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氮、磷养分有效性对森林凋落物分解影响的研究进展

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摘要: 通过对相关研究文献的综述结果表明,氮(N)和磷(P)是构成蛋白质和遗传物质的两种重要组成元素,限制森林生产力和其他生态系统过程,对凋落物分解产生深刻影响。大量的凋落物分解试验发现在土壤 N 有效性较低的温带和北方森林,凋落物分解速率常与底物初始 N 浓度、木质素/N 比等有很好的相关关系,也受外源 N 输入的影响;而在土壤高度风化的热带亚热带森林生态系统中,P 可能是比 N 更为重要的分解限制因子。然而控制试验表明,N、P 添加对凋落物分解速率的影响并不一致,既有促进效应也有抑制效应。为了深入揭示 N、P 养分有效性对凋落物分解的调控机制,“底物的 C、N 化学计量学”假说、“微生物的 N 开采”假说以及养分平衡的理论都常被用于解释凋落物分解速率的变化。由于微生物分解者具有较为稳定的 C、N、P 等养分需求比例,在不同的养分供应的周围环境中会体现出不同的活性,某种最缺乏的养分可能就是分解的最重要限制因子。未来的凋落物分解研究,应延长实验时间、加强室内和野外不同条件下的 N、P 等养分添加控制试验,探讨驱动分解进程的微生物群落结构和酶活性的变化。

关键词:凋落物分解;N;P;养分有效性;微生物;酶

Effect of nitrogen and phosphorus availability on forest litter decomposition

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Abstract: Nitrogen (N) and phosphorus (P) are the two most important elements for building plant proteins and genetic material, limiting forest production, and other ecosystem processes, and they profoundly affect litter decomposition. Litter-quality parameters, particularly initial lignin and N contents, ratios of C:N, and lignin:N often correlate strongly with rates of litter mass loss in temperate and boreal forests. Furthermore, soil N availability and N addition also affect litter decomposition. In tropical and subtropical forests, where highly weathered soil is frequently observed, P could be more important than N in inhibiting litter decomposition. However, P has not been considered in most current ecosystem carbon cycling models, but fertilization experiments show different responses of litter decomposition rates to nutrition addition. Synergistic, antagonistic, and neutral effects can be observed. Both the “basic stoichiometric decomposition theory” and “microbial nitrogen mining” hypothesis have been used to explain litter decomposition rate variations with nutrition addition. Regarding rigid C:N:P ratios in microbial decomposers, different nutrition sources could result in altered microbial activity, and limited nutrient supplies could result in restricted litter decomposition. To clearly understand the effects of N and P regulation on decomposition, we need longer decomposition experiment durations, more intensive field and laboratory fertilization experiments, and simultaneously, microbe and enzyme dynamics in the decomposition process should be further

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investigated.

Key Words: litter decomposition; N; P; nutrient availability; microbes; enzymes

植物凋落物的分解向土壤归还养分,向大气释放 CO_2,是生态系统物质循环和能量流动的重要环节[1-2]。自从 Bocock and Gilbert 于 1957 首次使用凋落物分解袋技术以来,关于凋落物分解的文章逐年稳定递增,利用 Web of Science 进行搜索,发现迄今为止文章总数已经超过 8000 篇(图 1)。1990 年后,人们密切关注全球升温及与之相伴的大气 CO_2浓度升高等环境问题,因此对分解过程调控机制的深入了解变得尤为迫切[3-5]。

