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氮沉降增加情景下植物-土壤-微生物交互对自然生态系统土壤有机碳的调控研究进展

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摘要:大气氮沉降增加倾向于促进受氮限制陆地生态系统地上生物量,但是对地下碳过程和土壤碳截存的影响结果迥异,导致陆地生态系统“氮促碳汇”的评估存在很大的不确定性。大气氮沉降输入直接影响微生物活性或间接影响底物质量,改变凋落物和土壤有机质(SOM)的分解速率和分解程度,进而影响土壤有机碳(SOC)的积累与损耗过程。过去相关研究主要集中在土壤碳转化过程和碳储量动态方面,缺乏植物-微生物-SOM 交互作用的理解,对土壤碳截存调控的生物化学和微生物学机理尚不清楚。本文以地下碳循环过程为主线,分别综述了氮沉降增加对植物地下碳分配、SOC 激发效应、微生物群落碳代谢过程的影响,深入分析 SOM 化学稳定性与微生物群落动态的关系。该领域研究的薄弱环节体现在:①增氮倾向于降低根系的生长和周转,对根际沉积碳分配(数量和格局)的影响及驱动因素不明确;②虽然认识到氮素有效性影响土壤激发效应的方向和强度,但是氧化态 NO_3^- 和还原态 NH_4^+ 输入对有机质激发效应的差异性影响及潜在机理知之甚少;③微生物碳利用效率(CUE)是微生物群落碳代谢的关键表征,能够很好地解释土壤碳的积累与损耗过程;由于缺乏适宜的测定方法,难以准确量化土壤微生物的 CUE 及微生物生物量的周转时间;④增氮会抑制土壤真菌群落及其胞外酶活性,对细菌群落组成的影响尚未定论,有关 SOM 化学质量与土壤微生物群落活性、组成之间的耦合关系尚不清楚。未来研究应基于长期的氮添加控制实验平台,结合碳氧稳定性同位素示踪、有机质化学、分子生物学和宏基因组学等方法,深入分析植物同化碳的地下分配规律、微生物碳代谢和周转、有机质化学结构与功能微生物群落的耦合关系等关键环节。上述研究将有助于揭示植物-土壤-微生物交互作用对 SOC 动态的调控机制,完善陆地生态系统碳-氮耦合循环模型,有效降低区域陆地碳汇评估的不确定性,并可为陆地生态系统应对全球变化提供科学依据。

关键词:大气氮沉降;地下碳分配;有机质稳定性;激发效应;碳素利用效率

Regulation of plant-soil-microbe interactions to soil organic carbon in natural ecosystems under elevated nitrogen deposition: A review

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Abstract: Increased atmospheric nitrogen (N) deposition generally promotes aboveground biomass in N-limiting terrestrial ecosystems, but the effects on underground carbon (C) processes and soil C sequestration remain controversial. This leads

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to considerable uncertainties in the evaluation of the C sequestration capacity caused by N deposition in terrestrial ecosystems. Atmospheric N deposition affects soil organic C (SOC) accumulation and depletion by directly changing microbial activity and/or indirectly changing substrate quality, and thereby changing the soil organic matter (SOM) decomposition. Previous research primarily focuses on soil C transformation processes and storage dynamics; however, limited information is available on the interaction among plants, microorganisms, and SOM, especially the biophysical and biochemical mechanisms involved in regulating plant-microorganism-SOM interactions with soil C sequestration. In this review, we summarize the effects of elevated N deposition on plant belowground C distribution, SOC priming effect, and microbial C metabolism, and analyzed the relationship between SOM chemical stability and microbial community dynamics. We identified a number of research topics which are in urgent needs of mechanistic investigation in the following decades: first, increased N input tends to reduce root growth and turnover, but the effects on C allocation in rhizosphere and associated mechanisms are unclear; second, although N availability can affect the direction and magnitude of the SOM priming effect, the contrasting effects of oxidized NO_3^- and reduced NH_4^+ and the potential mechanisms on SOM priming effect are far from certain; third, microbial C use efficiency (CUE) is a crucial characterization of C metabolism of microbial communities, the bottleneck process for soil carbon emission. It is challenging to accurately quantify the microbial CUE and microbial turnover time owing to a lack of appropriate measurement methods; fourth, increased N input inhibits the activities of soil fungal communities and their extracellular enzymes, but the effects on the activity and composition of the soil bacterial community are inconsistent; moreover, the association between SOM chemical quality and soil microbial activity and composition is elusive. Therefore, we call for a long-term N control experiment platform to fully investigate the above-mentioned topics in a systems perspective. The most advanced techniques, such as stable C and oxygen isotopic tracer, organic matter chemistry, molecular biology, and macro genomics, will be used to analyze the belowground allocation of the plant-assimilated C, microbial C metabolism and turnover, and coupling between the SOM chemical structure and microbial functional groups. This long-term experiment could help understand the mechanism of plant-soil-microbial interaction and its contribution to SOC dynamics, improve the soil carbon models, and reduce the uncertainty of regional C sink assessment, and further lay a cornerstone for scientific managing terrestrial ecosystem in a changing world.

