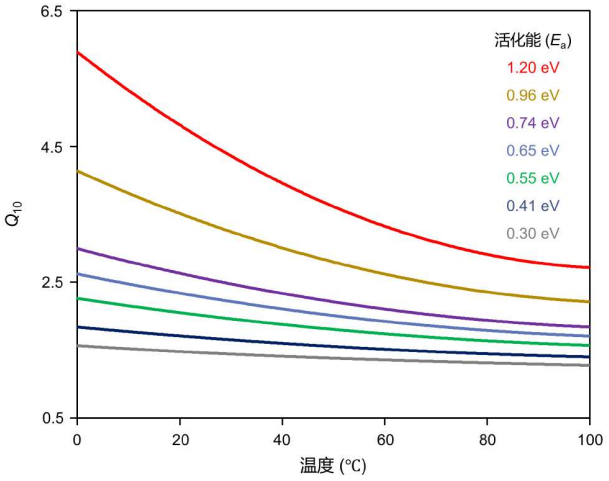


图 3 温度、活化能和土壤有机碳分解温度敏感性(Q_{10})之间的关系(根据Arrhenius公式$R_s = Ae^{-\frac{E_a}{RT}}$建模)

Figure 3 Relationship among temperature, activation energy, and the temperature sensitivity of SOC decomposition (Q_{10}) (modeled based on the Arrhenius equation $R_s = Ae^{-\frac{E_a}{RT}}$)

跨气候带的地理尺度研究从“时空替代”角度上进一步支持SOC分解的适应性调节. Giardina和Ryan[105]指出, 不同气候带森林土壤的碳周转时间差异并不显著, 提示温度并非决定碳周转速率的唯一因素. Sistla等人[106]在北极苔原20年增温实验中未观察到SOC显著变化, 多项增温实验综合分析也发现模拟增温对土壤碳库的净影响有限[98,107]. 关于微生物呼吸的热适应, 研究普遍发现单位微生物呼吸速率与年均温呈负相关[108~110], Alster等人[111]则发现呼吸最适温度(T_{opt})和拐点温度(T_{inf})随背景温度升高而上移, 进一步表明, 土壤微生物呼吸存在明显热适应性. Li等人[110]基于我国森林与高寒草地共298个土壤样品的室内培养实验, 发现微生物最小呼吸温度(T_{min})随年均温升高而显著升高, 揭示了土壤微生物呼吸热适应性的显著地理分异格局, 表明微生物呼吸过程适应其长期所处的温度环境.

4.2 表观热适应的驱动机制

SOC分解对长期增温的适应性响应是生态系统“外部限制”和微生物“内部调节”共同作用的结果. 在生态系统层面, “底物耗竭”是经典解释之一: 增温加速易分解SOC周转, 使底物质量与可利用性逐渐下降, 土壤呼吸和Q_{10}随时间降低[112,113]. 增温引起的土壤干燥也会抑制微生物活性, 对SOC分解形成负反馈[96,114]. 此外, 增温通过改变氮有效性、植物群落组成和凋落物性质等间接调控SOC分解[115]. Luo等人[101]在草原实验中观察到增温初期碳释放迅速增强而后趋于稳定, 很好地印证了底物耗竭的作用.

在微生物层面, 群落组成重组和生理功能调节是热适应的重要途径. 微生物可通过“物种筛选”实现对增温环境的群落优化, 或通过膜脂改组、增强酶热稳定性和热激蛋白表达等生理机制提高耐热性[116~118]. 部分长期增温试验提示, 微生物群落可能发生进化性适应, 形成更高效的代谢通路以降低单位碳损失. Bradford等人[108]在跨气候带研究中发现, 长期处于较高温度条件下的微生物单位生物量呼吸速率下降、代谢效率提升, 直接支持热适应机制.

目前关于底物耗竭与微生物适应在热响应中的相对贡献仍存在争议. 模型研究常认为仅考虑底物耗竭即可解释Q_{10}下降[119], 但也有实验发现, 即便在底物供应充足条件下, 长期增温后微生物呼吸仍下降[3], 表明热适应具有独立作用. 总体上, SOC分解的“表观热适应”更可能是多过程耦合的综合结果, 不同生态系统中主导机制的权重受底物供应、群落结构与环境背景共同影响. 哈佛森林试验提出的四阶段响应模式[102]综合体现了底物耗竭、微生物演替与养分限制的交互作用.