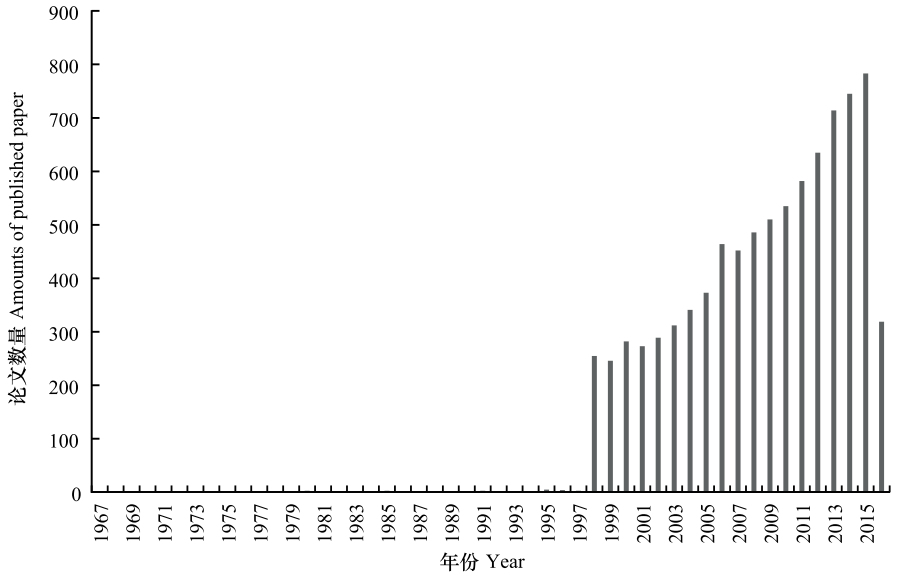

图 1 近 50 年有关凋落物分解发表的 SCI 文章

Fig.1 The papers on litter decomposition published included in SCI in the past 50 years

凋落物分解的调控机制极其复杂,涉及物理、化学和生物学过程,但主要可以归纳为两个方面,其一是凋落物本身质量,即其物理化学性质和养分的含量,其二是分解的外在环境,特别是气候因子(温度、水分)以及土壤或枯枝落叶层的养分含量和有效性[1,6-7]。过去的研究表明在全球和区域的尺度上,气候是调控凋落物分解的首要因素,但在局域尺度上,表征凋落物质量的养分含量指标以及分解环境中的养分有效性则起至关重要的作用[8-13]。N、P 是陆地生态系统植物生长最重要的两种限制性养分[14-16],在全球变化背景下,自然或人为驱动的这两种元素输入变化,必将对凋落物分解产生重要影响,进而影响全球的碳平衡或碳预算。然而,N、P 养分有效性的改变如何影响凋落物的分解,以及分解过程中的微生物学机制等尚待阐明,直接影响到碳循环模型的构建和对生态系统碳吸存潜力的预测。

1 不同来源的 N 对凋落物分解的影响

化石燃料的燃烧、化肥的使用以及固 N 作物的栽培等人类活动,把 N 从惰性的形态(N_2)转化为活性的形态,如 NH_3(Haber Bosch 制氮法)、NO_x。而活性 N 经脱 N 作用形成 N_2的速度小于活性 N 形成的速度,导致这些活性 N 在大气、土壤和水体中储藏[17],并在未来相当长的时间内持续增加[18]。活性 N 的增加引发了平流层臭氧耗竭、酸沉降、海岸带富营养化以及淡水的生产等环境问题,同时也提高了生态系统的净初级生产力[19-20],增加了生态系统 C、N 储量。为了进一步了解 N 输入持续增加情况下,生态系统碳输出的变化,需要明确 N 对凋落物分解的效应。

大量的凋落物分解研究表明,分解速率与 N 相联系的各种指标有很好的相关关系。这体现在凋落物自

身的 N 含量、C/N、木质素/N,土壤环境中的 C/N、N 含量以及外源添加的 N 量对分解产生的不同效应。

1.1　凋落物底物的 N 含量对分解的影响

“底物的 C、N 化学计量学”假说认为,微生物分解者与分解底物之间存在 C、N 化学计量学的差异,这种对分解者生理学上的基本约束驱动凋落物分解和养分的释放[21-23]。一般来说,新鲜凋落物的 C/N 比高于微生物分解者,微生物需要从周围环境(土壤或降水)获取养分来维持其自身的生长需求[24-25]。此外,大量的研究发现在分解早期,凋落物初始 N 含量以及与 N 相关的底物质量指标和凋落物分解速率有很好的相关关系[20-21],证明 N 对凋落物分解的限制作用。尽管以上证据都是间接的,但 C/N 比和木质素/N 的比率等指标常被用于预测凋落物的分解速率[20,23,26-27],同时也被一些碳循环模型采用。

1.2　土壤 N 有效性对凋落物分解的影响

在热带山地生态系统的土壤年龄序列中,凋落物在养分有效性高的土壤中分解最快,而在养分有效性低且限制了地上部分生产力的土壤中分解最慢[28-29]。Hobbie[30]在美国明尼苏达州的研究发现,分解速率与土壤 N 有效性有显著的相关关系。土壤养分有效性对分解的限制作用还表现在分解者和植物之间的正反馈环,在低养分的土壤中,凋落物分解受到限制而减缓养分循环,进一步降低植物的养分有效性,限制植物的生产力;而较低生产力的植物,凋落物归还的数量和质量都较低,抑制了分解[31]。在温带森林生态系统研究表明,高土壤 N 有效性提高细根底物的质量,进而影响了细根的分解速率[32]。

