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北方森林土壤微生物化学计量不平衡响应机制研究进展

蒋 帅，王庆贵*

黑龙江大学现代农业与生态环境学院，黑龙江 哈尔滨
Email: *qgwang1970@163.com

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摘 要

微生物与其资源间的化学计量不平衡决定了微生物的元素限制，这将改变其碳与养分的利用效率，最终影响微生物驱动的生物地球化学循环。人类活动引起的一系列全球变化，例如，气候变暖、大气CO_2浓度升高、氮沉降等会显著改变环境中资源养分的可利用性，这将导致微生物与其资源间的化学计量不平衡，最终影响微生物的代谢和养分循环过程。作为陆地生态系统最稳定的碳库，高纬度的北方森林对气候变化高度敏感，其碳储存的变化将会改变全球碳收支。本文结合以往研究中微生物应对化学计量不平衡的适应策略，对全球变化背景下北方森林土壤微生物应对资源改变的适应机制及研究进展进行了综述，以期进一步理解微生物分解者对陆地生态系统养分循环的调节作用。

关键词

土壤微生物，生态化学计量学，化学计量不平衡，元素利用效率，胞外酶化学计量

Response Mechanism of Soil Microbial Stoichiometry Imbalance in a Boreal Forest: A Review

Shuai Jiang, Qinggui Wang*

College of Modern Agriculture and Ecological Environment, Heilongjiang University, Harbin Heilongjiang
Email: *qgwang1970@163.com

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*通讯作者。

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Abstract

The stoichiometric imbalance between microbes and their resources determines the element limitation of microbes, which will change their carbon and nutrient utilization efficiency, and ultimately affect the biogeochemical cycle driven by microbes. A series of global changes caused by human activities, such as climate warming, elevated atmospheric CO_2 concentration, and nitrogen deposition, will significantly alter the availability of nutrients in the environment, which will lead to changes in the stoichiometric imbalance between microorganisms and their resources, and ultimately affect microbial metabolism and nutrient cycling processes. As the most stable carbon pool in terrestrial ecosystems, the high-latitude boreal forests are highly sensitive to climate change, and changes in their carbon stocks will change the global carbon budget. In this paper, we reviewed the response mechanism and research progress of soil microorganisms in boreal forests to resource changes under the background of global change, combining with the adaptation strategies of microorganisms in response to stoichiometric imbalance in previous studies, with a view to further understanding the role of microbial decomposing in regulating nutrient cycling in terrestrial ecosystems.

Keywords

Soil Microbes, Ecological Stoichiometry, Stoichiometric Imbalance, Element Utilization Efficiency, Extracellular Enzyme Stoichiometry

1. 引言

北方森林作为陆地生态系统最稳定的碳库，其碳储量达到(272 ± 23) Pg 碳[1]，相当于大气圈中碳储量的 50% [2]。然而，在气候变化的背景下，高纬度北方森林生态系统正面临着明显的全球变暖，这可能导致森林中稳定的碳库碳释放和相关土壤功能的改变[3]，进而导致生态系统功能发生变化。土壤微生物作为全球生物地球化学循环的重要参与者，具有广泛的生理与功能多样性，在凋落物分解、土壤有机质的转化、土壤碳固存以及养分循环等过程起到重要的作用[4] [5]。土壤中大量的有机碳被微生物转化、储存和呼吸[6]。虽然微生物生物量仅占土壤有机质的小部分，但它很大程度驱动了生态系统尺度上的碳(C)、氮(N)和磷(P)的循环[7]。因此，研究土壤微生物对碳氮磷循环的调控机制对认识全球变化背景下生物地球化学循环具有重要意义[8]。

微生物与其基质之间的化学计量关系是控制元素循环的一个重要因素[7]。这些元素的比例是对自然复杂性的简化[9]，微生物可以通过生态化学计量学理论与生态过程联系起来[10]。生态化学计量学理论(Ecological Stoichiometry Theory, EST)作为一个重要的方法被广泛应用于从亚细胞尺度到生态系统尺度营养动态、限制和生物量生产的预测[10] [11]。其中，化学计量不变性(即内稳态)是微生物生态化学计量学的核心概念。根据“Shelford 耐受定律”可知，即使外界环境不断变化，有机体会具备一个负反馈机制，即消费者与底物的化学计量比保持一种相对稳定的格局，这种相对稳定的状态被定义为“内稳态”[12]。基于全球范围的研究显示，作为土壤微生物的重要资源，植物凋落物在植物物种、生命形式以及系统发育类群之间存在较大的差异[13] [14]，因而凋落物的 C:N:P 比值很宽且具有较大的变异性[15]。虽然，随

