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长期氮添加对温带落叶阔叶林优势植物叶片次生代谢产物的影响

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摘 要 植物次生代谢产物(PSM)与植物的生长发育、抵御生物与非生物胁迫的能力密切相关, 在植物对环境的适应策略中发挥至关重要的作用。然而, 目前森林生态系统中植物叶片PSM如何响应长期氮添加尚不清晰, 限制了对氮沉降背景下树木抗性及森林生态系统稳定性变化的理解。该研究基于连续12年的氮添加实验平台, 选取了北京东灵山温带落叶阔叶林中的乔灌层优势植物, 包括白桦(*Betula platyphylla*)林的优势植物白桦和毛榛(*Corylus mandshurica*), 以及蒙古栎(*Quercus mongolica*)林的优势植物蒙古栎和大花溲疏(*Deutzia grandiflora*), 旨在探究两种林型的土壤理化性质、4种植物的叶片酚类PSM (总酚、黄酮和单宁)含量及乔木生长对长期氮添加的响应。结果表明, 白桦林土壤水分和养分含量均高于蒙古栎林; 氮添加显著降低了白桦林的土壤pH和蒙古栎林的土壤含水量, 并增加了蒙古栎林的土壤全磷含量。整体上, 白桦林和蒙古栎林的优势植物的叶片酚类PSM含量对氮添加的响应并不一致, 表现为白桦林呈上升趋势, 而蒙古栎林则呈下降趋势, 尤其是在高氮添加处理下较为显著。4种植物的叶片酚类PSM含量与叶片养分含量存在权衡关系, 并受到土壤水分和养分的调控。此外, 氮添加后, 白桦的相对生长速率呈下降趋势, 而蒙古栎则呈上升趋势。这些结果暗示氮沉降背景下不同林型差异化的养分分配及生长-抗性平衡策略。相较于白桦林, 水分和养分相对贫瘠的蒙古栎林在长期氮沉降的影响下很可能较早出现脆弱性相关(如昆虫植食性水平增加, 病原菌丰度上升等)的问题。

关键词 氮沉降; 温带落叶阔叶林; 植物次生代谢产物; 土壤理化性质; 养分分配策略

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Effects of long-term nitrogen addition on leaf secondary metabolites of the dominant plant species in a temperate deciduous broad-leaved forest

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Abstract

Aims Plant secondary metabolites (PSMs) are closely related to plant growth, development, and the ability to resist biotic and abiotic stresses, playing a crucial role in plant adaptation strategies to the environment. However, the response of leaf PSMs to long-term nitrogen (N) addition in forest ecosystems remains insufficiently studied, which largely limits our ability to grasp the changes in tree resistance and forest ecosystem stability under N deposition.

Methods Our study is based on an 12-year N addition experiment platform, focusing on four dominant plant species in the temperate deciduous forest of Donglingshan: including the plants *Betula platyphylla* and *Corylus mandshurica* in the birch forest and *Quercus mongolica* and *Deutzia grandiflora* in the oak forest. We investigated responses of soil physicochemical properties in two forest types, leaf phenolic PSMs (i.e., total phenolic, flavonoid, and tannin) contents of four plant species, and tree growth to long-term N addition.

Important findings The results showed that soil water and nutrient contents of birch forest were higher than

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those of oak forest. N addition significantly decreased soil pH in birch forest and soil water content in oak forest, and increased soil total phosphorus content in oak forest. Overall, the responses of dominant plant species to N addition exhibited contrasting trends, with leaf PSMs showing an increasing trend in the birch forest and a decreasing trend in the oak forest, particularly under high N addition treatments. The leaf phenolic PSMs contents of the four plant species exhibited a trade-off with leaf nutrient contents which was regulated by soil water and nutrient availability. Additionally, after N addition, *B. platyphylla* showed a decreasing trend in relative growth rate, whereas *Q. mongolica* showed an increasing trend. These results suggested different nutrient allocation and growth-defense balance strategies among different forest types under N deposition. Compared to the birch forest, the oak forest, which was relatively poor in water and nutrients, was likely to experience vulnerability-related issues (e.g. increased levels of insect herbivory and higher abundance of pathogens) earlier under the influence of long-term high N deposition.

Key words nitrogen deposition; temperate deciduous broad-leaved forest; plant secondary metabolites; soil physicochemical property; nutrient allocation strategy

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大气氮沉降已成为全球性的生态环境问题, 我国是全球氮沉降热点区域之一(Vet et al., 2014; Wang et al., 2017)。虽然当前我国氮沉降速率已趋于稳定, 但相比美国和欧洲, 仍处在较高水平(Yu et al., 2019; Wen et al., 2020), 尤其是我国东部森林生态系统面临较严峻的氮沉降压力(Du et al., 2016)。长期或过量的氮输入可能产生富营养化效应(Simkin et al., 2016; Weldon et al., 2022), 对森林生态系统产生不利影响, 如加剧土壤酸化(Lu et al., 2018)、增加植物病原菌的丰度(Wu et al., 2021)和病虫害发生的风险(Throop & Lerdau, 2004; Martínez et al., 2024), 导致生物多样性锐减(Bobbink et al., 2010; Midolo et al., 2019)、生态系统生产力及稳定性下降等(Gundale, 2022; Schulte-Uebbing et al., 2022)。

