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氮沉降影响土壤磷与ECM和SAP真菌关系研究进展

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摘　要

氮沉降深刻影响生态系统养分和物质循环，提升生态系统生产力，最终将会影响全球气候变化。随着氮沉降增加，土壤养分尤其是土壤磷将会受到显著影响。土壤微生物在驱动土壤与植物之间养分循环、养分供给方面具有重要作用，逐渐成为氮沉降变化背景下的重点研究对象。本文通过综述近年来的相关研究论文，重点分析了ECM和SAP真菌及其功能，探讨了氮沉降背景下土壤磷变化及其对ECM、SAP真菌的影响，揭示了氮沉降如何影响土壤磷与ECM和SAP真菌关系。该文可为氮沉降背景下土壤磷与真菌群落互作关系的深入研究提供基础数据。

关键词

氮沉降，土壤磷，ECM真菌，SAP真菌

The Effect of Nitrogen Deposition on the Relationship between Soil Phosphorus and ECM and SAP Fungi: A Review

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Abstract

Nitrogen deposition profoundly affects the nutrient and material cycle of ecosystems, and ultimately enhances ecosystem productivity and affects global climate change. With the increase of N deposition, soil nutrients, especially soil phosphorus, will be significantly affected. Soil microorganisms play an important role in driving nutrient cycling and nutrient supply between soil and plants, and have gradually become the focus of research under the background of N deposition. In this study, we reviewed the related research papers in recent years and analyzed the ECM and SAP fungi and their functions, discussed the changes of soil phosphorus and its effects on ECM and SAP fungi under the background of N deposition, and revealed the effect of N deposition on the relationship between soil phosphorus and ECM and SAP fungi. This research can provide basic data for further study on the interaction between soil phosphorus and fungal community under the background of N deposition.

Keywords

Nitrogen Deposition, Soil Phosphorus, ECM Fungi, SAP Fungi

1. 引言

人类活动导致了一系列气候变化，诸如气候变暖、降水格局改变、极端天气现象频发、酸雨、氮沉降等，给社会经济发展带来了严重威胁[1]。活性氮排放速率从 20 世纪 60 年代开始持续增加，工业活动的密集化导致大量的氮排放至生态系统。氮沉降长期干扰生态系统状态，一方面增加了系统生产力，另一方面也造成土壤酸化，导致生物多样性的丧失[2] [3]。先前有研究表明，氮添加能够提高土壤养分有效性，促使土壤养分发生改变，尤其是磷的改变[4]。正如陈等人汇总相关研究证明，氮沉降能够影响土壤磷循环，主要表现在凋落物的养分循环上[5]。Magill 对哈佛森林生态系统研究发现，氮沉降会降低凋落物的产量[6]；周等人对于天然常绿阔叶林进行氮添加对照试验也发现，增氮会抑制凋落物产量，从而导致回归土壤的磷含量减少[7]。但也有学者发现了相反结果，Block 等人研究发现氮沉降量高的森林磷含量显著高于氮沉降量低的林地[8]；Magill 在其早期生态研究中表明，氮沉降增加了森林凋落物产量[6]。土壤磷作为重要的养分在生态系统中发挥着重要作用，同时也是影响植物生长和土壤真菌群落的关键影响因子[9] [10]。因此，在氮沉降增加背景下，加强对土壤磷元素的研究，将有助于进一步了解土壤养分与土壤微生物功能的互作关系。

土壤微生物是生态系统中不可或缺的重要组分，土壤有机质的转化与土壤养分循环都离不开土壤微生物。例如，一些土壤微生物能够与植物互作，影响土壤养分尤其是磷的吸收与转化[11]；土壤微生物还能够参与生物的扰动裂解过程，驱动土壤碳氮循环。菌根真菌与植物共生得到了广泛的证据支持，能够发挥出叠加的生态价值。ECM 共生真菌(Ectomycorrhizal fungi, ECM)与 SAP 腐生真菌(Saprotrophic fungi, SAP)同处于一个生态位，存在激烈的竞争关系，且具有相似的养分转化功能。近年来研究发现，ECM 真菌与 SAP 真菌对于环境变化响应敏感，并与土壤环境息息相关[12]。因此，二者成为真菌体系中专家学