Key Words: atmospheric nitrogen deposition; belowground C allocation; soil organic matter stability; priming effects; carbon use efficiency

当前全球碳循环研究中的一个关键科学问题是“失踪碳汇”(missing C sink)的分布与驱动机制[1]。过去150年,人类活动导致大气氮沉降增加了3倍[2],显著提高了受氮限制的陆地生态系统碳储量,是正确解释“失踪碳汇”的重要途径[3]。然而,目前有关氮沉降驱动陆地生态系统固碳的效率以及时空格局还存在很大的不确定性,不同学者估计的“氮促碳汇”变化范围为16—400 kgC/kgN[4-11]。相对于植被碳汇,有关氮沉降增加情景下土壤碳储量的演变方向也存在分歧,包括增加[12]、降低[13]和不变[14]等3种结论。增氮引起土壤碳汇增量变化范围为0—70 kgC/kgN [7, 15-17],同样存在很大的不确定性。

大气氮沉降输入提高生态系统氮素的可利用性,直接改变土壤微生物群落的数量和组成,抑制根系和凋落物分解的速率和程度[18],进而增加或降低土壤有机质(SOM)的储量和稳定性[19];另外,大气氮沉降输入提高植被生产力,改变凋落物产量和生化属性[20],通过底物可利用性来调节土壤微生物群落的结构和功能[21],间接影响SOM的累积速率(图1)。土壤有机碳(SOC)库对增氮的响应取决于生态系统类型[22]、土壤深度[23]、SOC组成[24]、施氮类型和剂量[25]等要素。就植物-土壤-微生物群落系统而言,增氮会自上而下改变SOC的周转过程与稳定性,理论上会产生以下4种影响:①外源性氮输入会改变植物同化碳的再分配,根际沉积碳的数量和质量的变化进而影响活跃微生物群落组成[26];②氮素有效性增加会抑制微生物胞外酶活性,降低微生物群落获取碳源的能力,提高其碳素利用效率[27];③氮素富集会改变微生物群落之间的交互作用和竞

争关系,进而改变分解微生物群落的组成[28];④氮素富集会降低凋落物的分解速率和程度,增加类木质素化合物的氧化程度和稳定性,进而促进 SOM 的积累[29]。然而,上述 4 个科学假设缺乏系统的实验验证,其内在的微生物分子生态学机理未得到很好的理解,也没有被融入到当前主流的生物地球化学模型之中[30]。

过去 30 年,尽管自然陆地生态系统对大气氮沉降增加的响应研究得到了充分的重视,但是主要侧重于生态系统碳氮转化过程与土壤碳储量动态,缺乏植物-土壤-微生物群落的交互作用及其调控机制的研究,对 SOC 积累与损耗的微生物学机理研究也不够系统深入。探讨植物-土壤-微生物群落三者交互作用及其对土壤碳储量动态的调控作用,研究有助于完善陆地生态系统碳-氮循环耦合模型,深入认识 SOC 截存与损耗的机理,有效降低区域陆地“氮促碳汇”评估的不确定性,并可为陆地生态系统应对全球变化提供科学依据。鉴于此,本文以地下碳循环过程为主线,分别综述氮富集对植物地下碳分配、SOC 激发效应、微生物群落碳代谢过程的影响,深入分析 SOM 化学稳定性与微生物群落动态的关系。论述过程中我们试图标注各个领域的薄弱环节,明确未来可能的研究重点,期望起到抛砖引玉的效果。