为应对干旱、土壤贫瘠等胁迫性环境条件, 植物进化出了多种防御性状, 以维持生长代谢, 同时降低因植食性昆虫取食所带来的损害风险(Agrawal & Fishbein, 2006)。其中, 植物次生代谢产物(PSM)在调控植物对生物和非生物胁迫的响应中发挥着重要作用(Jamieson et al., 2017; Erb & Kliebenstein, 2020; Tak & Kumar, 2020)。总酚(TP)、黄酮(FLA)、单宁(TA)等酚类化合物是高等植物中最常见的PSM, 尤其是在森林树木生长、发育及其与植食性昆虫互作方面的研究中备受关注(Lämke & Unsicker, 2018)。前人研究表明, 在植物不断适应其生存环境的过程中, 这些化合物可能已经同时进化出特定的生理和生态功能(Holopainen et al., 2018)。例如, 总酚作为酚类化合物的总和, 是植物叶片表征化学防御能力的综合指标(Hanley et al., 2007)。黄酮被认为具有抵御病原菌侵染的功能(Tan et al., 2022)。单宁可导致蛋白质类物质功能丧失(李明等, 2007), 被认为是对植食动物起威慑作用的主要物质。因此, 在全球变化加剧的背景下, 研究PSM对全球变化因子的响应, 有助于深入理解植物与环境之间的内在联系, 对于评估树木的抗逆性及森林生态系统面临的风险具有重要意义。

前人开展的模拟氮沉降实验发现, 植物的PSM通常表现出高度可塑性和营养敏感性(de Long et al., 2016)。氮输入会通过影响土壤、根际微生物等(Li et al., 2021; Lv et al., 2024)对植物地上部分的PSM合成与累积产生显著影响(Liu et al., 1999)。例如, 在瑞典亚北极苔原灌丛植被带, 氮添加降低了群落水平上杜鹃花科矮灌木的酚类化合物的含量(de Long et al., 2016)。类似地, 高浓度的氮添加可诱导挪威东南部温带海洋性气候区云杉(*Picea asperata*)针叶中的多种酚类化合物浓度降低并改变其组成(Nybakken et al., 2018)。另外一些研究却发现, *Athrixia phylicoides*、青钱柳(*Cyclocarya paliurus*)叶片的总酚和黄酮含量会随氮添加的剂量增加呈现出先增加后降低的趋势(Tshivhandekano et al., 2018; Deng et al., 2019; 秦健, 2023)。可见, 植物PSM含量对氮沉降的响应很可能存在物种特异性, 但是目前不同物种PSM响应氮沉降的研究依然十分有限。此

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外, 目前的氮添加实验年限大多较短(<10年), 或者是基于盆栽实验开展, 用来模拟自然森林生态系统中树木对长期氮沉降的响应存在一定的局限性。

资源可用性假说(resource availability hypothesis)通常被认为是解释植物防御模式最成功的理论(Coley et al., 1985), 该假说预测, 在资源丰富的环境(例如土壤水分、养分)中生长的植物, 将更多地投资于生长, 而较少地投资于防御。这一观点与生长分化平衡假说(growth-differentiation balance hypothesis)的观点相呼应, 后者认为: 在资源充足时, 植物以生长为主, 而在资源受限时, 植物以分化为主(Wareing & Phillips, 1981; Herms & Mattson, 1992)。此外, 已经有许多研究证实了叶经济性状(如叶片养分含量)与叶片PSM含量的权衡关系(程思祺等, 2022), 即资源获取型策略的物种有较低的防御能力(Morrow et al., 2022)。因此, 结合森林生境条件、植物养分状况及树木生长, 研究植物如何对以氮沉降为代表的环境变化产生次生代谢的适应性调整, 有助于揭示氮沉降背景下的植物养分分配策略。

在氮沉降背景下, 温带森林存在较大的生产力提升和碳汇潜力(Schulte-Uebbing et al., 2022; Xing et al., 2022), 但同时也很可能面临着植食性昆虫取食和病虫害发生频率升高的风险, 影响森林生态系统结构、功能和稳定性(Dobor et al., 2024)。为了深入理解温带森林不同树种PSM含量及其对氮沉降的响应, 为解析氮沉降背景下温带森林植物-植食性昆虫间互作的过程与机制做好铺垫, 本研究选择了北京市东灵山两种温带典型森林, 分别是白桦(*Betula platyphylla*)林和蒙古栎(*Quercus mongolica*)林, 探究其优势植物叶片酚类化合物含量对长期氮添加的响应。该研究区位于东亚高氮排放和高氮沉降的热点地区——京津冀地区的周围(Zhang et al., 2021), 属于氮限制型森林系统(冯继广和朱彪, 2020)。本研究依托北京大学生态学系建立的中国东部森林养分添加实验平台(NEECF) (Du et al., 2013), 在连续12年施氮实验样地中, 以白桦林和蒙古栎林内的优势乔木和灌木为研究对象, 探究长期氮添加下4种优势植物的叶片酚类化合物(总酚、黄酮和单宁)的影响。同时, 结合土壤理化性质、叶片养分及树木生长, 解析温带森林在氮沉降背景下的次生代谢适应机制。

1 材料和方法

1.1 研究区概况

研究区域位于北京市东灵山森林生态系统定位研究站(39.96° N, 115.43° E, 海拔1 300 m)。该区域属于暖温带半湿润季风气候, 年平均气温为5.4 ℃, 年降水量为650 mm, 背景大气氮沉降速率约为15 kg·hm^{-2}·a^{-1} (Du et al., 2013)。主要土壤类型为褐土(根据中国土壤分类系统), 土层厚度为90–120 cm (邹安龙等, 2019)。白桦林乔木层优势物种为白桦, 伴有少量黑桦(*B. davurica*)和山杨(*Populus davidiana*), 灌木层常见物种包括毛榛(*Corylus mandshurica*)、巧玲花(*Syringa pubescens*)、六道木(*Zabelia biflora*)和土庄绣线菊(*Spiraea ouensanensis*)等; 草本植物主要包括舞鹤草(*Maianthemum bifolium*)、蒙古风毛菊(*Saussurea mongolica*)和三脉紫菀(*Aster ageratoides*)等。蒙古栎林乔木层优势物种为蒙古栎, 伴有少量黑桦和大叶白蜡(*Fraxinus chinensis* subsp. *rhynchophylla*)等; 林下灌木常见物种包括大花溲疏(*Deutzia grandiflora*)、小花溲疏(*D. parviflora*)、六道木、土庄绣线菊和胡枝子(*Lespedeza bicolor*)等; 草本植物主要包括野青茅(*Deyeuxia pyramidalis*)、蒙古蒿(*Artemisia mongolica*)和银背风毛菊(*S. nivea*)等(姚辉等, 2015)。