者进行对比研究的重要对象。大量研究表明，氮沉降对 ECM 真菌存在显著负效应，正如 GrmanE 等人研究发现，氮沉降会导致真菌多样性和丰富度的降低[13]；Verlinden 等人研究也发现，氮沉降的增加会导致 ECM 真菌生物量和产量减少[14]。同时，李等人研究还发现氮沉降会导致 ECM 真菌菌丝量减少，降低真菌生产力[15]。但也存在相反的结果报道：Hendricks 等人在 2016 年的模拟氮沉降实验中发现，氮添加下 ECM 真菌生物量显著增加[16]。相较于 ECM 真菌研究，SAP 研究较有不足，更多倾向于氮添加对 SAP 真菌的正向效应。例如，Zhou 等人研究和 She 等人研究都表明氮沉降会增加土壤中 SAP 真菌比例[17] [18]；Zhao 等人最新研究也发现，氮添加能够增加 SAP 真菌的丰富度与相对丰度[19]。有证据表明，氮沉降下 ECM 与 SAP 真菌群落丰度存在显著的负相关关系[20]。但也有人发现，ECM 真菌与 SAP 真菌在调节磷限制转化功能方面存在相似性[21]。ECM 真菌与 SAP 真菌都会受到外源氮的调控，揭示氮沉降增加背景下土壤磷含量变化同 ECM 真菌与 SAP 真菌之间的关系具有重要意义。

2. ECM 真菌与 SAP 真菌简介

ECM 真菌能够与植物根系共生形成外生菌根，ECM 真菌的菌丝不能伸入植物细胞，只能着生在细根表面形成菌套，其菌丝能替代根毛的作用，帮助根系吸收养分和水分[22]。

SAP 真菌为腐生真菌，是一系列营腐生活的真菌，需要在土壤中从死亡的动植物残体中获取自身需要的养分，属于异养生物。SAP 真菌是生态系统中不可缺少的分解者[23]，能够促进土壤中动植物养分归还，维持生态系统养分平衡。

3. ECM 真菌与 SAP 真菌功能

3.1. ECM 真菌功能

ECM 真菌能够与超过 90%的 ECM 树种共生，利用树木光合作用产生的碳作为吸收土壤氮元素的驱动力，促进植物根系养分吸收，提升根系代谢能力[24]。它还可以通过转化不能被根系直接吸收的多肽和蛋白质中的氮来供给植物宿主，促进植物养分吸收，维持宿主养分平衡，从而促进植物生长[25]。因此，ECM 真菌能有效缓解土壤氮限制，提升土壤养分的有效性，促进土壤碳氮循环[24] [26] [27] [28] [29]。ECM 真菌存活过程中能够分泌多种天然激素，增强宿主的抗逆性与免疫力。同时，ECM 真菌还可以直接产生磷酸酶以及扩大根系吸收更多的磷[29] [30]，在磷限制的土壤条件下，ECM 真菌发挥着关键的作用。

3.2. SAP 真菌功能

SAP 真菌在土壤的碳氮循环中发挥着重要作用。它们具有分泌大量氧化酶和广泛降解富碳凋落物的能力，是森林中木质纤维素的主要分解者[22]。它们可以分解复杂的有机物，促进生态系统的碳氮循环[20]，以维持土壤稳定[31]。

4. 氮沉降的影响

4.1. 氮沉降对土壤磷的影响

土壤磷是植物生长必不可少的营养元素，植物吸收土壤磷促进细胞分裂以及能量合成，参与植物各项生命活动[22]。自然界的磷以有机磷和无机磷两种形式存在，植物可吸收利用的磷被称之为有效磷，其中最重要的是储存在土壤有机物中容易分解和矿物中容易随土壤移动分解的磷。人类活动导致的氮沉降，通过改变生物对于土壤磷的需求而影响生态系统的磷循环[22]。

工业革命以来，人为活动增加了全球氮沉降速率，导致大量的氮输入生态系统[32] [33]。更多的学者

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综述多年氮沉降实验结果，发现氮添加促进了植物对于土壤磷的吸收[34]，降低了土壤磷的有效性；氮沉降也可能造成土壤酸化，促使土壤磷离子与 Al^{3+}结合，抑制根系对磷的吸收，导致土壤磷的有效性降低[35] [36]。如 Yang 等人通过不同梯度氮添加实验研究发现，土壤有效无机磷和有机磷含量都随着氮添加的增加而减少[37]。也有证据表明，增加氮的输入会导致植物对磷的需求增加[37] [38] [39]，刺激植物对磷的利用，导致植物磷浓度下降[25]。生态系统中磷的主要来源是依靠岩石风化以及少量的大气沉积[40]，氮沉降的急剧增加，磷输入相对较少，导致生态系统氮磷输入不平衡[39] [41] [42] [43]，最终导致磷限制。

