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氮磷添加对植物地下觅食性状影响的研究进展

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摘要: 植物地下觅食性状对于植物的养分获取和环境适应至关重要。氮磷有效性作为关键驱动因子, 深刻影响植物地下养分获取策略。本文介绍了植物地下觅食性状的划分, 包括吸收根性状(形态、构型、增殖)、菌根性状(菌根真菌侵染率、菌丝密度)和分泌性状(根系碳分泌速率、根系酶活性), 阐述了氮磷添加对不同觅食性状的影响。研究发现: 氮磷添加对吸收根性状的影响因树种和养分条件而异, 植物会通过改变其形态、构型、增殖特征来优化资源吸收; 菌根真菌通过差异化策略(如丛枝菌根真菌依赖菌丝拓展无机养分吸收, 外生菌根真菌分泌酶分解有机质)调控植物地下资源获取, 但氮磷添加普遍抑制菌根侵染率; 根系酸性磷酸酶和硝酸还原酶作为反映植物对磷氮获取与代谢的关键指标, 其活性受氮磷添加显著调控。本文还探讨了地下觅食性状之间的协调机制, 包括性状间的协同与权衡、资源分配中的成本效益优化。针对当前研究的不足之处, 提出从氮磷养分的交互作用、根系分泌性状与吸收根及菌根性状的协同响应机制、野外成熟植物的原位观测、不同菌根类型树种觅食策略等方面进一步研究, 旨在深入理解植物地下养分获取策略及其对环境变化的适应机制, 为森林生态系统的经营管理提供科学依据。表 2 参 95

关键词: 氮磷添加; 地下觅食性状; 吸收根; 菌根共生; 分泌性状

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Research progress on the effects of nitrogen and phosphorus addition on plant belowground foraging traits

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Abstract: Plant belowground foraging traits are crucial for plant nutrient acquisition and environmental adaptation. Nitrogen (N) and phosphorus (P) availability, as key driving factors, have a profound impact on plant belowground nutrient acquisition strategies. First, it introduces the classification of plant belowground foraging traits. This include absorptive root traits (morphology, architecture, and proliferation), mycorrhizal traits (mycorrhizal fungal colonization rate and hyphal density), and exudation traits (root carbon exudation rate and root enzyme activity). Subsequently, it illustrates the effects of N and P addition on these foraging traits. Regarding absorptively root traits, studies have shown that the effects of N and P addition vary depending on tree species and nutrient conditions. Plants optimize resource acquisition by altering their morphology, architecture, and proliferation characteristics. For mycorrhizal traits, mycorrhizal fungi regulate belowground resource acquisition through differentiated strategies (For example, arbuscular mycorrhizal fungi rely on hyphal extension for inorganic nutrient uptake, while ectomycorrhizal fungi secrete enzymes to decompose organic

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matter), however, N and P addition generally suppress mycorrhizal colonization rates. As for exudation traits, root acid phosphatase and nitrate reductase, which are key indicators reflecting plant P and N acquisition and metabolism, were significantly regulated by N and P addition. Next, it also explores the coordination mechanisms among belowground foraging traits. This includes synergies and trade-offs among traits, as well as cost-benefit optimization in resource allocation. Finally, addressing current research gaps, future research directions are proposed, focusing on N-P interactions, the synergistic response mechanisms among root secretory traits, absorptive roots, and mycorrhizal traits, in situ observations of mature plants in the field, and foraging strategies of different mycorrhizal types of tree species. These directions aim to deepen our understanding of plant belowground nutrient acquisition strategies and their adaptation mechanisms to environmental changes, providing a scientific basis for the management of forest ecosystems. [Ch, 2 tab. 95 ref.]