1.2 实验设计

氮添加实验采用完全随机区组设计。实验开始于2011年7月, 白桦林和蒙古栎林各有3个区组, 每个区组设置对照(CK, 0 kg·hm^{-2}·a^{-1})、低氮(N50, 50 kg·hm^{-2}·a^{-1})和高氮(N100, 100 kg·hm^{-2}·a^{-1}) 3种氮添加处理, 每种处理重复3次, 共18个样方。氮添加梯度的设置是参考了全球其他同类实验的设置梯度, 同时综合考虑NEECF平台上不同森林类型站点的可比性(设置依据详见Du等(2013))。样方大小为20 m × 20 m, 样方之间设置10 m的过渡带。由于北京地区政策管控, 在该站点采用尿素($CO(NH_2)_2$)代替硝酸铵(NH_4NO_3)作为氮源。每年生长季(5–10月)的每月月初, 将相应质量的尿素彻底溶解于30 L水中, 用喷雾器均匀喷洒于氮添加样方。对照样方仅喷洒相同质量的清水。

1.3 样品采集

研究对象分别为白桦林的优势乔木白桦和优势灌木毛榛, 蒙古栎林的优势乔木蒙古栎和优势灌木

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大花溲疏。于2023年7月初, 在白桦林、蒙古栎林每个样地内随机抽取3株乔木和3株灌木。每个植株采集20–40片成熟叶片, 乔木样树是利用高枝剪采集目标树树冠中下层叶片, 采样高度尽量一致。采集的叶片置于放有冰块的保温箱中, 快速送至实验室。随后, 利用烘箱在65 ℃下烘干至恒质量, 利用高通量组织研磨仪(Tissuelyser-II, 上海净信实业发展有限公司, 上海)粉碎后进行次生代谢产物和叶片养分含量的测定。

在目标树周围50 cm处, 去除枯枝落叶层, 使用手持式钢土钻收集3个0–20 cm土壤的子样本并混合成一个样品。将每个土壤样品分为两份子样品, 第一份子样品测定鲜质量后, 在105 ℃下烘干至恒质量获得干质量, 从而计算土壤含水量(SWC); 第二份子样品风干后粉碎、过筛, 用以测定土壤全碳(STC)、土壤全氮(STN)、土壤全磷(STP)含量和土壤pH。

1.4 样品测定

1.4.1 土壤理化性质测定

使用元素分析仪(Elementar Vario EL III, Elementar, Hesse, Germany)测定土壤全碳和全氮含量, 使用电感耦合等离子体发射光谱仪(ICP-OES, Thermo 6300, Thermo Scientific, Waltham, USA)测定土壤全磷含量。土壤pH通过将10 g土壤样品溶于蒸馏水中(水土质量比2.5:1), 利用pH计测定悬浮液pH得到。

1.4.2 叶片养分含量测定

使用元素分析仪测定叶碳含量(LCC)和叶氮含量(LNC), 使用电感耦合等离子体发射光谱仪测定叶磷含量(LPC)。

1.4.3 叶片次生代谢产物含量测定

采用福林-酚比色法测定总酚含量(李静等, 2008), 以没食子酸(Gallic acid, Sigma-Aldrich, Saint Louis, USA)为标准物质。具体步骤如下: 称取充分研磨后的80 mg叶片粉末样品, 加入2 mL 70%乙醇并充分振荡。超声浸取15 min后, 放入高速离心机离心(8 000 r·min^{-1}, 10 min), 分离上清液。取40 μL上清液, 依次加入1.8 mL福林酚试剂和1.2 mL 7.5%的碳酸钠溶液, 避光静置1.5 h。以不含没食子酸标准溶液的试管为对照, 使用紫外可见分光光度计(UV-3300, 上海美普达仪器有限公司, 上海)测定溶液在765 nm波长下的吸光值。

采用硝酸铝-亚硝酸钠-氢氧化钠络合法测定黄酮含量(宋元清等, 2005), 以芦丁(Rutin, Sigma-Aldrich, Saint Louis, USA)为标准物质。具体步骤如下: 量取1 mL测定总酚过程中提取的样品滤液, 依次加入0.3 mL 5%的亚硝酸钠溶液、0.3 mL 10%的硝酸铝溶液和4 mL 4%氢氧化钠溶液。每添加一种溶液后, 需充分振荡并静置, 最后用蒸馏水定容至10 mL。以不含芦丁标准溶液的试管为对照, 使用紫外可见分光光度计测定溶液在510 nm波长下的吸光值。

采用钨酸钠-磷钼酸比色法测定单宁含量(中华人民共和国农业部, 2008), 以单宁酸(CAS: 1401-55-4)为标准物质。具体步骤如下: 称取10–20 mg叶片粉末样品, 加入4 mL 60%乙醇, 超声浸取10 min并过滤, 加入60%乙醇定容至5 mL, 得到样品溶液。取1 mL样品溶液至试管中, 依次加入0.3 mL钨酸钠-磷钼酸显色剂、0.5 mL 7.5%的碳酸钠溶液和3.2 mL水, 摇匀并静置30 min。以不含单宁酸标准溶液的试管为对照, 使用紫外可见分光光度计测定溶液在760 nm波长下的吸光值。