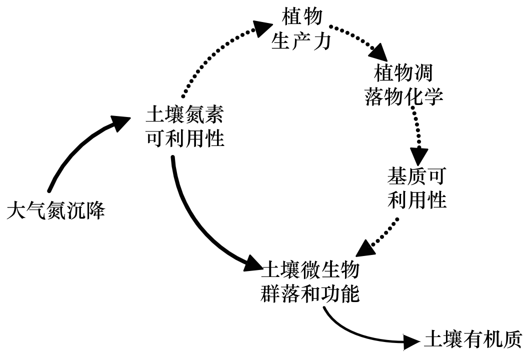

图 1　氮沉降对自然生态系统植物和微生物群落的影响

Fig.1　Effects of nitrogen deposition on plant and microbial communities in natural terrestrial ecosystems

实线为直接影响,虚线为间接影响

1　增氮对植物地下碳分配的影响

在自然生态系统(森林和草地)中,细根生产支配着地下净第一性生产力(BNPP),根源碳对 BNPP 的贡献约为 40%—60%,如果不考虑根际沉积会显著低估 BNPP[31]。增氮通常促进植物生长和地上生物量的积累,GPP 不同组分间的权衡关系以及异速生长约束支配着这一分配格局[32]。增氮对地下碳分配的影响不一致[33-34]。增氮能够刺激[35]、抑制[36]或不影响[16]根系动态,根系对增氮的非线性响应取决于生态系统的氮饱和阶段[37]。Meta 分析结果表明,增氮显著增加所有生态系统根系现存碳储量[34],如果不包括农田生态系统,施氮增加根系碳输入的幅度较小[33]。根据最优碳分配理论,当受氮限制时,植物投资更大比例的碳到根系中以获取更多的氮;而当氮丰富时,增氮会降低植物分配到根系碳的比例。此外,增氮还会显著降低根系的生长和周转速率,暗示地下碳截存潜力将下降[38]。不同的氮类型对根系碳分配的影响存在一定的差异,NO_3^--N 富集会减少侧根的生长,对根系碳分配的抑制效应更大[39]。根系碳周转对增氮的响应符合成本-效益理论,只要获取养分的效益超过维持自身存活的碳成本时,根系活性就能维持[40]。因此,土壤氮素有效性增加会提高根系的氮吸收速率和代谢活性,但是根系生命周期会变长,周转速率降低[35]。

土壤微生物生长在很大程度上依赖于植物源有机碳。植物通常以根际沉积物的形式为根际微生物提供碳源。根际沉积物包含渗出物(如小分子有机酸、氨基酸和糖)、分泌物(如酶)、细胞死亡的溶出物以及粘液[41]。尽管根际沉积物在植物碳归还量中所占的比例较小,但对根际微生物群落影响巨大[42]。菌根是联系植物与土壤的桥梁和纽带。外生菌根(ECM)的土壤碳固持作用一般强于丛枝菌根(AM)。植物向外生菌根真菌投入更多的光合产物,且外生菌根残余物富含难分解的化学物质,有益于土壤碳持留[43];此外,外生菌根真菌吸收有机氮,致使腐生微生物受氮限制,进而抑制 SOC 的分解[44]。通常 ECM 样地(凋落物、土壤富含有机氮,C/N 宽)和 AM 样地(凋落物、土壤库富含无机氮,C/N 窄)对增氮的响应不同,生态化学计量学是响应的主要驱动力。增氮倾向于降低 ECM 样地土壤微生物获氮酶的投资(相对于获碳酶而言),增加氮矿化速率,降低微生物碳需求;相反,增氮不影响 AM 样地异养微生物的活性,增加土壤净硝化和 NO_3^- 的移动性[45]。除了改变根际微生物群落活性,增氮还会改变根际碳沉积。利用原位 $^{13}CO_2$ 脉冲标记技术,Curry 等[26]研究发

现增氮促进苏格兰泥炭地植物叶片碳固定,但是光合同化碳的地下分配取决于植物功能型,总体上降低向根系分泌物中转移的碳量,植物表现出明显的保守性。基于^{14}C-CO_2标记实验,Ge 等[46]研究发现施氮增加水稻茎和根系生物量,促进光合同化碳向根际和 SOC 的转移。上述有限、迥异的结果表明,目前我们对增氮条件下不同植物功能群同化碳的地下分配规律缺乏明确的认识,特别是根际碳沉积与微生物群落组成对氮素类型是否存在差异性响应,以及两者交互作用如何调控 SOC 储量动态。