因此, 底物限制与微生物热适应并非相互排斥, 而是在不同时间尺度上共同塑造SOC分解对增温的响应: 短期响应主要受底物可利用性和酶动力学调控, 长期响应则更多反映群落重组与代谢适应. 生物与非生物因子通过影响反应活化能、代谢通路与群落结构, 决定SOC分解温度响应的时间轨迹, 也构成陆地碳循环预测中的重要不确定性来源[120]. 未来研究亟需通过长期、多因子交互控制实验, 结合多组学与稳定同位素示踪, 系统解析热适应的过程网络, 并将关键微生物参数纳入地球系统模型.

5 总结与展望

SOC分解对温度的响应是土壤碳-气候反馈过程的关键环节, 对气候变化背景下土壤碳库的稳定性和动态具有深远影响. 随着实验方法与模拟手段的不断发展, 关于温度敏感性的形成机制和空间异质性方面已取得了重要进展. 本文综述了相关研究, 重点总结

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了生物因子(植被类型、微生物群落、CUE)和非生物因子(温度、水分、养分、底物特征及物理-化学保护)对SOC分解温度敏感性的影响机制. 现有研究表明, 这些因子通过“碳质量-温度”关系、不同碳库对温度响应差异等途径发生耦合, 形成多层次、多过程交织的调控网络. 在此框架下, 学界初步揭示了Q_{10}在全球尺度上的显著水平空间异质性, 并识别出沿土壤剖面的垂直分布特征, 尤其是在强矿物保护和深根系统共存的深层土壤中, SOC对温度的响应规律明显有别于表层, 应引起更多关注.

尽管如此, 当前研究仍面临若干关键挑战:

(1) 实验设计与尺度局限. 多数增温实验在时间上偏短、空间上偏局地, 难以代表生态系统长期响应和区域异质性. 未来应依托联网增温平台和土壤剖面增温装置[121], 结合长期监测数据, 通过多站点、多情景的综合分析提高结论的可推广性.

(2) 微生物调控机制解析不足. 现阶段研究多侧重DNA水平的群落结构与功能潜力分析, 难以区分“潜在功能”与“实际活性”. 未来有必要加强转录组层面的功能基因表达追踪[122], 并引入稳定同位素探针等技术[31], 在“基因-群落-过程”多层级上解析微生物调控SOC分解温度响应的机理.

(3) 模型参数化与尺度集成有待加强. 现有碳循环模型在参数精细化与动态预测方面仍显不足, 往往忽视土壤空间异质性、剖面层次性以及碳输入与分解之间的时滞效应. 未来模型应在两方面同步推进: 在机制层面, 将微生物驱动过程纳入SOC分解建模框架, 重点引入CUE、酶活化能动态变化及微生物热适应等过程参数, 推动从经验温度响应函数向过程模型转变, 并利用长期观测、同位素示踪与组学数据对参数进行约束与不确定性评估; 在尺度集成层面, 构建“微生物-群落-生态系统-区域”多层级过程映射与参数传递机制, 结合长期监测、遥感与机器学习等手段, 实现Q_{10}参数的区域化校正与动态更新. 在气候变化情景下, 未来研究还需结合共享社会经济路径(SSPs)与典型浓度路径(RCPs)开展SOC温度响应模拟[47], 系统评估不同情景下土壤碳库变化及碳-气候反馈的时空演变. 通过机制深化与模型改进相结合, 有望提高区域和全球尺度碳循环预测的可靠性, 为制定土壤碳管理策略和推进国家“碳中和”目标提供坚实的科学基础.

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Progress in understanding the temperature sensitivity of soil organic carbon decomposition

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Soil is the largest organic carbon reservoir in terrestrial ecosystems, and even subtle changes in the rate of soil organic carbon (SOC) decomposition can markedly alter atmospheric CO_2 concentration, thereby influencing the trajectory of climate change. In recent years, with ongoing global warming, increasing attention has been paid to the temperature response of SOC decomposition and its underlying mechanisms. This paper provides a systematic review of advances in the temperature sensitivity of SOC decomposition, with a particular focus on biotic and abiotic controls, horizontal spatial patterns, vertical profile heterogeneity, and the dynamic responses and adaptive processes of SOC decomposition to temperature change. Synthesizing current evidence, we show that the temperature sensitivity of SOC decomposition exhibits pronounced spatiotemporal heterogeneity and is jointly regulated by microbial processes, substrate properties, and physico-chemical protection mechanisms. Future research should further quantify the spatiotemporal variability of SOC decomposition temperature sensitivity and its drivers, and explicitly incorporate microbially mediated processes into terrestrial carbon cycle models, in order to improve predictions of soil carbon-climate feedbacks and provide a stronger scientific basis for achieving carbon neutrality targets.

soil organic carbon, soil carbon decomposition, temperature sensitivity, global warming, carbon neutrality

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