氮富集使生态系统养分限制模式从氮限制转变为磷限制，这在不同陆地生态系统中已得到证实[34] [38] [42]。氮沉降下能够显著增加地上生物量，这将促进生态系统对于磷的需求[44]。地上生物量增加的同时最终会导致凋落物的质量增加，凋落物氮磷比增加[42] [45]。正如 Zhang 等人研究发现，地上地下生物都趋向于吸收稳态比例的养分，当凋落物氮磷比增加，土壤氮元素归还远远超过磷元素归还，这可能会降低依赖于氮有效性的相关磷元素有效性，降低净磷矿化率，增加生态系统尺度的磷限制[38] [46]。

4.2. 氮沉降对 ECM 真菌的影响

ECM 真菌能够与植物形成共生体，相互依存。ECM 菌根真菌在根系生长过程中占有重要地位[47] [48] [49]。ECM 真菌与植物形成共生体，最重要的功能就是帮助植物获取土壤中的氮。有研究表明，ECM 真菌能够在氮限制的条件下保持增长[50] [51]。同时，ECM 真菌能够吸收土壤中的 NH_4^+ 和 NO_3^- 供给植物生长，并利用土壤中的有机氮促进土壤氮循环[49]。因此，ECM 真菌必将会受到氮沉降的影响。

在氮限制条件下，ECM 真菌可以通过转化不能被根系直接吸收的多肽和蛋白质中的氮来供给宿主，有效缓解土壤氮限制[25] [28] [51]。氮沉降增加了土壤氮养分有效性，植物细根能够获取足够氮源，则会降低细根对于 ECM 真菌的依赖[13]，从而降低 ECM 真菌的多样性与丰富度。氮沉降会导致真菌子实体减少，降低 ECM 真菌的生产力。但也有学者发现，在其他子实体减少的同时，有一种菌种：管形鸡油菌 (Cantharellus tubaeformis) 在氮沉降下却提高了自身生产力[52]，这可能与特定真菌对环境的适应有关。

氮添加增加了土壤氮有效性，同时也影响了 ECM 真菌根尖生物量与菌丝的产生，用来调节植物对于 ECM 真菌碳供给和碳分配之间的平衡[53] [54]。有研究表明，随着氮沉降的增加，根尖生物量将会减少[55]。正如 Verlinden 等人对于氮沉积下 ECM 真菌的研究中发现，氮沉降的增加会导致 ECM 真菌生物量和产量减少，这可能是氮沉降能够增加土壤氮利用效率，植物供给 ECM 真菌碳的比例减少所致[14]。

尽管对于氮沉降影响 ECM 真菌的相关研究中，消极影响的报道占据主动，但也有报道显示一定量的氮输入可以对 ECM 真菌产生积极影响。Hendricks 等人在 2016 年的模拟氮沉降实验中发现，氮添加能够导致 ECM 真菌生物量的增加[16]，出现了与前人研究相反的结果。相似的，Kalliokoski 等人在 2010 年的研究中发现 ECM 菌丝体的产生与土壤氮肥力息息相关，越肥沃的土壤 ECM 菌丝体的产量反而越高[56]。这就说明氮添加导致 ECM 真菌的变化不仅仅只依靠氮氮素含量，还与其本身生存环境有关，与初始土壤养分密切相关。

4.3. 氮沉降对 SAP 真菌的影响

SAP 腐生真菌承担着土壤养分分解的重要角色，与 ECM 真菌同处一个生态位，共同参与土壤碳循环[57]。同时，SAP 真菌与 ECM 真菌存在一定的竞争关系，称之为“Gadgil 效应”，他们通过对于土壤养分的竞争，促进土壤碳的积累[58] [59]。这将会导致 SAP 真菌活性的降低，减少土壤有机质的分解[27] [60]。

SAP 真菌与 ECM 真菌相互竞争，ECM 真菌能够受到氮沉降的调控，SAP 真菌也必将受到氮沉降的影响。Maaroufi 等研究发现高氮添加量能影响 SAP 真菌的群落组成[54]。近些年的研究也表明，子囊菌

对于氮添加存在积极响应，这间接证明氮沉降会导致土壤中 SAP 真菌比例增加[17] [18]。Zhao 等最新研究中发现，氮添加能够增加 SAP 真菌的丰富度与相对丰度，远远大于降水的影响[19]。SAP 真菌群落主要受到土壤肥力的影响，尤其是土壤有机碳的影响[61] [62] [63] [64]。氮含量也是影响 SAP 腐生真菌的关键影响因素[61] [62]，SAP 真菌的组成与 C:N 和 N:P 显著相关。有机肥的添加也可以提高 SAP 真菌的活性、多样性和生物量[65] [66]，土壤 SAP 真菌群落也会随着土壤肥力梯度变化而变化[20] [67]。

