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氮沉降对植物病原菌影响的研究进展

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摘 要

氮沉降是影响所有陆地生态系统结构和功能的重要环境因子，对植物和病原菌及其交互作用均产生重要影响。然而，关于氮沉降对植物病原菌影响的研究往往被忽视。植物病原菌作为一种存在于不同生态系统中和已知所有植物谱系中的生物类群，对于调节植物运输和吸收、生长发育以及抵御病害能力等均具有重要意义。基于此，本文综述了近年来的相关研究文献，分别从氮沉降对植物病原菌(细菌和真菌)侵染特性、生长发育、多样性和丰富度的影响以及植物－病原菌的互作关系等方面进行了系统分析，提出了应重点关注的研究领域和方向，旨在为病原菌生态功能及其对气候变化的响应研究提供科学依据。

关键词

氮沉降，病原菌，多样性，丰富度，植物－病原菌交互作用

Research Progress on the Effects of Nitrogen Deposition on Plant Pathogens

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Abstract

Nitrogen deposition is an important environmental factor affecting the structure and function of all terrestrial ecosystems, which has important effects on plants, pathogens and their interactions.

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However, studies on the effects of nitrogen deposition on plant pathogens are often neglected. Plant pathogens are a biological group present in different ecosystems and known in all plant lineages. It is of great significance for regulating plant transport and absorption, growth and development, and disease resistance. Based on this, this paper reviewed the relevant research literatures in recent years, and systematically analyzed the effects of nitrogen deposition on the infection characteristics, growth and development, diversity and richness of plant pathogens (bacteria and fungi), as well as the interaction between plants and pathogens. The research fields and directions that should be focused on were proposed to provide scientific basis for the study of the ecological function of pathogens and their response to climate change.

Keywords

Nitrogen Deposition, Pathogens, Diversity, Richness, Plant-Pathogen Interaction

1. 引言

植物病原菌在自然植物群落中发挥着双重且非常重要的作用[1] [2]。它既是造成植物疾病的主要病原体，也会对生态系统的结构和功能、生长和发育、生物多样性等造成严重威胁和灾害[3]。然而，植物病原细菌和真菌作为植物病原菌两类重要的类群，其侵入植物组织内利用活的根组织来提取营养物质，导致根系形态发生改变并对其产生显著影响[4] [5]。同时，植物根际病原菌也可以诱导植物改变根际群落和增加有益菌群进一步提高抵御病害能力，从而促进植株生长[6] [7]。

氮是植物必需的营养元素，是植物生长发育的重要元素，对植物抵抗病原菌方面起着重要作用[8]。然而在过去的一个世纪里，由于人类在全球范围内的活动，燃烧过量的化石燃料、过度的使用化肥以及汽车尾气的过量排放，导致人为氮沉降比自然氮沉降显著增加，使得大量活性氮(Nr)进入陆地生态系统中，从而导致了全球性的氮沉降问题[9] [10] [11]。在大气中活性氮主要通过干、湿两种途径沉积将局部氮循环扩散到全球尺度，从而影响了森林生态系统的平衡[12] [13]。目前，中国大气氮含量从 1980 年的 13.7 kg Nhm^{-2} 持续增加到 2010 年的 19.6 kg Nhm^{-2}，预计到 2050 年氮沉降速率将再次翻倍[14] [15]。上世纪，由于欧洲和北美比中国率先进入工业化进程，导致活性氮排放量增大。然而，随着经济的发展，逐渐认识到氮沉降所带来的负面问题。因此，到 21 世纪之后氮沉降有所缓和[16]。相比之下，北美和欧洲在 2006 年到 2008 年的总氮沉积分别为 5.9 kg Nhm^{-2} 和 9.8 kg Nhm^{-2} [17] [18]。此外，有数据显示，我国氮沉降在 2000 年将达到顶峰，在 2011 年到 2015 年下降了 21% [19]。即便如此，当下全球仍然面临着减少活性氮排放和氮沉降对人类健康和环境的负面影响[20]。在中国北方地区，由于集约化的生产模式，总氮沉降的速率达到了 22.6 kg Nhm^{-2}，而过量的氮沉降又会诱发一系列的环境问题[21]。例如，氮沉降可以改变生物地球化学循环[12]、改变生态系统结构和功能[22]、改变土壤性质(造成土壤酸化)以及影响生态系统碳循环，进而影响全球气候变化[23]。其中由氮沉降引起的植物特性变化也将对植物病原菌产生显著的影响[24]。事实上，大部分植物中都存在植物－病原菌互作现象。因此，为进一步揭示大气氮沉降对植物病原菌的影响及其机制，本文分别从氮沉降对病原菌侵染特性、生长发育、病原菌多样性、病原菌丰富度以及对植物病原菌互作关系的影响等方面对以往研究进行了系统分析，提出应重点关注的研究领域和方向，旨在为病原菌对生态系统功能造成的影响提供技术支持。