2 氮素有效性对 SOC 激发效应的影响

增加凋落物的输入会降低土壤碳库,该现象称为“激发效应”[47]。激发效应是由于外源底物的添加激活土壤中的微生物,促进它们对 SOM 的分解。根据激发方向可分为正激发和负激发效应,根据有无机质参与可分为表观激发和真实激发[48]。当添加的外源底物远低于微生物量时,由于微生物自身内部代谢和周转导致 CO_2释放的过程,并不涉及 SOM 周转,因此表观激发对土壤碳库没有影响。但是当添加的底物剂量远高于微生物量时,微生物优先利用外源底物的能量,降低对 SOM 的分解,因此会出现负激发。随后,当外源底物的能量耗尽之后,促使被激活的微生物分解 SOM 来获取所需的养分和能量,从而产生正激发。基于全球培养实验的集成分析,发现正激发效应可促使有机质分解增加 3.8 倍,而负激发效应导致 SOM 分解减少 50%[49]。激发效应的产生机制主要包括:①共代谢理论[50];②底物偏好理论[51];③氮挖掘理论[52];④化学计量学理论[53]等。正激发产生机理以微生物激活作用、微生物竞争与演替、养分挖掘和化学计量学为主,而负激发产生机理以底物偏好利用和毒害作用为主。微生物的种类和大小[51]、植物类型和物候[54]、土壤动物对微生物的取食[55-56],均会影响激发效应的强度。非生物因素如底物质量[57]、数量[58]和土壤属性(温度、水分、土层、养分状态)也会影响微生物群落对底物的利用,进而影响激发效应的强度和方向[59-62]。

外源底物添加造成的激发效应的强度和方向主要取决于不同微生物在不同养分有效性下的竞争作用。土壤中包括 r 策略和 K 策略两种功能迥异的微生物种群,r 策略主要利用新添加的底物,能够利用有限的资源快速生长繁殖;K 策略微生物能量来源于 SOM 分解,生长缓慢。在低氮有效性的条件下,K 策略微生物在竞争中处于优势,微生物会迅速利用底物的能量合成胞外酶,分解 SOM 获取必需的养分。在高氮有效性条件下,r 策略微生物生长更迅速,添加的外源底物满足微生物的化学计量平衡,增加微生物对养分的需求,此时 r 策略微生物起主导作用[63]。在土壤氮素有效性较低的条件下,微生物的活性较低,添加氮素后微生物迅速利用氮素保持自身的化学计量平衡,增加微生物活性和胞外酶的分泌,产生正激发效应促进 SOM 分解[64]。相反,在富氮或氮饱和条件下,微生物会优先利用相对易分解、新添加的底物,产生负激发效应,抑制 SOM 分解[51]。施氮能够降低或增加 SOM 的激发效应。Hartley 等[65]研究发现,单独添加葡萄糖显著刺激亚北极 SOM 分解,产生正激发效应;而同时添加硝酸铵和葡萄糖时,显著降低了激发效应的强度,体现的是微生物氮的挖掘机制。在添加两种不同质量的亚热带森林叶凋落物(杉木和桤木)后,Zhang 和 Wang[66]也发现激发效应的强度具有显著性差异,添加无机氮导致两种凋落物的激发效应强度出现不同程度的降低。相反,Chen 等[53]研究指出,同时添加蔗糖和无机氮造成的激发效应显著高于单独添加蔗糖造成的激发效应,化学计量学理论能够很好地解释这一现象。实际上,氮的挖掘理论与化学计量学理论并不矛盾(图 2)。在氮素有效性较低时,激发效应主要取决于 K 策略微生物,此时激发效

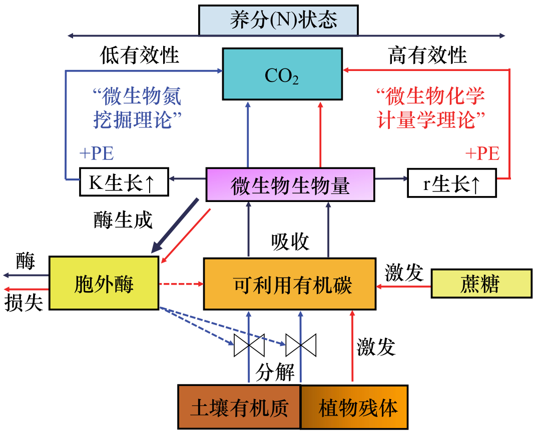

图 2 养分挖掘理论与化学计量学理论关系[53]