着植物资源分解转化为有机质，资源化学计量变异性降低[16]，但同其他资源一样，有机质的 C:N:P 在不同生态系统类型的群落中也存在着显著差异[17]。已有研究表明，资源 C:N 增加 10 倍的同时，微生物生物量 C:N 仅增加 1.3 倍[17]。因此，土壤微生物必须应对时空变化导致的资源化学计量的失衡。

微生物应对元素失衡的适应机制已被报道[8] [15] [18]，可以总结为以下四个主要方面：第一，微生物化学计量可塑性，即微生物可以调节其生物量 C:N:P 比例满足基质元素组成的变异[9] [19]；第二，微生物胞外酶化学计量的调整，微生物通过分泌胞外酶改变直接底物的元素组成，胞外酶会优先分解满足其营养需求的化合物[20] [21] [22]；第三，微生物资源利用效率的调整，微生物吸取底物后，通过调节元素利用效率使元素矿化并排出多余元素[15] [23]；第四，通过分解来自外部来源的基质，最有效地获取相对稀缺元素的微生物丰度会增加[24]。尽管以上四种机制已被提出，但每种机制的相对贡献程度需要进一步评估。因此，本文围绕以上四种微生物适应机制，综述目前北方森林土壤微生物应对化学计量不平衡响应的研究进展。通过分析当前研究不足，进一步提出亟需关注的科学问题。

2. 化学计量可塑性的研究进展

微生物生物量 C:N:P 对化学计量不平衡响应主要有两种调节机制，即微生物通过过量储存元素(非内稳态)或通过改变群落结构和生物量化学计量同步变化来适应化学计量的不平衡[15]。尽管以往的研究报道了微生物生物量 C:N:P 具有恒定的摩尔比(60:7:1) [25]以及全球范围内微生物 C:N:P 为 42:6:1 [17]，但生态化学计量学的另一重要理论——“生长速率理论”认为生物体通过改变他们的 C:N:P 比值适应生长速率的改变[12]。高生长速率意味着富含磷的核糖体 RNA 的投资，导致 N:P 值的减小[26]。Zhou 等[27]整合分析发现土壤有机碳和全氮对土壤微生物 C:N 的解释度与气候条件的解释度相一致，这说明面对资源的变异，微生物会表现出非内稳态。同样 Xu 等[17]研究也报道了资源 C:N 与微生物生物量之间的正相关，尽管这种关系随着资源比的变异表现出强烈的抑制。因此，微生物生物量 C:N:P 对资源 C:N:P 变化的调整，即非内稳态，可能有助于微生物群落适应化学计量失衡。相比土壤微生物的非内稳态调节，许多研究认为微生物生物量 C:N:P 的可塑性是由于微生物群落结构的变化导致的[5] [8] [15] [24]。Zhou 等[5]通过整合分析的方法得到，随着演替变化，土壤碳氮比显著增加的同时，真菌/细菌比例快速增加。这种为适应资源由高质量向低质量变化，微生物群落做出的由 r 对策向 k 对策的转变，可能表明了群落结构和生物量化学计量的同步变化是导致微生物化学计量可塑性的原因。然而，导致微生物群落变化的可能原因有很大的不同[15]，因此对于微生物化学计量可塑性的机制还需进一步的研究。

最近一项对北方森林火烧后不同植被恢复阶段的研究发现，尽管土壤 C:N 发生显著改变，微生物生物量 C:N 仍保持不变[28]，在受到严重干扰后，土壤微生物会主动调节其生物量 C:N。相反，土壤微生物 C:P 和 N:P 的变化较大，这可能与资源磷过量有关，此时微生物变得非常不稳定[19]，以多聚磷酸盐形式的细胞磷储存可达到累积干质量的 10%~20% [29]，从而强烈的影响微生物生物量的 C:N:P。然而，与全球尺度的研究相反，土壤微生物生物量 C:N 与真菌/细菌之间没有发现高度的相关[28]。此外，对北方森林氮沉降的研究发现，施氮会导致土壤微生物氮(MBN)的增加，导致 MBC:MBN 显著降低[30] [31]，但微生物 C:N 的改变与细菌和真菌的优势地位转变无关[30]。尽管微生物很大程度上存在内稳态，土壤微生物生物量 C:N:P 也表现出相对的弹性，在群落和不同生态系统类型之间存在显著的差异，但 C:N:P 的变化是否可能预测微生物群落(结构)有待进一步研究。

3. 消费者维持“内稳态”机制的研究进展

微生物养分需求与其资源之间的化学计量不平衡导致 C 和养分(N/P)循环发生改变，进而导致 C:养分(N/P)释放比率发生变化，这被称为消费者驱动的养分循环理论(Consumer-Driven Nutrient Recycling