Key words: nitrogen and phosphorus addition; belowground foraging traits; absorptive roots; mycorrhizal symbiosis; exudation traits

氮和磷是植物生长发育所必需的大量元素，它们在土壤中的有效性直接影响着植物的生长和分布。近几十年来，化石燃料和农业氮肥的广泛使用导致全球氮沉降增加，一些地区甚至达到氮饱和状态，超过了生态系统的临界负荷，对森林生态系统产生了显著的负面影响^[1]。过量的氮输入打破了生态系统的氮磷平衡，特别是在热带和亚热带森林中，进一步加剧了土壤磷限制^[2]。由于土壤中的磷易被固定且迁移性较弱，植物难以有效吸收和利用^[3]，这使得氮和磷成为制约陆地生态系统生产力的主要因素。

在森林生态系统中，植物主要通过根系和菌根从土壤中获取养分。然而，养分资源的空间分布往往呈现高度异质性，形成所谓的“养分斑块”^[4]。这种异质性对植物的地下觅食策略提出了严峻挑战，同时也推动了植物地下性状的适应性进化。研究表明，根系在形态和生理等功能上表现出显著的分化，例如 MCCORMACK 等^[5]将细根划分为吸收根和运输根：吸收根具有直径小、代谢快、寿命短、成本效益比低等特点，主要承担养分和水分的吸收功能，对环境变化表现出更高的可塑性；而运输根则主要负责养分的运输和储存^[5-6]。这种功能分化使植物能够更高效地适应异质养分环境。

本文系统介绍了植物地下觅食性状的划分，阐述了氮磷养分添加对地下觅食性状的影响，探讨了地下觅食性状之间的协调机制，并提出了当前研究的不足和未来发展方向，旨在深入理解植物地下养分觅食策略及其对环境变化的适应机制，为森林生态系统的经营管理提供科学依据。

1 植物地下觅食性状的划分

植物的生长和生存依赖于对土壤中养分的有效获取。地下觅食性状是植物为了获取养分而进化出的一系列性状，包括吸收根性状、菌根性状和分泌性状^[7-8]，详见表 1。形态、构型等吸收根性状能够使植物更精准地占据土壤中养分丰富的斑块，从而增强养分的获取效率^[9-10]。与菌根真菌共生可增加根系养分吸收的有效性，因为菌根真菌能够通过菌丝网络扩大根系的吸收范围，进入根系无法到达的区域^[11]。根系分泌物可以促进吸附在土壤矿物上的养分释放，或用于刺激土壤微生物的活性，增加矿化率和获得与有机质复合的养分^[12]。这些地下性状能够促进植物对不同类型土壤资源(如易获取或较复杂的有机/无机资源)的获取，而不同资源库的利用成本与收益则取决于土壤养分背景^[13]。

2 氮磷添加对植物地下觅食性状的影响

氮磷添加通过改变植物的资源分配策略，显著影响根系形态、菌根共生效率及根系分泌物动态，进而重塑根际生态过程。这些响应具有物种和环境的依赖性，但整体表现为从“高投资-高获取”向“低成本-高效率”策略的适应性转变^[8, 14]。