1.3　外源添加的 N 对凋落物分解的影响

分解养分限制的直接证据只能通过施肥实验,在增加外源提供的养分情况下,考察凋落物分解速率是否提高。然而凋落物分解对外源 N 输入的响应并不一致,既有促进作用[33-34]、抑制作用[35-36],还有研究发现没有明显的作用[33,37]。

N 添加对凋落物分解的促进或抑制作用以及影响的程度大小与很多因素有关,除凋落物本身质量外,还有诸多其他因素,如气候、大气 N 沉降水平以及施 N 肥的类型、网袋的孔径大小等。Knorr 等[38]的综合分析表明,N 施肥改变了凋落物的分解速率,但分解响应的方向和程度受到施肥的量、大气氮沉降水平以及凋落物质量交互作用的调节。当施肥量为氮沉降水平的 2 – 20 倍时,或者氮沉降水平达 5 – 10 kg N ha^{-2} a^{-2},再或者凋落物质量差(高木质素含量)时,凋落物分解受到抑制;在高 N 施肥的情况下(大气氮沉降的 20 倍),或氮沉降水平在 5kg N ha^{-2} a^{-2}以下,或高质量的凋落物(低木质素含量)时,凋落物分解被促进。因此,特定生态系统中,分解过程对 N 施肥的响应受到 N 沉降水平的影响,长期高 N 沉降下的生态系统可能获得了适应性,在人为施 N 肥的情况下凋落物分解反应程度较小。

从有机质中获得 N 的过程非常复杂,N 分布在多种等级的混合物以及腐殖大分子中,因此微生物的 N 获取策略与特定种群的 C 底物偏好有密切联系[39-40]。在 Moorhead and Sinsabaugh[41]提出的以分解者集团为基础的凋落物分解模型中,把微生物分成三大类:分解活性蛋白质的机会主义者(opportunists)、需要外源 N 输入分解木质纤维素的专性分解者(decomposers)和利用氧化酶打开腐殖质获得所需的 C 和 N 的“淘金分解者”(miners)。

在多样的 C 和 N 获取策略情况下,外源 N 添加试验中发现土壤胞外酶活性的响应差异便不难理解了。因此,近年来很多研究者倾向于从酶活性变化的角度来解释 N 添加对分解的影响[42]。用酶活性的变化来解释 N 添加对分解的影响得到了多个研究的支持[42-46]。如 Fog[47]发现在高 N 的情况下,白腐担子菌被分解纤维素的子囊菌所竞争性排除,这种对木质素分解的抑制作用导致添加 N 对分解的中性效应或负效应。Craine 等[48]研究也认为,是 N 的添加降低负责分解惰性 C 的微生物活性 C 有效性,抑制了负责惰性有机 C 中“N 开采”的酶(如酚氧化酶、过氧化物酶)的生产[41,49],从而限制了凋落物的分解。添加 N 不仅改变了酚氧化酶,还有其他微生物获取 C、N、P 酶的活性,这些酶活性的变化能较好的解释凋落物分解速率的变化[49-51]。酶活性对外源 N 的不同响应,与样地土壤养分有效性[53-54]、凋落物木质素含量[54-55]、凋落物和土壤的 C/N 比[46,56]以及微生物生物量[57]有关。测定酶活性使我们能够直接跟踪微生物群落对凋落物性质和环境变量的功能响

应[44],但由于植物-凋落物-微生物交互作用具有潜在的复杂性,在地表植被、凋落物化学性质、土壤 C/N 比和 N 有效性不同的多种林地上,凋落物分解速率和土壤的酶活性同时会对外源 N 添加做出何种响应,目前尚不清楚。目前,DGGE、PLFA 以及高通量测序技术的成熟和应用,必将推进对 N 沉降背景下不同生态系统凋落物分解过程中微生物群落和酶活性的动态变化的准确刻画。

2 P 对凋落物分解的影响

长期复杂的成土过程中形成了土壤在地理学上的分异,中高纬度地区的土壤较为年轻, N 含量较少,而低纬度地区土壤古老, P 含量有限[58]。P 和 N 对初级生产力以及其他生态系统过程的限制作用已经在多种多样的陆地生态系统中被证明[16]。与 N 不同,土壤 P 来源于岩石风化,每个生态系统发生时都有一个固定 P 储量,随生态系统发育,P 不断流失且不能轻易得到补充。这导致老的土壤中 P 的总量和生物有效性都较低,从而对生态系统 NPP、凋落物分解等其他生态学过程产生了深刻的影响[28,15]。