1.5 树木相对生长速率测定

对于叶片采样的白桦和蒙古栎目标树, 我们连续12年监测了树木胸径的变化情况。2011年10月, 用精度为0.1 cm的软尺对样方内所有植物测量初始胸径(DBH, 树高1.3 m处), 并将样方内所有DBH ≥ 3 cm的树进行编号, 挂牌, 并安装铝制自动测树器。待测树器稳定后, 每年定期用精度为0.01 mm的电子游标卡尺测量测树器窗口的变化。然后, 根据窗口大小的差值计算树木当年的胸径值, 进而计算相对生长速率(RGR) (Tian et al., 2017)。主要参考以下公式:

$$\mathrm{DBH}_t = \mathrm{DBH}_1 + \frac{X_t - X_1}{\pi \times 10}$$

$$\mathrm{RGR} = \frac{\ln(\mathrm{DBH}_t) - \ln(\mathrm{DBH}_1)}{\Delta t}$$

式中, DBH_t表示当年胸径值, DBH_1表示2011年10月初始胸径值, X_t表示该年窗口值, X_1表示初始窗口值, π表示圆周率, Δt为树木生长测定年限。本研究计算了2011年10月至2023年10月共12年的相对生长速率。

1.6 数据处理与统计分析

所有统计分析与作图均在R 4.3.3软件中进行。使用R包“lme4” (Bates et al., 2022)构建混合效应模

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型, 探究两种林型土壤理化性质的差异、氮添加对两种林型土壤理化性质、4种优势植物叶片PSM以及两种优势乔木相对生长速率的影响, 并将区组设置为随机因子。在进行统计分析之前, 使用R包“DHARMa” (Hartig, 2022)检验模型残差的正态性。除蒙古栎林的土壤含水量对氮添加的响应以及土壤全碳含量在两种林型间的差异模型外, 其他模型均通过了正态性检验。对不满足正态分布的数据, 进行了对数转换处理。当模型的固定效应显著时, 采用最小显著性差异(LSD)法进行不同处理间的多重比较。使用R包“factoextra” (Kassambara & Mundt, 2017)中的主成分分析(PCA)对4种植物的6个变量(包括叶片PSM和养分含量)降维分析。采用一般线性模型探究土壤理化性质与PC1的相关关系(其中灌木的土壤理化性质采用样地水平数据匹配)。进一步区分白桦林与蒙古栎林中优势植物6个变量的PCA, 并使用*t*检验探究多变量性状空间中样本在不同氮添加处理间的差异。以上数据分析中, 若$p < 0.05$, 则认为差异具有显著性。

2 结果和分析

2.1 长期氮添加对白桦林和蒙古栎林土壤理化性质的影响

氮添加降低了蒙古栎林的土壤含水量, 尤其是高氮处理下较为显著(图1A)。在施氮处理下, 白桦林和蒙古栎林的土壤pH均呈下降趋势, 尤其是在白桦林中土壤pH下降尤为明显(图1B); 土壤磷含量则呈升高趋势, 尤其是在蒙古栎林中升高较为显著(图1E)。然而, 在施氮处理下, 两种林型的土壤碳和氮含量均未出现显著变化(图1C、1D)。

2.2 长期氮添加对4种优势植物叶片酚类次生代谢产物含量的影响

整体上, 白桦林和蒙古栎林的优势植物叶片酚类PSM含量对氮添加的响应存在差异, 表现为白桦林的叶片PSM呈升高趋势, 蒙古栎林则呈下降趋势, 尤其是在高氮处理下下降较为明显。具体而言, 高氮添加显著提高了白桦叶片的总酚含量, 但对其他3种植物无显著影响(图2A); 低氮和高氮添加均降

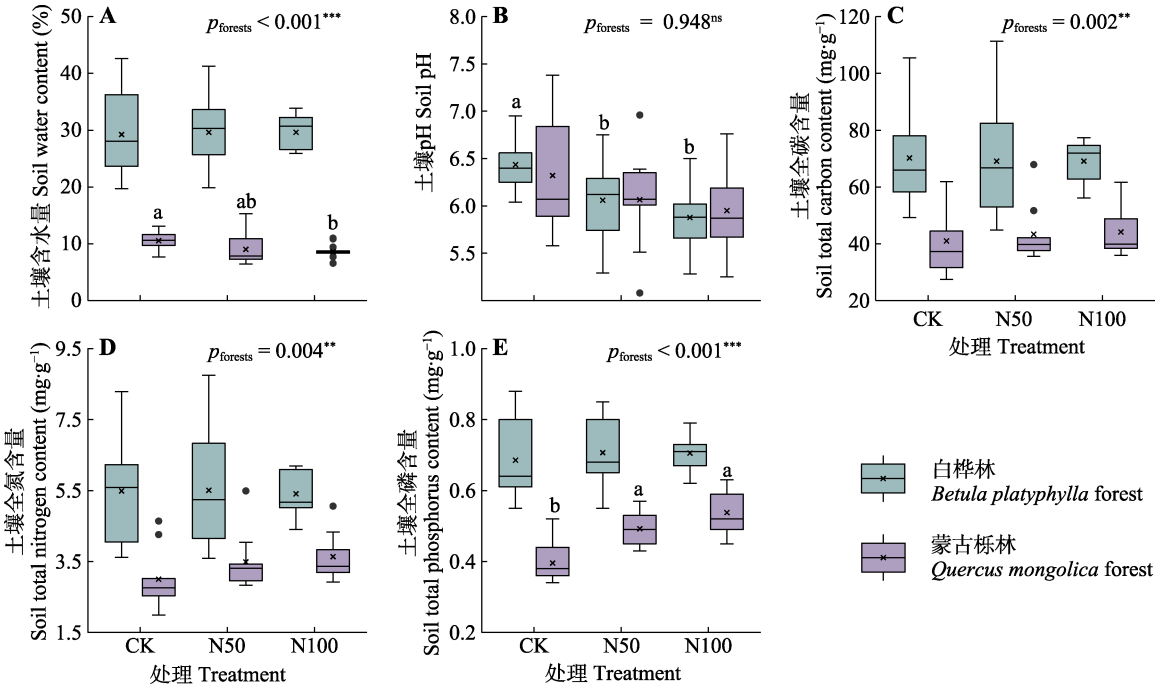


图1 氮添加对白桦林和蒙古栎林土壤理化性质的影响(n = 9个体× 3处理× 2林型= 54)。“×”表示该组数据的平均值点。每个子图右上角标注了不同林型间的统计差异p值(ns, $p > 0.05$; **, $p < 0.01$; ***, $p < 0.001$)。不同小写字母表示处理组间差异显著($p < 0.05$)。CK, 对照, 0 kg N·hm^{-2}·a^{-1}; N50, 低氮, 50 kg N·hm^{-2}·a^{-1}; N100, 高氮, 100 kg N·hm^{-2}·a^{-1}。