2. 氮沉降对植物病原菌侵染和生长的影响

2.1. 氮沉降对植物病原菌侵染特性的影响

在复杂的生态系统中，病原菌数量丰富，对宿主有很大的影响[25]。然而，通过病原菌来调控植物群落中病原菌的侵染研究少之又少[26] [27]。我们也只能通过以往这些研究，可知侵染会造成草地生物量生产的减少[28]，而氮沉降也只是直接或间接地改变侵染的驱动因素之一[29]。其中氮沉降影响病原菌侵染方式有：一是增加植物氮浓度直接影响病原侵染率，二是通过氮富集改变植物生长速率，进而改变植物物种丰富度，间接影响病原菌侵染途径[30] [31] [32]。具体而言，植物病原菌可以通过侵入细胞壁而进入植物内部(如叶内或者根内病原菌)，或不与植物进行直接接触(如植物根际土壤微生物)，在植物赖以生存的环境周围通过分泌多种代谢产物而对植物生理生化特性及其功能产生显著影响[13] [33] [34]。例如，植物病原菌侵染植物叶片后，会抑制氮素的运输和吸收，从而导致寄主植物的光合能力减弱[35]。此外，也有研究发现，当根际土壤中有效氮含量增高时，就会造成 NH_4^+-N 的积累，导致宿主植物的病情指数升高，进而提高植株的侵染率[36]。同时，高水平的氮添加也可以通过改变植物的解剖和生化特性和病原菌的来源，增加宿主抗性和补偿性生长(耐受性)，从而直接增加或减少病原菌的侵染率[37] [38]。然而，当土壤中有效氮含量下降时，植物又会依赖内在病原菌而抵御其他疾病的侵染。因此，这符合植物－氮营养模型，在提高其氮需求时，植物进入一种自我封闭状态，即任何额外氮肥的施入对生物量几乎没有影响[39] [40]。另外一种解释是，在施氮过程中，所产生的瞬时脉冲增加了真菌病原的攻击性，从而降低疾病侵染率[41]。此外，氮沉降对植物病原菌的影响也会随寄主植物类群的不同而不同，至今尚无一致的结论。Ishida 等[42]研究表明，氮添加没有对不同森林类型及其优势寄主植物根系真菌侵染产生显著差异，但有利于提高叶片的抗性[43] [44] [45] [46]。

基于上述，笔者都是从单一“氮角度”分析了不同氮水平的增加或减少以及直接或间接对病原菌的侵染和影响。然而，也有相关研究从植物生长策略和植物多样性丧失入手[47]，针对植物功能群和病原菌侵染的关系，详细阐述了快速生长的植物群落有更高的侵染率，导致病原菌的影响比生长缓慢的植物群落更弱[48] [49]，这符合生长－防御权衡假说。此外，在植物多样性丧失方面，当病原菌的宿主广泛分布在不同的群落时，单个病原菌的侵染会逐渐减少，因为宿主的丰度和病原菌传播较低[50] [51]。但是，在不同的群落中，单个病原菌的侵染也会逐渐加重，这是因为非专性病原菌的溢出和对外界无影响的病原菌的增加[52] [53]。因此，植物多样性可以影响单个病原菌(即专性程度和传播模式)，也可以对整个病原菌群落的侵染产生积极、消极或没有影响(即总体多样性效应)。

2.2. 氮沉降对植物病原菌生长的影响

在生态系统尤其是农业生态系统中，氮素是植物病原菌生长所需的重要营养元素，是病原菌从植物体内争夺的关键元素[54] [55]。在低水平氮添加处理下，植物病原菌受氮元素的影响较小，加之植物病原菌具有一定的特异性，所以对植物生长发育未产生明显影响。但是，也有研究学者提出不同意见：在氮沉降水平低的情况下(即低水平氮添加处理下)，也能显著影响植物生长以及植物相关微生物多样性[56]。有学者从另外一个角度对原生草原内生菌研究得出，内生菌对寄主植物的影响不仅受到氮素的影响，还会受到生物因子 AMF 和病原菌的影响。因此，内生菌也是影响植物生长不可忽视的因素之一[57]。然而，Dordas [58]的研究表明，随着氮水平的升高，活体营养性和半活体营养性病原体易感性也随之上升。在氮添加对水稻的研究中发现，总氮含量与稻瘟病易感性之间有显著相关性[59]，而氮素又是诱导真菌侵袭的主要因素。在高氮条件下，籼型水稻叶片全氮含量显著增加了 8.5%。因此，高氮会显著增加真菌病原菌基因的表达而降低植物的抵御能力，最终导致水稻的抗病性严重下降[60]。