Fig. 2 The relationship between nutrient mining theory and stoichiometry theory[53]

PE 为激发效应(priming effect)

应可以用氮的挖掘理论来解释，而化学计量学理论可解释 r 策略微生物的生长。尽管我们对激发效应的产生机制和影响因素已有一定的了解，但是有关不同形态氮素（NH_4^+ 和 NO_3^-）与不同来源底物（根系分泌物、凋落物）的交互作用对 SOM 激发效应的调控机理缺乏深入的分析，在深层土壤碳库影响的定量化方面仍然存在很大的不确定性。

3 增氮对微生物群落碳代谢的影响

微生物碳利用效率（CUE）是指分配给微生物生长所用有机碳与微生物群落组成所吸收的有机碳之比，它是微生物群落碳代谢的一个重要的综合指标[67]。理论上，微生物 CUE 被热力学限制在 0.88[68]，即微生物吸收的碳用于生长的部分不会超过 88%，因为微生物至少需要 12%的碳用于呼吸产生能量以维持其自身的生物量。然而，由于环境条件的限制，微生物生长和生物量的维持需要超过其最小的能量投入，土壤微生物 CUE 未达到理论上的最大值[69]。土壤生源要素化学计量学、底物质量、微生物群落组成均会影响微生物 CUE。在养分限制条件下（高碳/养分比），微生物被迫分配较多的碳和能量以获取所需养分，土壤呼吸 CO_2 排放较高，导致微生物 CUE 较低[67, 69]。当外源性底物的 C∶N∶P 比与微生物生物量 C∶N∶P 比（60∶7∶1—42∶6∶1）差异较大时，微生物必须分配更多能量生产胞外酶来获取缺失元素以维持其生物量；同时更多同化碳被用于微生物呼吸，导致微生物 CUE 下降[67, 69]。因此，养分富集农田土壤的微生物（尤其是细菌）生长效率普遍高于受氮限制的森林和草地土壤[70]。此外，碳和养分的可利用性也会影响微生物生物量的周转[71]。微生物 CUE 和土壤微生物生物量周转时间可能受有机碳浓度和质量的影响。降解复杂化合物需要多种胞外酶，而酶的合成需要消耗大量的能量和氮，所以降解复杂底物的微生物 CUE 较低[72]。由于微生物通过不同的代谢路径来同化不同类型底物，导致单位质量的同化碳具有不同的呼吸速率[73]。因此，植物类型、微生物群落组成以及不同来源的凋落物也会间接地影响微生物 CUE，真菌的 CUE 一般高于细菌[74]。目前测定微生物 CUE 的方法主要是基于 ^{13}C 标记底物，然而不同底物的微生物 CUE 差异巨大，该方法混淆了微生物碳利用效率与特定底物的利用效率[75]。最近，Spohn 等[76]建立了基于 ^{18}O-H_2O 标记技术计算微生物 CUE 的新方法，根据 ^{18}O-DNA 的增加量来计算土壤微生物的生长速率，再结合基础呼吸速率和微生物数量，可计算出微生物 CUE 和周转时间。