Fig. 1 Effect of nitrogen (N) addition on soil physicochemical properties in *Betula platyphylla* forest and *Quercus mongolica* forest (n = 9 individuals × 3 treatments × 2 forests = 54). The “×” symbol represents the mean value for each group. Each subplot displays the p-values for statistical differences between the forest types in the top right corner (ns, $p > 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Different lowercase letters indicate significant differences between treatments ($p < 0.05$). CK, control, 0 kg N·hm^{-2}·a^{-1}; N50, low nitrogen, 50 kg N·hm^{-2}·a^{-1}; N100, high nitrogen, 100 kg N·hm^{-2}·a^{-1}.

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低了大花溲疏的叶片黄酮含量, 但对其他3种植物无显著影响(图2B); 对于叶片单宁含量, 白桦在高氮添加处理下相比低氮添加显著升高, 而蒙古栎在高氮添加下显著降低, 大花溲疏在低氮和高氮添加下均显著降低, 毛榛则在不同氮处理间无显著差异(图2C)。

2.3 叶片酚类次生代谢产物与养分含量的权衡关系

4种优势植物的叶片PSM与养分含量PCA结果(图3A)显示, PC1和PC2的方差解释率分别为53.8%和18.3%, 累计解释率为72.1%。其中, PC1表明具有更高叶片酚类PSM (总酚、黄酮和单宁)含量的植物, 其叶片养分(碳、氮和磷)含量较低。PC1得分与土壤含水量和土壤养分含量呈显著负相关关系(图3B、3D–3F), 但与土壤pH无显著相关性(图3C)。进一步区分不同林型的PCA, 白桦林和蒙古栎林的PSM与叶片养分含量均在PC1上存在权衡关系, 且氮添加改变了每个林型内两种优势植物在多变量性状空间中的位置。白桦林两种优势植物的性状PCA结果(图4A)显示, PC1和PC2的方差解释率分别为34.0%和23.5%, 累计解释率为57.5%。氮添加使得白桦林两种植物有向PC1正端移动的趋势, 即PSM增大的方向, 其中高氮处理的PC1得分显著高于低氮处理。蒙古栎林两种优势植物的PCA结果(图4B)显示, PC1和PC2的方差解释率分别为56.1%和23.2%, 累计解释率为79.3%。氮添加使得蒙古栎林的两种植物有向PC1和PC2负端移动的趋势, 即PSM含量降低的方向, 其中高氮处理的PC2得分显著低于对照。

2.4 长期氮添加对两种林型优势乔木树种相对生长速率的影响

如图5结果所示, 氮添加后白桦的相对生长速率呈现下降趋势, 而蒙古栎的相对生长速率则呈上升趋势, 但均不显著($p < 0.05$)。

3 讨论

3.1 氮添加对白桦林和蒙古栎林土壤理化性质的影响

氮添加降低了温带典型森林土壤pH, 这与前人在氮添加模拟实验和全球尺度的meta分析的结果(Tian & Niu, 2015; Tian et al., 2018)一致。通常情况下, 氮添加会增加土壤中的H^+、NH_4^+或NO_3^-, 导致土壤中的盐基离子减少(Lu et al., 2014; Mao et al., 2017), 尤其是在氮饱和的情况下(Aber et al., 1998), 会出现明显的土壤pH下降现象(Höegberg et al., 2006; 高士杰, 2021)。关于土壤氮和磷含量对氮添加的响应, 前人研究发现, 温带森林中氮添加一般会增加土壤氮含量, 对土壤磷含量的影响存在较大