2.1 氮磷添加对吸收根性状的影响

在森林生态系统中，细根的关键功能往往与其形态特征密切相关。尽管已有大量研究探讨氮添加对

表 1 地下觅食性状描述

Table 1 Description of belowground foraging traits

项目	觅食性状	单位	描述	参考文献
吸收根形态性状	根直径	cm	反映细根结构、功能，与资源保护策略有关	[15–16]
	比根长	$\text{m} \cdot \text{g}^{-1}$	衡量养分吸收效率，与养分获取策略有关	[17–18]
	比表面积	$\text{cm}^2 \cdot \text{g}^{-1}$	反映养分吸收效率，与养分获取策略有关	[19]
	根组织密度	$\text{g} \cdot \text{cm}^{-3}$	体现根系生物量积累、植物生长与养分吸收活性，与资源保护策略有关	[16, 20]
吸收根构型性状	比分枝密度	g^{-1}	反映植物根系的环境适应力，同一序级的细根分枝越多，通常生长力和适应力越强	[21–22]
	比根尖密度	g^{-1}	表征养分吸收能力	[23]
吸收根增殖性状	根长生长速率	$\text{cm} \cdot \text{d}^{-1}$	反映植物探索土壤和获取养分的能力	[9]
	根质量生长速率	$\text{mg} \cdot \text{d}^{-1}$	表征植物对根系生长的资源投入及其功能效率	[9]
菌根性状	菌根菌侵染率	%	衡量植物根系与菌根真菌共生关系强度	[24]
	菌丝密度	$\text{m} \cdot \text{g}^{-1}$	衡量菌丝在特定环境中分布和生长强度，能够捕捉共生的功能性质，对养分添加敏感	[25–28]
分泌性状	根系碳分泌速率	$\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$	衡量根系向土壤中释放碳化合物的速率。分泌速率越高，根际微生物代谢活性越强，促进养分循环和有机质分解	[12, 29]
	根系酸性磷酸酶	$\text{nmol} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$	分解有机磷释放无机磷，是植物适应低磷环境、提升磷利用效率的关键	[30–31]
	根系硝酸还原酶	$\text{nmol} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$	植物氮代谢的关键酶，催化硝酸盐转化为亚硝酸盐供植物利用，其活性决定氮利用效率	[32]

细根形态性状的影响，但研究结果并不一致 (表 2)。不同植物细根形态性状对磷添加的响应也表现出显著的种间差异。例如：在低磷胁迫环境下 ($4 \text{ mg} \cdot \text{kg}^{-1}$)，杉木 *Cunninghamia lanceolata* 于胁迫初期表现出更大的根表面积、根长和根体积增量^[33]。磷添加处理 ($0.1 \text{ g} \cdot \text{kg}^{-1}$, P_2O_5) 显著提高了白羊草 *Bothriochloa ischaemum* 细根的比根长和比表面积^[34]；当单株施磷量为 6 或 $8 \text{ g} \cdot \text{株}^{-1}$ 时，色木槭 *Acer mono* 的根直径和比根长均显著增加^[35]；而 RYSER 等^[36] 发现，在每周分别添加 0.21、1.04 和 5.22 mg 磷条件下，羽状短柄草 *Brachypodium pinnatum* 和鸭茅 *Dactylis glomerata* 根组织密度未呈现显著变化。可见，氮磷添加对细根形态性状的影响因物种特性和养分条件而异，植物会通过改变其形态特征来优化资源吸收^[16]。

根系构型指同一根系中不同类型的根在生长介质中的空间造型和分布^[21]。细根构型对养分条件的变化比较敏感，植物通过调整细根构型参数来提高对养分的吸收^[37]。氮添加增加了亚热带丛枝菌根树种的分枝密度^[24]。然而，COMAS 等^[38] 研究发现，养分的提高会导致根系分枝数、根尖密度和分枝密度显著降低，这可能与养分过剩条件下植物资源分配策略的调整有关。此外，杨丽君等^[23] 对杨树 *Populus* 的研究表明，施肥显著提高了表层土的分枝比和分枝密度，表明复合养分添加对细根分枝性状具有协同促进作用。磷添加对分枝性状的影响与氮添加有所不同。LIU 等^[24] 对亚热带树种的研究显示，磷添加增加了根的分枝密度，但降低了分枝比。这种变化可能是植物在磷添加条件下的一种适应性策略，即通过增加分枝密度来扩大根系的觅食范围，同时将更多资源分配给一级根的生长，而非二级根。上述研究表明，根系构型对养分输入的响应具有显著异质性，氮、磷或复合养分添加可能通过不同机制 (如资源分配权衡、觅食范围优化) 驱动分枝密度、分枝比等性状的差异化调整。