在生态系统中，寄主植物防御能力的降低也可能促进了更多样的病原菌的入侵。例如，在对欧洲白杨的研究中，15~150 kg Nha^{-1} 氮添加显著抑制生长缓慢和单宁含量高的基因型，并有利于生长迅速和单宁含量低的基因型[61]。施氮可导致颤栗叶中次生化合物浓度降低，包括单宁酸、沙霉素、震颤霉素和总酚等具有抗真菌病原作用的类型[62] [63]。此外，持续的氮输入(来自肥料使用和氮沉积)，通过改变土壤性质来增加土壤真菌植物病原体的相对丰度，而其相对丰度的增加转化为更高的定植率(来自土壤中病原体的植物组织)，从而进一步影响植物的生长和存活[64]。在不同氮添加处理水平下对盆栽植物叶片生长研究发现，在对照水平下，植物叶片氮浓度没有显著影响[65]，而在高氮水平下，通过增加叶片氮浓度，促使 C_4 草的病原菌负荷加重(病原体负荷是由寄主植物丰度加权的疾病严重程度表征)，从而对 C_4 草的生长造成了影响[66]。

3. 氮沉降对植物病原菌多样性的影响

氮沉降通过改变土壤环境因子，显著增加了对植物病原菌多样性和对生态系统功能的影响[45]。Wu 等[67]在研究根系相关病原真菌多样性对长期氮沉降响应时得出，长期氮添加没有改变根相关真菌的总丰度(基于根葡萄糖胺浓度)或根系相关植物病原菌的相对丰度和物种丰富度。然而，长期的氮添加增加了植物病原真菌在属水平上的 Shannon 多样性和均匀性，并影响与养分吸收和宿主防御相关的其他真菌。此外，根据 Jung 等[68]和 Kwak 等[69]在嗜亚硝基植物对病原菌多样性影响的研究发现，噬氮植物 *A. nudicaulis* 和植物病原菌的丰富度显著正相关，而与 Shannon 多样性或丰富度没有明显关系。而另外一种噬氮植物 *M. canadense* 和植物病原菌多样性没有相关性。但是在林下 *A. nudicaulis* 和 *M. canadense*，这两种嗜氮植物的总丰度却和植物病原菌的丰富度呈现显著正相关。因此，发现大多数与根系相关的病原菌是非专性的。并且，这进一步证明了长期氮添加是可以通过增加易亲硝化植物在群落水平上的优势来增加病原菌多样性的[70] [71]。

Karst 等[72]的田间试验研究结果表明，氮添加同样增加了病原真菌的多样性。具体来说，黄斑文尿菌是与氮添加相关的主要病原体，该物种已知会导致胡杨的叶和芽枯萎病[73] [74]。与此同时，根据“氮病假说”指出，高氮有效性增加了植物的适口性和对病原菌的敏感性，这是由于代谢速率、组织氮浓度和比叶面积的增加所造成[66] [75]。并且，Nguyen 等[76]对 47 项研究进行的 Meta 分析中，发现氮素添加会增加植物真菌病的严重性(即病原菌丰度)。氮添加正在导致当地乡土植物物种的急剧减少，以及包括高海拔草甸在内的许多生态系统的功能组成的转变[70] [77]。因此，氮的添加可能会通过改变土壤性质或寄主植物物种丰富度来影响土壤植物病原体的相对丰度[78]。

4. 氮沉降对植物病原菌丰富度的影响

植物病原菌在自然生态系统中起着双重且非常重要的作用[2] [79]，而长期氮沉降会通过增加植物病原菌的相对丰度而严重威胁生态系统健康。另外，一系列的非生物和生物因素也是影响植物病原菌丰度的关键推手[70]。具体而言，在农业生态系统中，营养物质的输入就是增加植物病原菌丰度的主要因素之一[80]。例如，高氮添加可以显著提高植物代谢率、组织氮浓度、特定叶面积，进而增加植物的适口性和对病原菌的易感性[75]。在自然生态系统中，“稀释效应假说”认为，随着宿主物种丰富度的增加，病原菌丰度是降低的[81]，而通过在天然草地生态系统、植物－土壤反馈或高寒草甸系统都显著印证了这一稀释效应[70] [82] [83]。