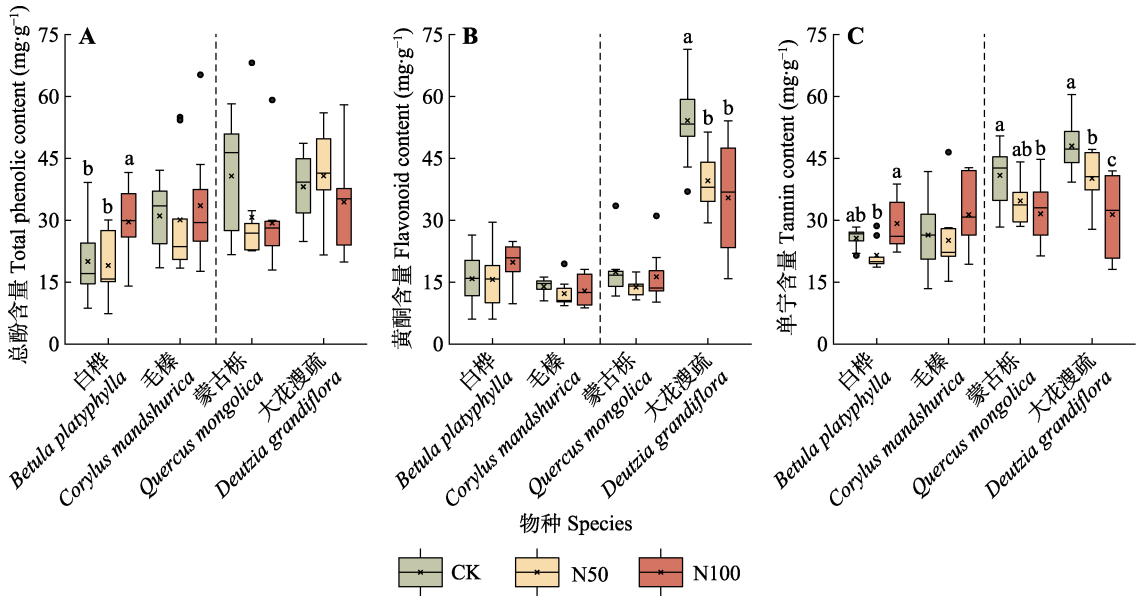


图2 氮添加对温带落叶阔叶林4种优势植物叶片酚类次生代谢产物含量的影响(n = 9个体× 3处理× 4物种= 108)。“×”表示该组数据的平均值点。不同小写字母表示处理组间差异显著($p < 0.05$)。CK, 对照, 0 kg N·hm^{-2}·a^{-1}; N50, 低氮, 50 kg N·hm^{-2}·a^{-1}; N100, 高氮, 100 kg N·hm^{-2}·a^{-1}。

Fig. 2 Effects of nitrogen addition on leaf phenolic secondary metabolites content of four dominant plants in temperate deciduous broad-leaved forest (n = 9 individuals × 3 treatments × 4 species = 108). The “×” symbol represents the mean value for each group. Different lowercase letters indicate significant differences between different treatments ($p < 0.05$). CK, control, 0 kg N·hm^{-2}·a^{-1}; N50, low nitrogen, 50 kg N·hm^{-2}·a^{-1}; N100, high nitrogen, 100 kg N·hm^{-2}·a^{-1}.

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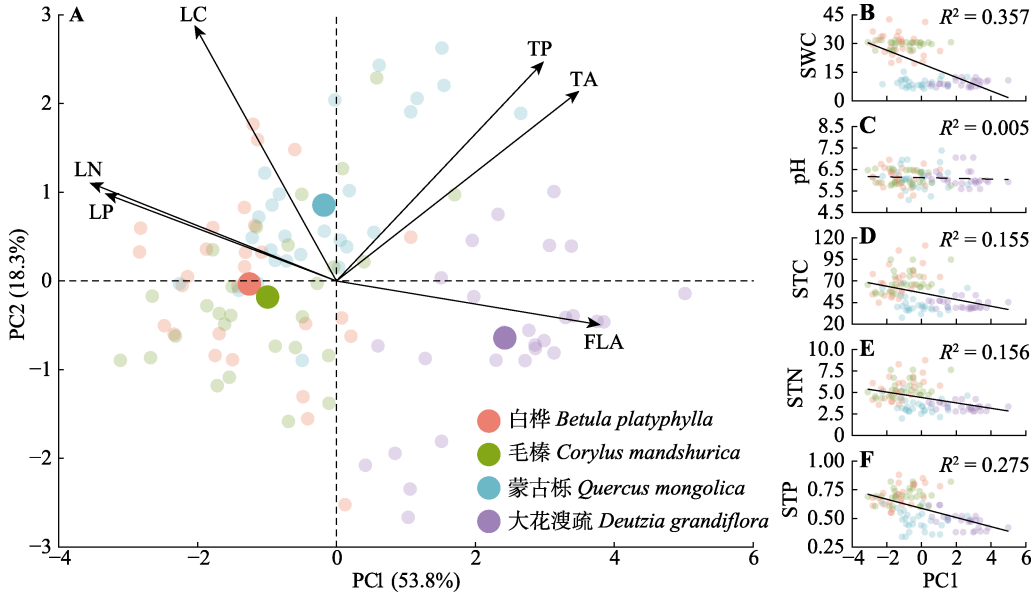


图3 4种温带落叶阔叶优势植物的叶片酚类次生代谢产物与养分含量的主成分(PC)分析图(**A**)以及第一主成分(PC1)与土壤理化性质的相关性(**B–F**) (n = 9个体× 3处理× 4物种= 108)。不同颜色代表不同的物种。深色点代表每个物种的平均值，浅色点代表样本点。当p < 0.05时回归线用实线表示，否则用虚线表示。FLA，黄酮含量; LC，叶碳含量; LN，叶氮含量; LP，叶磷含量; pH，土壤pH; STC，土壤全碳含量; STN，土壤全氮含量; STP，土壤全磷含量; SWC，土壤含水量; TA，单宁含量; TP，总酚含量。

Fig. 3 Principal component (PC) analysis diagram of leaf phenolic secondary metabolites and nutrient content for four dominant plants in temperate deciduous broad-leaved forest (**A**) and relationship between the first principal component (PC1) and soil physicochemical properties (**B–F**) (n = 9 individuals × 3 treatments × 4 species = 108). Different colors represent different species groups. Deep-colored dots represent the mean values of each species, while light-colored dots represent the sample points. The regression line is depicted with a solid line if p < 0.05, otherwise with a dashed line. FLA, flavonoid content; LC, leaf carbon content; LN, leaf nitrogen content; LP, leaf phosphorus content; pH, soil pH; STC, soil organic carbon content; STN, soil total nitrogen content; STP, soil total phosphorus content; SWC, soil water content; TA, tannin content; TP, total phenolic content.