增殖性状是表征植物地下觅食策略和资源分配模式的重要指标。土壤缺氮通常会促进主根生长以及部分侧根伸长，但不刺激侧根分化；在极度缺氮条件下，侧根分化几乎完全缺失^[39]。这种响应机制可能是植物在氮限制条件下优先将资源分配给主根以探索更深层土壤养分的策略。而土壤缺磷条件下，植物根系通常表现为变细长，生长出更多的侧根和根毛，通过增加根表面积提高对磷的吸收效率^[40]。WILLIAMSON 等^[41] 对拟南芥 *Arabidopsis thaliana* 研究进一步表明，低磷有效性通过增加侧根密度和长度来促进侧根生长，同时通过抑制细胞伸长来减缓初生根生长。张进如^[32] 对亚热带天然常绿阔叶林的研究发现，短期氮添加 ($<6 \text{ a}$) 增加了细根长度和生物量，长期施氮则会导致细根长度和生物量减少。TAYLOR 等^[42] 对火炬松 *Pinus taeda* 的研究表明，长期施氮处理显著降低了细根长度和生物量，这可能是由于氮

表 2 不同树种根系形态性状对氮添加的响应

Table 2 Responses of root morphological traits in different tree species to nitrogen addition						
根系性状	树种	树龄/a	氮添加水平	氮添加时间/a	对氮添加的响应	参考文献
直径	红松 <i>Pinus koraiensis</i> 、臭冷杉 <i>Abies nephrolepis</i> 、花楷槭 <i>Acer ukurunduense</i>	—	2.5、5.0 g·m ⁻² ·a ⁻¹	8	增大	[43]
	油松 <i>Pinus tabuliformi</i>	50	3、6、9 g·m ⁻² ·a ⁻¹	3	增大	[44]
	日本柳杉 <i>Cryptomeria japonica</i>	28	336 kg·hm ⁻² ·a ⁻¹	3	减小	[45]
	米老排 <i>Mytilaria laosensis</i>	22	30 kg·hm ⁻² ·月 ⁻¹	1	减小	[46]
	毛竹 <i>Pleioblastus amarus</i>	—	50、100、300 kg·hm ⁻² ·a ⁻¹	7	无显著变化	[47]
	黄槿 <i>Phellodendron amurense</i>	30	10 g·m ⁻² ·a ⁻¹	5个月	无显著变化	[48]
	日本柳杉	28	336 kg·hm ⁻² ·a ⁻¹	3	增大	[45]
	杉木 <i>Cunninghamia lanceolata</i>	2	40、80 kg·hm ⁻² ·a ⁻¹	1	增大	[49]
	雪岭云杉 <i>Picea schrenkiana</i>	—	10 kg·hm ⁻² ·a ⁻¹	1	增大	[50]
	油松	50	3、6、9 g·m ⁻² ·a ⁻¹	3	减小	[44]
比根长	毛竹	—	300 kg·hm ⁻² ·a ⁻¹	7	减小	[47]
	水曲柳、落叶松 <i>Larix gmelinii</i>	17	100 kg·hm ⁻² ·a ⁻¹	1	减小	[51]
	落叶松	—	75 kg·hm ⁻² ·a ⁻¹	8	减小	[52]
	米老排	22	10、30 kg·hm ⁻² ·月 ⁻¹	1	无显著变化	[46]
	北美山杨 <i>Populus tremuloides</i>	2	高氮(100%A层土壤)、 低氮(20%A层与80% C层土壤混合)	—	无显著变化	[53]
	湿地松 <i>Pinus elliotii</i>	28	10 kg·hm ⁻² ·a ⁻¹	1	无显著变化	[54]
	雪岭云杉	—	5 kg·hm ⁻² ·a ⁻¹	1	增大	[55]
	米槠 <i>Castanopsis carleisii</i>	43	15.6 mg·kg ⁻¹	5个月	减小	[56]
	日本扁柏 <i>Chamaecyparis obtuse</i>	100	31.8 mg·kg ⁻¹ 47.2 mg·kg ⁻¹	原位土壤氮肥力	减小	[57]
	日本柳杉	28	336 kg·hm ⁻² ·a ⁻¹	3	无显著变化	[45]
组织密度	米老排	22	10 kg·hm ⁻² ·月 ⁻¹ 30 kg·hm ⁻² ·月 ⁻¹	1	无显著变化	[46]
	杉木	43	18 mg·kg ⁻¹	5个月	无显著变化	[56]
	木荷 <i>Schima superba</i>	5	50、100、150 kg·hm ⁻² ·a ⁻¹	4	无显著变化	[58]