5. 氮添加对土壤磷与 ECM 和 SAP 真菌关系的影响

自然界中有很多有机磷不能直接被生物吸收利用，需要依赖微生物的分解。植物各种生命活动都需要磷的参与，但研究一致显现出氮沉降导致生态系统磷含量降低的趋势[35]-[43]。微生物在磷转化的过程中起到关键作用，例如微生物能参与磷的矿化以及菌根真菌促进磷有效性吸收等[68]。Khalid 等对不同磷梯度下土壤微生物属性进行研究时发现，低磷位点的 ECM 真菌多样性和丰富度显著高于高磷位点，SAP 真菌却没有显著变化。低磷状态下，子囊菌门(Ascomycota)显著增加，高磷状态下担子菌门(Basidiomycota)显著增加，这也间接反映出 ECM 真菌对低磷状态的亲和性和 SAP 真菌高磷状态的亲和性[69]。Khalid 等选择的研究地点位于昆明市和楚雄市的交接处，是典型的富磷地域。因此，高磷状态抑制了 ECM 真菌多样性，也导致 SAP 腐生菌群落结构发生变化。

微生物群落与磷含量变化之间的关系已经被很多证据证实[70] [71]。长期氮沉降下，生态系统将会向磷限制转变。根据资源优化理论，ECM 真菌将通过调节土壤磷形态缓解植物磷限制[72]，SAP 真菌能够促进凋落物分解，促进土壤磷循环。因此，ECM 真菌与 SAP 真菌必将受到磷限制的影响。正如 Zheng 等最新的研究发现，ECM 真菌 Shannon 多样性指数与土壤有效磷显著正相关，ECM 真菌群落会受到磷限制的强烈影响[73]。因此，氮沉降降低土壤有效磷可能间接影响 ECM 真菌多样性。SAP 真菌通过分解复杂有机物获取碳素已被广泛研究，但最新研究发现，ECM 真菌基因表达中也具有分泌降解有机物各种酶的能力[74]。这说明 ECM 真菌本身也具有降解有机质的能力，即使 ECM 真菌对于有机质分解能力存在明显差异[75]，但这一能力却被忽视了很久。

ECM 真菌还可以直接产生磷酸酶，扩大根系吸收更多的磷[22]。最近研究表明，ECM 和 SAP 真菌的磷酸盐转化功能极为相似，SAP 真菌和 ECM 真菌都通过分泌有机酸和产生水解及氧化外酶来促进氮和磷的活化[21] [76] [77]。在氮沉降下，土壤磷含量发生变化，ECM 和 SAP 真菌可能缓解磷限制这一现象。此外，ECM 和 SAP 真菌对磷的响应不仅依赖于土壤提供的磷，同时可能还依赖于磷和氮的相互作用[21] [77]。

6. 总结与展望

6.1. 总结

我们综述了氮沉降对于土壤磷含量、ECM 和 SAP 真菌群落影响的相关研究，系统地梳理了氮沉降下土壤磷含量与真菌群落的关系，虽然相关研究广泛开展，但仍存在较大的局限性。氮沉降对于磷含量产生负面影响的研究已经被大多数学者认同，但大多数研究都关注氮沉降对磷含量的直接作用，并没有探究更深层次的机制影响。

前人研究更多关注的是单一层面的影响，例如：氮沉降对于磷的影响，对于 ECM 真菌、SAP 真菌的影响。并没有系统考虑多元素之间的关系，也没有考虑真菌之间的协作与竞争是否影响最终结果，缺乏对于氮沉降(环境变化)、磷(养分)、真菌(微生物)之间相关关系的系统解释，这将成为未来的重点研究领域。

虽然 ECM 真菌与 SAP 真菌之间存在生态位重叠，但氮沉降对于 ECM 真菌的研究与对 SAP 真菌的

研究数量严重失衡，氮沉降如何影响 SAP 真菌群落的研究仍有空缺。

6.2. 展望

在以后氮沉降如何影响土壤磷含量的研究中，需要关注土壤因子之间的相互作用，地上地下的协作功能等。例如，氮沉降是否影响土壤微生物并导致磷含量的变化，微生物是否为承担这一过程的媒介等，亟需加强。

土壤磷对真菌群落的影响存在不同的结论，这可能是由原始土壤环境的不同所决定。因此，需要加强对原始土壤条件如何影响氮添加机制的对比研究。

虽然氮沉降与 ECM 真菌存在显著负效应已被报道，但相对立的研究结果依然存在。同时，氮沉降如何影响 SAP 真菌群落的研究仍有很大不足，因此需要更系统、全面地探索出现相反结果的原因，探寻真菌群落对氮沉降响应的普适性规律。

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