在热带亚热带的酸性土壤里, P 易于被其中的铁铝氧化物固定,发生强的吸附作用, N 相对过剩而由矿石来源的 P 等必要养分处于耗竭状态,全球气候变化下的 N/S 沉降更加剧了生态系统潜在的 P 限制[31,59-61]。研究已证实 P 有效性限制了热带、亚热带生态系统的 NPP(净初级生产力)。凋落物分解的初级阶段经常需要富集 P,说明新鲜凋落物中的 P 养分不足以维持分解者的生长,而凋落物分解速率常与 P 及其相联系的凋落物质量指标显著相关[1,62-66],表明凋落物分解可能受 P 限制。此外热带生态系统土壤高度风化,N 过剩而 P 有效性低,在此土壤上生长的凋落物也具有高 N/P 比的特征[59,67]。因此相比于 N,微生物在分解中更难以从凋落物本身及周围环境获得 P,根据李比希最小值定律(Liebig′s law of the minimum),P 可能是该区域凋落物分解更为重要的限制性因子。然而,现有的生态系统 C 循环机理模型很少考虑 P 的循环[40,68]。

不同于 N 的循环,P 循环可分为生物和地球化学循环。生物循环是指植物和微生物吸收的 P 在死亡后变成土壤有机 P,这部分的 P 能够被重新矿化和吸收;地球化学循环则是由于母岩风化或外源添加提供给生态系统的 P,与土壤矿物发生化学反应被固定在土壤中[69-71]。但有证据表明,微生物能迅速利用外源添加的 P,在生物吸收和土壤吸附有效 P 的竞争中起支配作用[72-74]。已有研究通过测定呼吸速率,探讨 P 添加后高度风化土壤凋落物分解过程中微生物活性变化,来解释 P 有效性对分解的限制作用[74-76]。而直接测定 P 添加对分解过程中微生物动态效应的研究很少,这是由于当前的生态系统模型都把土壤微生物当作一个黑箱[77-79]。

与 N 相比,人们对 P 与微生物结构和功能的关系了解较少[62]。在外源 P 添加的情况下,P 的有效性提高,微生物运用更少的能量获得 P[52,43],那么微生物是否重新分配它的资源,转向提高获得 C、N 的胞外酶活性呢? 这些酶的活性能用于解释 P 添加情况下凋落物分解速率的变化么? 土壤化学性质:如 pH,N、P 等养分有效性和凋落物质量的变化不仅影响酶的合成,同时影响细菌和真菌的比例及其群落结构的变化[45,79-80]。如富含养分的活性有机质由快速生长的细菌侵染,因其快速的细胞分裂需要大量富 P 的 RNA,而养分贫乏难分解的有机质易于生长真菌[81-83]。因而直接测定酶活性和主要微生物类群结构对凋落物性质和环境变量的响应,能获得对凋落物分解机理更为清晰的了解。

3 其他元素对凋落物分解的影响

N 和 P 是限制生态系统过程的两种关键元素,被大部分分解试验关注。目前的研究表明,北方森林和温带森林,富 N 比贫 N 的凋落物分解快[93];而低地热带雨林 N 相对丰富, P 含量随时间不断耗竭[45,94],从而使 P 在该区域凋落物分解中起主导作用[33,46,59,67]。除这两种元素外,尚有少量研究表明其它元素也在分解中有重要作用。

凋落物分解是个多种底物(如蜡类、酚类、木质素和纤维素等)连续降解的过程,需要微生物合成多种(metallomic enzymes)金属酶的参与[95],这个过程中会出现包括 N、P 等其它多种养分供应的不足。Kaspari[95]在热带低地森林的分解试验发现,P 的添加提高凋落物分解速率 33%而微量元素(如 B, Ca, Cu, Fe, Mg,

Mn, Mo, S, Zn)的添加则提高了 81%。这说明除 P 之外,另有其它元素可能参与并促进凋落物的分解。据统计,大约需要 25 种化学元素才能驱动整个生态系统碳循环过程中的树木生长、分解中的微生物繁殖[85]。如果要对限制凋落物分解的养分重要性进行排序,需设计析因实验,然而这样的试验目前仍很少[33,90]。

4　N/P 比率对凋落物分解的影响

Alfred Redfield 在 1958 年观测到,海洋浮游生物生物量中 C、N 、P 原子比为 106:16:1,这与海水中 C、N 、P 比例相似。这种化学计量学关系简洁的反映了有机体和环境之间的交互作用,被称为“Alfred 比率”,其有助于深入了解海洋生态系统 NPP 和 C 储量受养分限制的性质和程度,以及海洋中 N、P 生物地球化学循环过程。“Alfred 比率”在海洋生态系统的预测能力,推动生态学家在陆地生态系统寻找相似的养分格局和关系,因而诞生了一门新的学科—生态化学计量学,这门学科着眼于了解生态学交互作用过程中的多种化学元素的平衡[84-85]。然而,我们当前对化学计量关系以及其在陆地生态系统中的重要意义所知还很有限[86]。