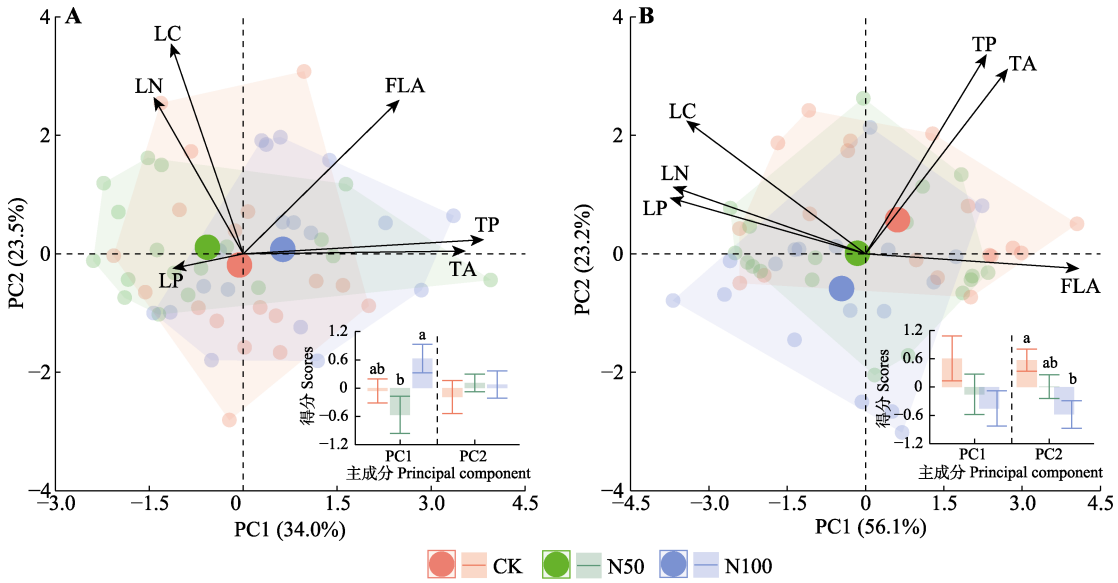


图4 白桦林(**A**)和蒙古栎林(**B**)优势植物叶片酚类次生代谢产物和养分含量的主成分分析图(n = 9个体× 3处理× 2物种= 54)。不同颜色代表不同的氮添加处理。柱状图表示第一(PC1)和第二主成分(PC2)得分在不同氮添加处理间的差异，不同小写字母表示不同处理间差异显著(p < 0.05)。FLA，黄酮含量; LC，叶碳含量; LN，叶氮含量; LP，叶磷含量; TA，单宁含量; TP，总酚含量。CK，对照, 0 kg N·hm^{-2}·a^{-1}; N50，低氮, 50 kg N·hm^{-2}·a^{-1}; N100，高氮, 100 kg N·hm^{-2}·a^{-1}。

Fig. 4 Principal component analysis diagram of leaf secondary metabolites and nutrient content for *Betula platyphylla* forest (**A**) and *Quercus mongolica* forest (**B**) (n = 9 individuals × 3 treatment × 2 species = 54). Different colors represent different nitrogen treatments. Barplots show PC1 and PC2 score differences across nitrogen treatments, with significant differences indicated by different lowercase letters (p < 0.05). FLA, flavonoid content; LC, leaf carbon content; LN, leaf nitrogen content; LP, leaf phosphorus content; TA, tannin content; TP, total phenolic content. CK, control, 0 kg N·hm^{-2}·a^{-1}; N50, low nitrogen, 50 kg N·hm^{-2}·a^{-1}; N100, high nitrogen, 100 kg N·hm^{-2}·a^{-1}.

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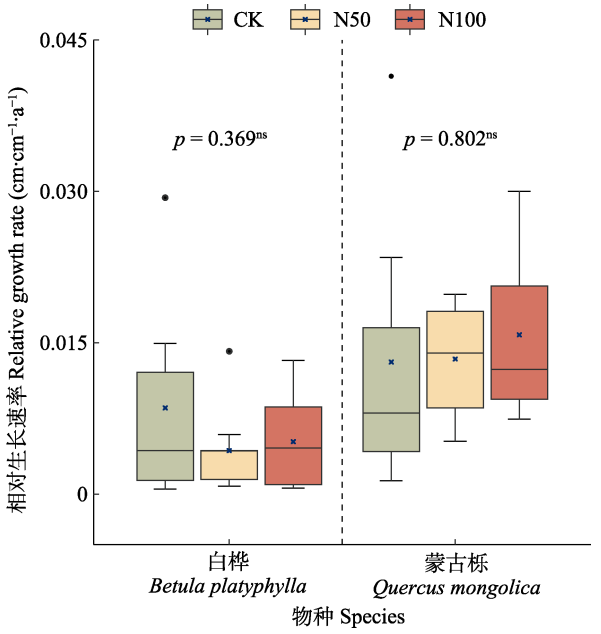


图5 氮添加对白桦和蒙古栎相对生长速率的影响(n = 9个体× 3处理= 27)。“×”表示该组数据的平均值点。“ns”代表每个树种的相对生长速率在不同氮添加处理间无显著差异(p < 0.05)。CK, 对照, 0 kg N·hm^{-2}·a^{-1}; N50, 低氮, 50 kg N·hm^{-2}·a^{-1}; N100, 高氮, 100 kg N·hm^{-2}·a^{-1}。

Fig. 5 Effects of nitrogen addition to the relative growth rate of *Betula platyphylla* and *Quercus mongolica* (n = 9 individuals × 3 treatments = 27). The “×” symbol represents the mean value for each group. “ns” indicates relative growth rate of each tree species have no significant differences among different nitrogen treatments (p < 0.05). CK, control, 0 kg N·hm^{-2}·a^{-1}; N50, low nitrogen, 50 kg N·hm^{-2}·a^{-1}; N100, high nitrogen, 100 kg N·hm^{-2}·a^{-1}.