氮沉降通过改变寄主植物物种丰富度来影响土壤和根系植物病原菌相对丰度的[78]。根据 Thalineau 等[54]研究发现，0~15 g/m^2 施氮处理水平与土壤植物病原菌的相对丰度呈显著正相关(ER = 13.72, De = 27.95)，而在预测病原菌相对丰度的一般线性模型中，土壤 NH_4^+ 解释了 66.96%的相对病原菌丰度变化，

土壤 NO_3^- 解释了 44.84%的相对病原菌丰度。基于上述，得出氮添加通过改变土壤性质，显著增加了不同处理下植物病原菌的相对丰度，并且确定了氮添加条件下的土壤病原菌丰富度直接取决于局部定植的相对强度[78]。然而，Soonvald 等[84]通过替代有机施肥处理对土壤和根系病原菌的研究发现，替代有机施氮处理中土壤病原菌相对丰度显著增加，且这种影响在生长季节尤为突出。

5. 氮沉降对植物–病原菌交互作用的影响

氮素被认为是陆地生态系统中植物生长的主要限制因子，生态系统氮输入不成比例的增加预计将加剧资源的限制，而病原菌在决定植物群落结构方面有重要作用[85]。因此，理解植物–病原菌的交互作用对氮富集的响应有着重要作用[58]。同时，植物类群和植物病原微生物之间复杂的交互作用也可以被多种环境因子影响。在这些非生物因子当中，也有研究表明，氮素有效性的变化可以改变植物、微生物和植物病原菌的昆虫载体的适合度[86] [87] [88]。它们依赖于氮素的媒介关系，氮富集可以增加或者减少病原菌负荷和抗性[89]。例如，土壤微生物和氮富集的相互作用能有效影响植物–病原菌的互作，可以通过多种机制介导植物与病原菌的交互作用，包括改变植物氮的获取量，也可以通过固氮、氮矿化和扩展根系网络来增加植物对氮素的获取[90]。并且根据 Yang 等[91]研究表明，高水平氮添加也可以降低植物病原菌类群，从而提高植物类群的抗病性。此外，也有田间试验证明了氮添加可以改变自然植物群落结构，加剧病原菌的发生和传播，增强寄主植物的抗性来降低疾病侵染程度[41]。氮添加还能改变植物类群和植物病原菌之间的竞争关系[92]，从而降低诸如植物叶氮含量，最终影响其光合速率[70]。与之相反，在青藏高原东部的高寒草甸进行的一项长期研究发现，10 g/m^2 氮添加也能够改变土壤性质，增加土壤真菌植物病原菌的相对丰度[93]，抑制难降解碳的形成以及降低微生物活性[94]。氮添加也能够导致草原生态系统稀有类群种类的丧失，从而加重了植物病原菌对于植物的侵害能力[95]。同时，也有研究发现在亚热带森林生态系统，外源氮添加可以通过改变土壤环境因子，显著增加植株对病原菌侵染的抵抗力[79]。尽管氮素能够影响植物–病原菌的互作已经被广泛证明，但具体的途径尚需进一步研究。

6. 结论与展望

本文综合考虑了陆地生态系统中氮沉降对植物病原菌侵染和生长、多样性和丰富度以及植物–病原菌交互作用的最新信息。基于对国内外不同氮添加对植物病原菌的研究，得出如下结论：我们发现不同氮水平处理是把双刃剑。适量的氮处理可以帮助植物依赖内在病原菌而抵制其他疾病的侵染[39]，并且有效促进植物生长和发育以及显著改变植物相关微生物多样性[56] [57]。然而，当氮处理超过一个临界值时，氮添加可以显著抑制植物生长、提高植株侵染、增加病原菌多样性以及增加植物病原菌的易感性[13] [72] [75]。与此同时，高水平氮添加也可以通过改变土壤理化性质和降低植物病原菌类群而增加病原菌相对丰度，提高植物类群的抗病性[91] [94]。

人类活动导致大气氮沉降显著增加，大量活性氮进入陆地生态系统，打破了原有的生态平衡，多数研究注重其负面影响，对于氮沉降引起植物病原菌变化的内在机制还存在很大争议，对氮沉降如何通过影响植物功能性状进而间接影响植物病原菌群落结构仍知之甚少。因此，合理运用高通量测序等技术手段，从不同角度对环境病原菌群落结构的变化进行分析，阐明氮沉降对植物病原菌群落组成和多样性的影响，进而揭示其对生态系统结构和功能的影响机制，是今后该研究领域的重点内容。此外，利用多尺度、多维度、跨区域的方法，科学构建氮沉降模型，对于厘清氮沉降对植物病原菌的影响机制至关重要。但当前关于模拟氮沉降对植物病原菌菌群变化的长期试验尚未系统开展，合理构建耦合生态系统地上和地下菌群变化的长期控制试验势在必行。

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