Theory, CNR) [10]。在微生物研究中，微生物严格的内稳态是消费者驱动的养分循环理论的核心假设[10]。面对化学计量的不平衡，土壤微生物会通过调整元素利用效率以及胞外酶的分泌维持其内稳态[24] [32] [33]。资源与微生物之间的不平衡反映了微生物的养分限制[24]。元素阈值比率(Threshold Elemental Ratio, TER)定义了生态系统从受养分(N/P)限制到能量(C)限制的转变[34] [35]，被认为与消费者驱动的养分循环密切相关(CNR)。TER 通过把生态代谢理论和化学计量理论结合在一起[10] [36] [37]，将微生物生物量化学计量学和元素利用效率联系起来，整合了微生物化学计量与胞外酶化学计量之间的关系[38]。总的来说，TER 是一种简单适用的预测微生物碳和养分通量的工具。

3.1. 微生物胞外酶的调整

土壤微生物群落通过分泌分解复杂有机物的胞外酶获取碳和营养物质[39] [40]。这些胞外酶通常是微生物代谢的限速步骤[41]，因此其相对丰度可作为微生物养分需求的指标[42] [43] [44]。生态酶化学计量学是生态化学计量学和生态代谢理论的交集[22] [45]。通常将土壤 C、N 和 P 转换的末端水解酶比例关系称为“生态酶化学计量”，主要包括：β-1,4-葡萄糖苷酶(β-1,4-glucosidase, BG)；β-1,4-乙酰葡糖胺糖苷酶(β-N-acetyl glucosaminidase, NAG)，亮氨酸氨基肽酶(*Leucine aminopeptidase*, LAP)；以及酸性/碱性磷酸酶(Acid/*Alkaline phosphatase*, AP)。基于全球范围的数据显示，胞外酶的化学计量受到很好的约束，其 C:N:P 比值接近 1:1:1 [42]。但胞外酶的化学计量在不同生态系统尺度存在显著变化，这可能受到气候环境，植被类型以及人类活动的影响[43] [46] [47] [48]。与温带地区相比，在磷限制的热带地区，BG:AP 和 NAG:AP 明显降低[8] [43]，因此，生态酶化学计量的变化可能反映了养分限制的变化[49]。资源分配理论认为，微生物群落通过优化资源配置生产细胞外 C-、N-和 P-获取酶，在土壤养分限制的条件下加速有机养分的释放，调整微生物生物量 C:N:P [32] [33] [50] [51]。但酶的生产需要能量和氮的投入，因此只有当酶产生的效益更大时这种调节才会发生[18] [52]。研究发现，强氮限制条件下，通过胞外酶的分泌调节底物氮可能不是微生物维持内稳态的适当策略，因为酶本身需要氮的投入，同时这还会增加元素的限制[52]。

北方生态系统土壤低温限制了分解者的活性，从而限制了氮(N)的释放，进一步限制了植物和微生物的生长[53] [54]。微生物通过合成胞外酶直接催化降解聚合土壤化合物[52]，因而细胞外酶活性同样会受到强烈的温度限制[55]。值得注意的是，基于季节的研究发现，北方生态系统夏季温度升高加速分解的同时，营养可用性的增加可能会通过调节微生物的生长或分解者群落特定成员的活动限制胞外酶活性[56]。对北方森林火烧序列的研究发现，胞外酶活性与真菌丰富度的变化一致，而与以往认为的火烧后土壤温度升高导致微生物活性增加的假设不一致[57]。此外，在北方森林不同树种的研究中发现，土壤 C、N、P 循环相关酶活性在不同优势树种的土壤存在差异，这可能对北方森林土壤的养分有效性产生影响[58]，通过研究胞外酶活性的变化可能对预测北方森林的养分循环具有重要意义。以往研究还发现氮含量有限的微生物可能无法将资源分配给细胞外酶[38]，因此，在普遍氮限制的北方森林中土壤微生物如何通过胞外酶化学计量应对资源化学计量变异的机制有待验证。

3.2. 微生物元素利用效率的调整

微生物面对资源与自身供求的不平衡时，如果不能直接改变资源的组成或调整自身生物量化学计量，微生物会通过调节进入生物量的元素分配方式维持化学计量[15]，即微生物会吸收任何基质，通过保留维持自身组成和代谢的限制元素，释放超过其需求的元素。微生物碳利用效率(Carbon Use Efficiency, CUE)定义为分配给生物量生产的碳占吸收碳的比例[59] [60]，已有研究发现氮有效性的提高增加了微生物的 CUE，这是因为微生物分配更多的 C 用于微生物量的生长，而不是用于获取氮[61] [62] [63]。此外，在 C 营养非常高的基质中，微生物可用 C 不能全部用于生物量的积累，而是通过溢流呼吸释放，这将大大降