说明：“—”表示未知。

过剩条件下植物将更多资源分配给地上部分的生长。LIU 等^[24]对亚热带树种的研究表明，氮磷钾复合肥添加显著提高了根长增殖，而氮、磷单独添加对增殖无显著影响，这表明养分交互作用对细根增殖性状具有协同效应。上述研究揭示，养分类型(氮、磷)、浓度梯度(缺乏或富集)及作用时间(短期与长期)共同塑造了根系增殖性状的响应模式。氮、磷匮乏分别驱动主根深拓与侧根扩张的差异化策略，而养分过量则通过碳-养分分配权衡抑制根系增殖。值得注意的是，复合养分输入可能通过协同效应放大根系可塑性，而单一养分管理可能低估植物对复杂环境的适应能力。

2.2 氮磷添加对菌根性状的影响

菌根是由特定真菌与植物根系形成的互利共生结构，是植物获取资源的重要器官。据统计约有 5 万种真菌与 25 万种植物形成菌根共生关系，而且陆地生态系统中高达 80% 的植物氮和磷是由菌根真菌提供的^[59]。这种菌根共生关系使根系觅食行为变得更为复杂多样，能够重塑植物地下资源获取策略，且其具体效应受到共生体种类的直接调控^[60-61]。菌根真菌主要分为丛枝菌根(arbuscular mycorrhizal, AM)真菌和外生菌根(ectomycorrhizal, ECM)真菌，它们在养分吸收和资源分配策略上存在显著差异。AM 真菌通过菌丝网络扩大根系养分吸收面积，提高土壤体积的占有率；在土壤无机养分斑块中，AM 真菌能够迅速增殖，从而增大对氮、磷的吸收^[62]。AM 真菌对无机养分具有较高的亲和力，同时部分 AM 真菌还能够从简单的有机化合物中获取养分^[63]，这种特性使 AM 真菌在低养分条件下具有显著优势。ECM 真菌通过分泌水解酶、纤维素酶和蛋白酶等促进有机质的分解^[62]，但在无机养分较高的斑块中可能会受到抑

制^[64]。与 AM 树种相比, ECM 树种通常表现出更强的养分利用保守性, 而 AM 树种则以较低的生物量投资和较高代谢率进行资源获取^[65]。

CHEN 等^[65]提出了一个模拟植物群落从养分富集区获取氮和磷的概念框架, 发现不同根形态和菌根类型的植物能够适应一系列营养异质性环境。菌根真菌侵染植物根系后, 能够显著改善宿主植物的养分吸收能力, 因此菌根侵染率常被用作表征根系菌根化程度的重要指标。MA 等^[66]对 AM 和 ECM 树种的整合分析表明, 短期氮添加增加了植物的地下碳分配, 进而提高了细根菌根侵染率, 且 AM 树种在氮添加条件下的生长表现优于 ECM 树种。然而, 耿鹏飞^[67]对红松的连续氮添加试验发现, 随着土壤氮有效性的增加, 菌根侵染率降低。这是因为在高氮条件下, 植物无须依赖菌根共生体即可直接从土壤中获取足够养分, 从而减少对菌根的光合产物分配, 导致侵染率下降。林子然等^[68]对紫花苜蓿 *Medicago sativa* 的研究表明, 在高磷添加条件下, 寄主植物磷营养状况得到改善, 菌根真菌的菌丝生长受到抑制, 导致菌根侵染率降低。类似地, 王婷等^[69]对杉木的氮磷添加实验发现, 在低氮条件下, 磷添加降低了菌根侵染率, 这是因为氮磷添加提高了土壤中的有效氮和有效磷含量, 杉木可以直接从土壤中吸收足够营养元素, 从而减少对菌根的依赖。相关研究表明, 菌根真菌侵染率的增加是植物根系应对缺磷条件的典型反应, 因为缺磷会促使植物通过增加菌根真菌的侵染来扩大与土壤的接触面积, 从而提高对无机磷的吸收能力^[70-71]。TRESEDER 等^[14]对 31 个树种的整合分析发现, 氮肥和磷肥的添加均导致菌根侵染率降低。可见, 菌根真菌通过改变细根功能性状, 显著影响植物的地下资源获取策略。