野外观测和模型模拟结果表明，施氮降低微生物活性、SOM 分解和 CO_2 排放[77-80]。施氮可能通过改变微生物群落活性和组成[81-82]以及底物的化学性质（如可分解性）来抑制土壤微生物呼吸，与微生物 CUE、胞外酶活性以及微生物生物量的变化有关[27]。其理论假设是：（1）氮限制条件下，增氮会导致更多的碳向微生物分配，而不是通过呼吸和胞外酶损失，导致微生物 CUE 增加，呼吸降低[69]，这可能与微生物群落组成向高 CUE 转变有关[83]。（2）增氮抑制了降解复杂底物（如木质素）的氧化酶活性。例如，增氮降低了北美温带森林土壤酚氧化酶活性[22]、木质素降解相关的功能基因丰度和基因表达[84]。（3）增氮通过减少分解微生物的生物量而降低呼吸[33]。增氮导致土壤酸化，增加 Ca^{2+}、Mg^{2+} 等阳离子的溶解与流失，土壤溶液中 Al^{3+} 浓度增加，对微生物产生毒害作用[85]。此外，土壤酸化也会抑制微生物胞外酶活性，金属离子的键合增加有机质中碳的稳定性，降低微生物获取碳的能力，进而降低微生物生物量和分解速率[86-87]。尽管已经对氮素富集条件下土壤微生物碳的代谢过程和响应格局做了一些探讨，但是氮素类型和剂量如何差异性地影响微生物碳代谢功能还不得而知；由于缺乏合适的测定方法，氮沉降增加情景下自然陆地生态系统土壤微生物碳利用效率及微生物生物量的周转时间尚未得到准确的量化。

4 SOM 化学稳定性与微生物群落动态的关系

SOC 是由不同分解阶段、不同驻留时间的有机质组分构成的混合物。森林和草地生态系统 SOC 储量和组成对增氮的响应呈现非线性，取决于生态系统类型、施氮剂量、施氮类型以及持续时间。例如，Malhi 等[88]研究发现，低剂量氮输入增加 SOC 和轻组碳（LF-C）含量，施氮剂量为 336 kg N hm^{-2} a^{-1} 和 224 kg N hm^{-2} a^{-1}

时,表层和亚表层 SOC 和 LF-C 含量分别达到最大值,随着施氮剂量的持续增加 SOC 和 LF-C 反而下降。基于 SOM 物理分组和同位素自然丰度技术,Fang 等[25]研究发现,低氮显著增加青藏高原高寒草甸 SOC 和颗粒态有机碳(POC)含量,而中氮和高氮导致土壤碳耗竭,SOC 由截存转变为损耗的大气氮沉降临界负荷为 20 kg N hm^{-2} a^{-1},并且铵态氮肥对 SOC 的损耗高于硝态氮肥。除了影响 SOC 的数量和组成外,施氮还会影响 SOM 的稳定性。Fang 等[89]利用 Biolog-eco 板法和三维荧光光谱(3DEEM)技术分别测定了青藏高原高寒草甸土壤微生物碳源利用活性和根际土壤 DOM 的化学组成,发现施氮刺激了土壤微生物活性,正激发效应降低 DOM 含量;施氮促进微生物优先利用小分子有机酸,提高土壤 DOM 的腐殖化系数,增加 DOM 的生物可降解性,不利于高寒草甸土壤碳累积。高剂量氮输入倾向于降低 SOM 中的活性组分(如烷氧基碳),而导致难以降解的芳香碳积累[90-91]。此外,大气沉降的 NH_4^+ 和 NO_3^- 能够结合到 SOM 骨架中,生成微生物难以降解的化合物(如杂环氮化合物),或通过氮键生成酚聚合物,进而促进 SOC 的积累[92]。

有机质化学结构的变化也会影响土壤微生物的底物利用,进而影响微生物群落的活性和组成,反之亦然。长期施氮会显著降低森林、草地等自然生态系统土壤微生物生物量[34],抑制腐生菌分泌木质纤维素水解酶,降低腐生微生物群落获取碳源(如纤维素、半纤维素)的能力[93];此外,氮沉降输入还会抑制白腐菌产生酚氧化酶,进而抑制木质素溶解酶生成,促进耐分解有机质的积累[94]。利用功能基因定量 PCR 和高通量测序技术,Hassett 等[95]和 Edwards 等[84]研究发现,施氮倾向于降低美国密歇根糖枫林土壤担子菌漆酶基因 *lcc* 的拷贝数(*lcc* 编码酚氧化酶),改变真菌群落组成(担子菌 OTUs/子囊菌 OTUs 增加),并且随着施氮时间的延长其抑制效应更加显著。同时,施氮倾向于降低凋落物分解速率和程度,增加类木质素化合物的氧化度和稳定性,进而促进 SOM 的积累[29]。潜在的生物化学机理是:高剂量的无机氮会抑制某些担子菌木质素水解酶的合成,以及编码酚氧化酶、锰过氧化物酶和木质素过氧化物酶的真菌基因转录下调,导致木质素降解下降[96]。木质纤维素水解酶基因转录下调会导致凋落物分解下降和 SOM 积累[97]。总体上,过去对氮沉降增加情景下森林土壤真菌功能基因表达和氧化酶活性演变研究较为深入,但是有关草地土壤细菌和真菌群落组成的变化如何代谢有机底物的机制仍不清楚,土壤微生物群落组成、SOM 化学结构的变化与 SOC 积累之间的耦联关系尚不清晰。