低 CUE [64] [65]。元素阈值比(TER)是分解者由 C 限制转向养分限制的临界基质 C:X (C:N，C:P)比值[7]。由于微生物根据养分需求调节其元素利用效率，因此 TER 将微生物化学计量学与元素利用效率联系在一起。当微生物群落在 C 限制且 N 过量时，即资源 C:N 小于 TERC:N 时，CUE 达到最大值并伴随氮利用效率(NUE)的减小。与之相反，当微生物受到 N 限制而 C 过量时，NUE 伴随 CUE 的下降而增加[24] [60]。

高 CUE 被认为可以促进土壤中微生物的生长并稳定碳，而 CUE 的减小可能意味着土壤碳储存的降低[59]，土壤微生物 CUE 已成为生物地球化学研究的重点[24]。在全球变化背景下，通过对土壤微生物 CUE 变化的研究，可能有助于理解北方森林的碳循环。例如，北方森林通常表现为氮限制，大气氮沉降的增加可能缓解了土壤养分限制，通过降低微生物底物的 C:N 提高微生物 CUE，微生物更有效的将 C 转化为生物量从而增加碳固存[59]。相比氮沉降，气候变暖会对北方森林产生强烈的影响，以往研究还发现，气候变暖可能会通过增加微生物活性及异氧呼吸速率降低 CUE [66]，同时 C 损失可能导致净氮矿化的增加，从而提高植物生产可利用氮[67]，这可以短期内增加生态系统的碳储量[68]，但长期的呼吸损失可能会降低土壤碳储量[59]。分解者 CUE 的变化可能也会带来间接的反馈，CUE 增加的同时会增加生产酶的资源进而增加分解减少 C 储存[69]。另一方面，TER 可能因微生物内稳态相对外部资源供应变化的维持程度有所不同[24]，CUE 的增加会减少 $TER_{C:N}$ 和 $TER_{C:P}$，提高微生物有机氮积累并减少植物氮的有效性，这可能会通过减少生产力降低土壤碳库，同时通过提高植物 C:N 增加微生物养分限制降低 CUE [59]。因此，同时对微生物元素效率、微生物胞外酶以及元素阈值的变化进行综合分析，能够更好的评价当化学计量不平衡改变时，微生物 CUE 的变化及其对地球化学循环的改变。

4. 微生物群落动态的响应

面对化学计量的失衡，土壤微生物还会通过原核生物固氮以及真菌菌丝体对磷和氮的迁移增加底物的氮和磷有效性[15]。由于固氮细菌仅占分解者群落的一小部分[70]，其固氮速率低于微生物呼吸速率[71]，因此面对化学计量的不平衡能否通过固氮细菌的调节还未证实[15]。相反，腐生真菌已被证明可以调节富营养斑块中的养分向贫养的生境转移，显著的缓解微生物与底物之间的化学计量不平衡[72]。但重要的是，真菌的这种调节作用，可能会影响资源驱动的细菌和真菌之间的竞争。已有研究提出微生物功能群相互作用的动态导致了群落水平上的适应，通过加速高 C:N 比凋落物的氮循环缓解氮限制，这一机制使得微生物能够克服资源与生物量之间的巨大失衡，而无需降低碳利用效率[73]。因此，有必要对群落水平的调节机制以及微生物群落驱动的化学计量响应展开研究。

5. 展望

尽管微生物应对资源变化的调节机制已被提出，但一系列的全球变化对微生物及其资源的直接或间接效应会影响微生物的适应对策[8]。特别是，化学计量不平衡的变化将导致微生物养分限制的变化，这将微生物元素利用效率与胞外酶活性和微生物群落特性的改变不同程度的联系起来。尽管微生物的不同机制同时运行，但其在不同时间和空间尺度上的贡献程度还需进一步讨论。而化学计量学概念为不同尺度养分循环的预测提供了可能。北方森林生态系统中储存了大量的碳，人们对北方森林在全球碳循环以及在该区域气候变化和碳循环之间的反馈作用越来越感兴趣。以往研究表明，胞外酶和微生物群落对化学计量不平衡协同响应可能改变了元素阈值比例，通过调节微生物的利用效率决定土壤和大气的碳交换[74]。总之，通过研究化学计量不平衡对调节微生物驱动的碳排放的作用，有助于我们更好的理解全球变化背景下北方森林资源质量的改变对该地区土壤碳储存的影响。

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