2.3 氮磷添加对根系分泌性状的影响

根系分泌物组成包括低分子量有机物(如糖类、氨基酸、有机酸等)、次生代谢物(如酚类化合物、黄酮类物质等)和酶类(如酸性磷酸酶、硝酸还原酶等)。根系分泌物的收集与分析技术(如根际原位收集法、离体培养法)因研究目标而异: 原位收集法可反映自然分泌动态但通量低^[8, 72]; 离体培养法可控制环境变量并实现高纯度分泌物获取, 但可能因根系损伤导致应激性分泌^[73]。该领域多采用液相色谱-质谱联用(LC-MS)进行代谢物定性与定量, 但需注意标准化提取流程以减少批次误差^[74]。以往对细根养分获取策略的研究主要集中在细根形态和菌根性状方面^[24, 64], 而对根系分泌性状, 特别是根系分泌诱导的根际酶活性的研究相对较少。其中细根酸性磷酸酶和细根硝酸还原酶是两类关键的分泌性状, 分别反映了植物对磷和氮的获取与代谢能力。

酸性磷酸酶是由真菌、细菌和植物根部分泌的一类酶, 能够催化有机磷化合物中磷酸键的水解, 释放出可被植物吸收的无机磷。酸性磷酸酶是植物在磷限制条件下获取有效磷的重要方式, 其活性高低反映了植物对磷的获取性策略^[75]。在低磷有效性土壤中, 植物通常通过提高酸性磷酸酶活性来增强对有机磷的活化能力。例如, 热带雨林植物在磷限制条件下表现出较高的磷酸酶活性^[76]。然而, 磷添加显著降低了米楮、杉木细根的酸性磷酸酶活性^[77]。MARKLEIN 等^[78]对 34 项研究的整合分析表明, 氮添加显著提高了磷酸酶活性, 这可能是因为氮添加促进了植物生长, 增加了对磷的需求, 从而刺激了酸性磷酸酶的分泌以活化更多的有机磷。

硝酸还原酶是植物氮素同化过程中的关键酶, 负责将硝酸盐还原为亚硝酸盐, 进而转化为氨供植物利用。硝酸还原酶的活性直接影响植物的氮代谢能力^[32]。氮沉降背景下, 土壤中硝酸盐含量增加会刺激植物体内硝酸还原酶活性的提高, 从而促进氮素的转化和同化。例如, 吴淑华等^[79]对常绿阔叶林 6 种植物的模拟氮沉降实验发现, 氮添加显著提高了植物体内硝酸还原酶的活性。此外, 根尖是氮素吸收和代谢最活跃的部位, 其硝酸还原酶含量较高, 能够快速同化吸收的氮素^[80-81]。在氮胁迫条件下, 植物的氮素代谢可能受阻, 导致硝酸还原酶活性降低。例如, 马祥庆等^[82]对杉木的研究表明, 氮胁迫显著降低了根系硝酸还原酶的活性。目前关于磷添加对硝酸还原酶活性影响的研究较少, 但磷作为植物生长的重要元素, 可能通过影响植物的氮代谢间接调控硝酸还原酶活性。

3 植物地下觅食性状间的协调机制

植物在异质养分环境中, 通过调控根系形态、构型、增殖、菌根共生和根系分泌等性状之间的相互作用, 形成了一套复杂的协调机制, 以优化养分获取并适应环境变化。这种协调机制通过多层次功能整合实现, 涵盖性状间的协同与权衡, 以及资源分配中的成本效益优化^[8, 83]。