5 存在问题与展望

目前关于外源性氮输入对自然生态系统土壤碳动态的影响已开展了一些探索,但总体上还不够深入,存在许多问题亟待解决。首先,植物根系碳输入对增氮的响应呈现抛物线变化,取决于生态系统氮素有效性、施氮的类型与持续时间。总的来说,施氮降低根系的生长与周转,但是根际沉积物对增氮的响应及其固碳效应十分复杂,与植被-菌根类型、生态化学计量学等要素有关,未形成统一的研究结论。其次,关于激发效应的 3 个阶段、4 种驱动机制及影响因素分析较为深入,认识到养分尤其是氮素强烈影响激发效应的方向及强度,但是氮素类型、土层深度及其交互作用对激发效应的贡献并不清楚。再次,微生物 CUE 是微生物群落碳代谢的关键表征,受底物生态化学计量学驱动,能够很好地解释氮沉降增加情景下土壤碳的积累与损耗过程;由于缺乏适宜的测定方法,目前还难以准确量化土壤微生物 CUE 及微生物生物量的周转时间。最后,SOM 化学质量与土壤微生物群落活性、组成之间存在复杂的交互作用,增氮显著抑制贫氮生态系统土壤真菌群落及其胞外酶活性,对细菌群落组成的影响结论多样,有关微生物群落代谢底物、SOC 积累的生物化学机制尚不清楚。

基于上述研究的薄弱环节和存在的问题,在未来几年内,氮沉降增加情景下植物-微生物-SOM 交互作用在以下 4 个方面亟待加强(见图 3):(1)增氮对植被地下碳分配及微生物活性的影响。基于长期氮沉降模拟控制试验平台,构建 $^{13}C-CO_2$ 脉冲标记实验,测定不同功能群植物茎叶、根系、土壤(根际土和非根际土)、土壤呼吸、土壤 DOC 中 ^{13}C 的持留量,量化新固定的碳从植物茎叶分配到地下不同组分库的比例;结合 ^{13}C-PLFA 技术,鉴定土壤利用根际沉积碳的主要微生物类群,分析氮素类型和剂量对土壤活跃微生物群落丰度和活性的影响。(2)底物质量与氮素类型对 SOC 周转的调控作用。采集长期增氮控制试验对照样方表层和深层土

壤样品，通过添加^{13}C 标记的葡萄糖、氨基酸、纤维素以及不同类型的氮肥（NH_4^+ 和 NO_3^-），构建底物质量和氮素类型完全交互的激发效应培养实验，测定并计算激发效应的等级以及底物和 SOC 来源 CO_2的比例，模拟研究氮沉降增加情景下根系分泌物和植物残体输入对不同深度 SOC 周转的影响，定量评估底物的激发效应对 SOC 动态的贡献。（3）土壤微生物碳代谢过程对氮素可利用性增加的响应。采集控制试验对照和施氮处理样方表层和深层土壤，利用不依赖于底物的同位素标记新方法，根据^{18}O 标记水（$H_2{}^{18}O$）结合到微生物 DNA 的^{18}O 数量，计算出微生物的增长速率和呼吸速率，评价氮素类型和剂量对微生物群落碳利用效率（CUE）和周转时间的影响，结合土壤微生物生物量、碳降解相关的水解酶和氧化酶活性，阐明氮素有效性增加影响 SOM 分解的微生物学机制。（4）氮沉降增加情景下微生物群落演变与 SOM 稳定性的耦联关系。采集不同处理样方植物根系和表层土壤样品，利用热裂解-GC-MS 和^{13}C 核磁共振技术测定根系和 SOM 的单体组成与化学结构，分析施氮类型和剂量对有机质化学稳定性（如降解程度、芳香度、疏水度）的影响；同时，利用反转录实时定量 PCR（rt-qPCR）技术扩增量化细菌 16S rRNA 基因和真菌 28S rRNA 基因丰度，利用克隆文库技术和系统发育树方法分析真菌和细菌的群落组成，探讨土壤分解菌群落变化与 SOM 动态之间的耦合作用。期望通过上述研究，能够较为全面地理解大气氮沉降增加影响自然陆地生态系统 SOC 积累与损耗的生物学机制。