微生物生物量 C 与土壤 C 有效性有很强的相关关系,同时也与土壤微生物中 N 和 P 的含量密切相关,这种养分之间的线性相关关系表明土壤微生物生物量 C 的增加依赖于充足的土壤 N 和 P 养分供应来维持微生物生长所需要的养分元素化学计量比[87]。植物叶片养分比率反映了土壤 N 和 P 的相对丰度从低纬度到高纬度的增长[58,98-99],而土壤微生物量中的 N/P 比率并不随着纬度的变化而变化,也与土壤中 N:P 供应比率没有相关关系,而是维持在类似“Alfred 比率”的比例[86]。土壤微生物相对严格的养分需求以及低纬度地区土壤低 P 有效性解释了 P 对这些生态系统微生物生物量和活性的限制[59,72,88,96,97],进而限制凋落物的分解。由于 N、P 有效性在不同生态系统间的差异,因此有些研究者认为 N 和 P 对生态系统过程(包括凋落物分解)限制的相对重要性也不同,当 N/P 比低时受 N 限制,当 N/P 比高时受 P 限制(通常认为 N/P 比<14 时受 N 限制,N/P 比>16 时受 P 限制,当 N/P 比在 14 和 16 之间受到 N、P 的共同限制)[83]。人类活动可以通过添加 P 而转变 P 限制的生态系统为其它养分限制系统,也可以通过有意和无意的影响其它养分(主要是 N)的供给,导致 P 限制生态系统的出现。例如,欧洲西北地区由于极端高水平的大气 N 沉降克服了许多生态系统的 N 限制而转变成首先受 P 限制的生态系统[46,89],在北美地区进行的控制试验也获得类似的结果[90-92]。

5　展望

凋落物分解是一个贯穿着淋溶、冻融粉碎等物理作用以及土壤生物参与的生物化学作用交织在一起的复杂过程,并最终通过微生物的作用释放 CO_2到大气,释放养分回归土壤中。对同一种底物而言,控制微生物活性的温度、水分条件以及微生物所需的养分有效性,决定了凋落物最终的分解速率。因此,当前凋落物分解研究存在以下主要问题:1.影响凋落物分解的 N、P 养分因素与其他因素同时存在或发生交互作用,导致难以确定影响分解的主导因素。且确定影响分解速率的因素时,常采用相关分析的方法。相关分析可以为确定主导因素提供很好的线索,然而需要控制试验加以验证;2.较少考虑 P 有效性对凋落物分解的影响。早期的分解研究主要集中在北方森林和温带森林,研究结果认为 N 及木质素/N 比是调控凋落物分解的主要因素,现有的生态系统过程模型也只考虑 N 的作用而忽略了 P,然而近年来热带、亚热带发育在高度风化土壤上生态系统的多项研究表明 P 对生态系统过程的限制作用。即使在热带和亚热带,不同生态系统或同一生态系统不同的发育阶段受 N、P 养分限制情况也不一致;3.分解底物的异质性。即便同种植物,其不同位置或不同时间产生的凋落物 N、P 养分含量具有较大的差异。4.较少考虑影响分解过程各种酶的活性和微生物群落结构的变化。N、P 无疑是生态系统过程中两种最重要的养分,但它们对凋落物分解的影响及作用机制尚未明确的阐述,影响了对全球环境变化下生态系统过程的预测。今后应着重通过室内结合野外的控制试验获取直接的证据,主要考虑以下几个方面的工作:

(1)养分添加试验是确定养分限制属性的良好手段,然而需要认真的考虑养分添加量以及观测的时间。养分添加量会改变生态系统养分受限性质,有效体现养分添加效应需要延长观测的时间。例如,现有的凋落

物分解试验大部分少于 2 年,有的凋落物在此期间尚处于分解的初期阶段。

(2)要充分考虑分解环境变化对 N、P 添加效应的影响。例如热带雨林凋落物分解过程中淋溶起主导作用,因此养分添加对凋落物的干质量损失没有显著影响,但却促进了凋落物淋溶部分物质的矿化分解。

(3)养分平衡对凋落物分解的作用。微生物分解者的生长有严格的化学计量学要求,是否某种养分有效性的缺乏限制了凋落物分解。

(4)通过对分解过程中微生物和酶活性变化的观测,揭示凋落物分解的机理,阐明养分添加对凋落物分解的不同效应,最终弄清楚不同生态系统凋落物分解的主要限制性因子。

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