3.1 性状间的协同与权衡

在养分贫瘠的环境中,植物通常通过调整根系形态和生理性状来提高养分获取效率。例如,植物可能通过增加比根长来扩大根系的吸收表面积,同时提升养分吸收速率,形成“形态扩张-生理活化”协同策略增强对资源匮乏环境的适应能力^[3]。然而,性状间的协同效应会随养分有效性梯度发生策略性转换:WEN等^[83]对温室作物根系的研究发现,当土壤中易利用养分富集时,具有竞争性形态性状的物种会减少根系分泌物或菌根共生体的碳投入,转而优先依赖形态性状实现快速吸收,体现了“形态优化-生理收缩”的资源分配权衡。HONVAULT等^[84]进一步印证了这种机制:较粗的根虽因吸收表面积受限而处于形态劣势,但通过根鞘释放更多的羧酸盐或磷酸酶(生理优势)形成功能补偿,而较细的根则以低生理成本维持高效吸收界面,这种“形态-生理功能互补”本质上是异质环境中资源分配策略的权衡表达。

3.2 成本效益优化

在成本效益上,植物通过根系和菌根共生体的协调作用,以最小的资源投入获取最大的养分收益^[85]。如根直径较细的树种,单位根长构建成本低,通过根长增殖扩大吸收面积,而根直径较粗的树种,单位根长构建成本高,则倾向于投资菌根真菌的细密菌丝网络,以更低碳耗实现广域养分勘探^[24]。在低氮或低磷条件下,植物依赖菌丝网络拓展(延伸至养分斑块)和代谢活化(分泌磷酸酶、有机酸等)高效捕获分散养分,此时菌根共生体的碳投资回报率显著高于自主根系探索^[86]。然而,随着土壤氮磷有效性升高,植物对菌根的依赖性普遍降低:高磷直接抑制菌丝生长和侵染率,而高氮削弱菌根真菌的有机养分分解能力,促使植物将碳资源转向根系直接吸收或地上部生长^[14, 24, 87]。这种“共生解耦”策略具有环境响应特异性,即当菌丝维持的碳成本超过其养分收益时(如高养分土壤),植物优先减少菌丝投资;但在特定逆境或有机养分主导环境中,保留菌根的抗逆功能或菌丝网络的定向养分捕获能力仍具有净收益优势^[88-89]。菌根共生策略的动态调整,本质上映射了植物在资源异质性环境中对“碳投入-养分收益”权衡的精准计算和适应性表达。

4 研究展望

已有研究探讨了氮磷添加对植物地下觅食性状的影响,但这些研究多局限于单一养分条件,很少考虑不同养分间的相互作用。氮磷交互作用可能对地下性状的响应产生协同或拮抗效应^[90-91],因此,探讨植物地下觅食性状对不同养分间交互作用的响应,有助于揭示植物适应复杂养分环境的机制,为森林生态系统的经营和管理提供科学依据。目前,根系分泌性状,特别是根系分泌物诱导的根际酶活性的研究相对不足。根系分泌物在调节根际养分有效性方面具有重要作用,但与吸收根和菌根性状的协同响应机制尚未得到充分研究。未来研究应更加注重将根系分泌性状与吸收根、菌根性状相结合,探讨三者对养分斑块的协同响应机制,并纳入根系经济空间框架^[7],这将有助于更全面地揭示植物在异质环境中的适应策略,并为理解植物地下觅食性状的功能整合提供新的视角。当前关于地下性状对异质斑块响应的研究多基于盆栽幼苗^[92-93],而针对野外成熟植物的原位研究相对缺乏。尽管盆栽便于控制条件,但难以完全模拟自然环境中复杂的养分动态和生物互作过程,因此,加强野外原位研究对于深入理解植物地下生态过程、揭示植物适应环境变化的机制以及预测生态系统对全球变化的响应具有重要意义。不同菌根树种在根形态和结构上具有一定的差异性^[25],且对养分吸收具有不同的偏好性^[94-95],这可能导致不同菌根树种在养分获取策略上存在根本差异。因此,加强不同菌根树种地下养分获取策略的研究,将对深入理解森林生态系统中不同菌根树种的共存至关重要。

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