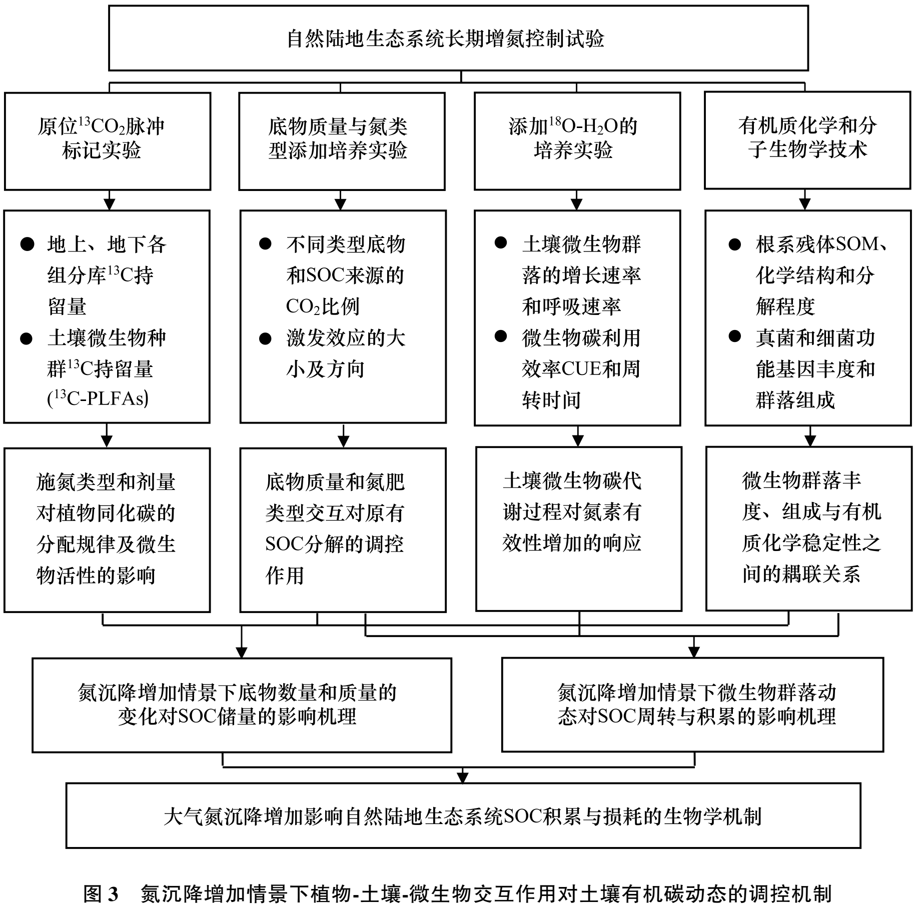

图 3　氮沉降增加情景下植物-土壤-微生物交互作用对土壤有机碳动态的调控机制

Fig.3　Mechanisms responsible for the regulation of plant-soil-microbe interactions to soil organic carbon dynamics under elevated nitrogen deposition

6　结论

外源性氮输入通过影响微生物群落活性和组成直接影响 SOM 分解，或通过改变底物数量和质量间接影响 SOC 的分解和累积过程。总体上，增氮倾向于促进地上生物量，抑制地下碳分配和根系周转。氮素有效性强烈影响 SOM 激发效应的方向和强度，取决于微生物生长的 r-K 策略和生态化学计量学特征。微生物 CUE

是衡量微生物群落碳代谢的重要表征，能够很好地解释土壤碳的积累与损耗过程，目前缺乏准确测定CUE的方法，稳定性碳氧同位素示踪是解决该问题较为理想的手段。SOM化学结构与微生物群落活性、组成紧密耦合在一起，增氮抑制真菌群落及氧化酶活性，对细菌群落组成的影响尚未形成定论，需要将有机质化学与分子生物学、宏基因组学方法紧密结合起来，深入地揭示增氮引起土壤碳积累与损耗的生物化学与微生物学机理。

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