差异(Deng et al., 2017)。在本研究中, 氮添加后土壤氮含量仅呈现微弱的上升趋势, 可能是因为样地的空间异质性以及氮的形式影响了施肥效率(Wright et al., 2011)。实验样地施用的尿素主要提供铵态氮, 具有较高的挥发性, 进一步削弱了施肥效果(邹安龙等, 2019)。此外, 这一结果可能还与植物根系吸收、土壤微生物活动等因素有密切关系(Li et al., 2021)。因此, 未来需进行更长时间的监测或针对性实验设计, 以深入探讨氮在土壤中的动态过程。本研究还发现, 氮添加后土壤磷含量呈升高趋势, 尤其是在蒙古栎林中显著升高。推测其原因, 可能是氮添加通过刺激微生物产生更多的磷酸酶或提高其活性, 加速有机磷的矿化(Marklein & Houlton, 2012; 陈美领等, 2016), 从而满足植物对磷的吸收和利用(Deng et al., 2016)。

3.2 植物叶片酚类次生代谢物产物含量与叶片养分、土壤理化性质的关系

本研究中, 4种植物的酚类化合物含量存在较大差异(图2), 这种差异可能源于不同树种的遗传背景, 同时也受到植物生长环境和生理状态的影响(李可鑫等, 2021; 郭思汝, 2024), 反映出森林植物对环境条件的不同适应策略和抗性。在PCA中, 第一主成分解释了4种植物6个性状(包括叶片养分和PSM)构成的性状空间53.8%的变异, 并且PSM指标分布在一轴的右侧, 养分指标则分布在一轴左侧(图3)。在区分林型后, 尽管解释度有所下降, 但性状分布仍然呈现类似的模式(图4)。这一结果与一项在温带森林中涵盖更多植物物种的研究结果(程思祺等, 2022)类似, 叶片养分、叶绿素含量和比叶面积等代表资源获取型策略的经济性状与酚类PSM等防御性状存在权衡关系, 即叶片养分状况较好的物种抗性较弱(Morrow et al., 2022)。通常认为, 植物吸收利用的养分来自土壤, 因此植物-土壤养分之间存在紧密的相关关系(Mosa et al., 2022)。本研究中4种植物的叶片PSM与养分还受到土壤水分、养分的调控(图2B–2F), 这也与资源可用性假说的预测(Coley et al., 1985)一致。此外, 蒙古栎林的土壤水分与养分条件明显低于白桦林, 其优势植物叶片具有较高的酚类PSM含量, 表明无论是乔木还是灌木对栖息地贫瘠环境的耐受性策略存在一致性。

3.3 氮添加对白桦林和蒙古栎林优势植物叶片酚类次生代谢物产物及优势乔木生长的影响

在氮添加条件下, 白桦林和蒙古栎林优势植物的酚类PSM表现出不同的响应趋势。整体上, 白桦林植物的PSM含量呈升高趋势, 蒙古栎林则呈下降趋势, 尤其是在高氮添加处理下较为显著(图2, 图4)。这表明两种林型在长期氮添加影响下的生长-抗性之间的平衡策略存在差异, 同时也验证了前人关于氮沉降介导的植物酚类化合物变化具有高度变异性的研究结论(de Long et al., 2016; Sun et al., 2020; Sun & Fernie, 2024)。

一般来说, 生态系统中氮的增加会导致酚类PSM积累量的减少(Sun et al., 2020; Lv et al., 2024), 但在过量氮添加的情况下, 叶片中的PSM含量往往会显著增加(Luo et al., 2008)。根据生长分化平衡假说, 在氮限制的森林生态系统中, 尤其是本研究中的温带蒙古栎林, 随着施氮量的增加, 植物很可能会优先分配资源给生长而非次生代谢产物的生产(Bryant et al., 1983; Wright et al., 2010; Endara & Coley, 2011)。因此, 树木中的酚类PSM的含量会减

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少。本研究中, 氮添加导致蒙古栎叶片黄酮含量以及大花溲疏的叶片黄酮和单宁含量的降低, 这可能说明植物将氮资源更多地分配到了生长而非代表抗性的PSM的合成。相反, 对于土壤水分和养分条件相对较好的白桦林, 高氮添加显著提高了白桦叶片总酚和单宁含量。这可能是高氮添加使得土壤中的氮可利用性超过了白桦生长所需的阈值, 从而促使白桦提高对总酚和单宁的能量投资以应对胁迫(Pant et al., 2021)。前人研究也观察到类似的现象: 当施氮水平超过植物正常生长所需时, 青钱柳幼苗和闽楠(*Phoebe bournei*)的叶片PSM含量也会显著增加(凌岩等, 2020; 刘沛书等, 2023)。

尽管缺乏灌木的生长数据, 但乔木的相对生长速率对氮添加的反应(图5), 即白桦呈降低趋势, 蒙古栎呈升高趋势, 在一定程度上佐证了生长分化平衡假说的预测。相较于白桦林, 水分和养分相对贫瘠的蒙古栎林在长期氮沉降的影响下很可能较早出现脆弱性相关的问题。具体来说, 这些问题可能表现为植物更容易遭受植食性昆虫取食(Throop & Lerdau, 2004)和病原菌侵染(Wu et al., 2021)的威胁, 从而增加植物的死亡率, 并对森林生态系统的稳定性构成更大挑战。因此, 通过选择性树种管理、土壤改良以及定期监测评估(Sun et al., 2020; 朱润铖等, 2024)等措施, 可以有效缓解氮沉降对森林生态系统的负面影响。

4 结论

本研究结合森林土壤条件、植物叶片养分及树木生长, 探究了温带落叶阔叶林中优势植物在氮沉降背景下的次生代谢适应特征。本研究发现, 4种优势植物的叶片酚类PSM含量与叶片养分含量存在权衡关系, 并受到土壤水分和养分的调控。整体上, 氮添加导致白桦林优势植物叶片酚类PSM含量呈上升趋势, 土壤条件较为贫瘠的蒙古栎林则呈下降趋势, 尤其是在高氮添加处理下, 这一变化尤为显著。这一结果表明, 不同林型植物的养分分配策略可能导致树木功能(生长和抗性)对氮沉降呈现差异化响应。研究结果有助于我们理解温带落叶阔叶林对氮沉降的次生代谢适应机制, 并为评估森林抵御环境变化的能力提供科学依据。鉴于植物防御和抗性机制的复杂性, 未来的研究应进一步纳入其他次生代谢物种类, 并综合考虑地下根系次生代谢物、土壤微生物、叶片虫食和树木生长与死亡率等多维度因素, 以全面评估氮添加对森林生态系统健康的潜在影响。

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