

原始森林土壤 NH_4^+ / NO_3^- 生境特征 与某些针叶树种的适应性

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摘要: 在陆地生态系统中, 生存地段的土壤养分环境构成了植物的“营养生境”。植物在长期进化过程中往往产生对原生营养生境的生态适应, 其中对 NH_4^+ 和 NO_3^- 两种无机氮源的吸收、利用特性便可能是这种适应的一个重要方面。由于硝化抑制(限制)或微生物对 NO_3^- 的强烈吸收、固持作用, 酸性、弱酸性的原始森林土壤中 NH_4^+ 含量大都远高于 NO_3^- , 从而形成了以 NH_4^+ 占绝对优势的“氮营养生境”。很多针叶树种(尤其是演替晚期阶段占优势者)对其长期所处的 NH_4^+ 优势生境产生了充分适应, 以致对非还原态氮(NO_3^-)的吸收、利用能力严重下降。这些针叶树往往表现出典型的“喜铵性”, 而在 NO_3^- 优势环境中则会引起氮代谢失调和生长下降。从氮同化酶、高耐铵性、根对 NH_4^+ 和 NO_3^- 的相对吸收能力及 NO_3^- 吸收的反馈控制、养分关系与养分平衡、根部碳流失、光合作用及耐荫性等多方面阐述了喜铵针叶树适应的生理生化机制。这种生态适应可能是顶极森林群落维持长期稳定的重要机制之一, 而采伐干扰后 NO_3^- 明显增加的立地条件则可能会导致喜铵的“原优势针叶树种”更新困难。在温带退化森林生态系统恢复与重建过程中, 顶极针叶树种对 NH_4^+ 营养生境的固有适应性是必须充分考虑的问题。

关键词: 森林土壤; 铵态氮; 硝态氮; 针叶树种; 生态适应; 生理生化机制

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Soil NH_4^+ / NO_3^- nitrogen characteristics in primary forests and the adaptability of some coniferous species

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Abstract In terrestrial ecosystems, soil nutrient regimes at a plant's living site generally represent the plant's "nutrition habitat". Plant species frequently well adapt to their original "nutrition habitat" during a long process of evolution, and the apparent preference for ammonium or nitrate nitrogen source (NH_4^+ or NO_3^-) might be an important aspect of the adaptation. Plants typically favor the nitrogen form most abundant in their natural habitats.

Nitrate has been recognized as the dominant mineral nitrogen form in most agricultural soils and the main nitrogen source for crops, but it is not usually the case in forest ecosystems. A large number of studies show that the "nutrition habitats" associated with primary forest soils are typically dominated by NH_4^+ rather than NO_3^- , generally with NO_3^- content much lower than NH_4^+ . Low levels of NO_3^- in these forest soils generally correspond to low net rates of nitrification. The probable reasons for this phenomenon include: (1) nitrification limitations and/or inhibitions caused by lower pH, lower NH_4^+ availability (autotrophic nitrifiers can't successfully compete for NH_4^+ with heterotrophic organisms and plants), or allelopathic inhibitors (tannins or higher molecular weight proanthocyanidins) in the soil; or (2) substantial microbial acquisition of nitrate in the soils which makes net nitrification rates substantially less than gross nitrification rates even though the latter are relatively high.

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Many coniferous species (especially such late successional tree species as *Tsuga heterophylla*, *Pinus banksiana*, *Picea glauca*, *Pseudotsuga mezesii*, *Picea abies* and etc.) fully adapt to their original NH_4^+ -dominated "nutrition habitats" so that their capacities of absorbing and using non-reduced forms of nitrogen (e.g. NO_3^-) substantially decrease. These conifers typically show distinct preference to NH_4^+ and reduced growth due to nitrogen metabolism disorder when NO_3^- is the main nitrogen source. The physiological and biochemical mechanisms that account for the adaptation to NH_4^+ -dominated systems (or limited ability to use NO_3^-) for the coniferous species include:

- (i) distribution and activity of enzymes for catalyzing nitrogen reduction and assimilation, generally characterized by lower nitrate reductase (NR);
- (ii) greater tolerance to NH_4^+ or rapid detoxification of ammonium nitrogen in the roots;
- (iii) lower capacity of absorption to NO_3^- by roots that might be controlled by feedback regulations of certain N-transport compounds, such as glutamine;
- (iv) relations and balance between nitrogen and other elements (such as Ca^{2+} , Mg^{2+} , and Zn^{2+} etc.). Some NH_4^+ -preferred conifers might be more adapted (tolerant) to lower base cation conditions;
- (v) NO_3^- nutrition, rather than NH_4^+ , that may lead to the loss of considerable quantities of organic and inorganic carbon to the surrounding media and mycorrhizal symbiont and probably contribute to slower growth;
- (vi) the metabolic cost of reducing NO_3^- to NH_4^+ that may make shade-tolerant conifers favor the uptake of reduced nitrogen (NH_4^+).

The adaptation of late successional conifers to NH_4^+ -dominated habitats has profound ecological implications. First, it might be an important prerequisite for the climax forest communities dominated by these conifers to maintain long-term stability. Second, primary coniferous or coniferous-broadleaved forests have been widely perturbed because of commercial exploitation, where the soil ammonium nitrogen pool tends to be largely transformed to nitrate after disturbance. In such a situation, the coniferous species that were dominant in undisturbed ecosystems may become poor competitors for nitrogen, and the site will be occupied by early successional (pioneer) plants better adapted to nitrate utilization. In other words, the implicit adaptation of many conifers dominant in undisturbed communities to ammonium nitrogen will cause difficulties in their regeneration on disturbed sites, which must be taken into account in the practical restoration of degraded temperate forest ecosystems.

Key words: forest soil; ammonium; nitrate; coniferous trees; adaptation; physiological and biochemical mechanisms

现代生态学中所涉“生境”概念,既可泛指某类生物经常生活的习惯性局域生态环境,也可特指某生物群体或个体目前所处的具体位置,强调现实生态环境^[1]。在自然生态系统中,植物种的生境由其生存地段的土壤和小气候等要素组成,它为该植物直接提供了各种环境资源和个性化的生活条件。由于植物所需的矿质养分资源基本上是从土壤中获取,因此生存地段的土壤养分环境便构成了其营养生境(nutrition habitat)。

在长期进化过程中,植物往往产生对特定营养生境(原生营养生境)的生理适应(physiological adaptation)和形态适应(anatomical adaptation),以致分化出不同的营养基因型或不同营养特性的生理生态类群。例如,植物在土壤低磷胁迫的长期选择压力下,常形成根系形态的改变与特化、专性根分泌物(如有机酸和胞外磷酸酶)大量增加及根对溶液中低浓度 H_2PO_4^- 的有效吸收(低 C_{min} 和 K_m) 等适应机制,以提高对土壤磷的吸收能力^[2,3]。又如,长期适应了石灰性土壤的植物(喜钙植物, calcicole)对高浓度的 Ca^{2+} 同时具有忍耐和逃避功能,并形成特异性的缺铁适应机制—诱导原生质膜产生还原酶或根分泌麦根酸类(mugineic acid, avenic acid)植物铁载体(phytosiderophore)^[4]。由于对土壤养分吸收、利用和运转(translocation)的特性差异,因而植物有着多种不同的养分效率(nutrient efficiency)模式^[5]。实际上,通常所说的“喜肥植物”和“耐瘠植物”也很可能是不同物种对其原始生境中的土壤肥力状况长期适应的结果。

氮是植物必需的大量元素之一,通常植物在生长发育过程中吸收的氮要高于其它矿质元素,因而氮常成为限制植物生长的主要元素^[6]。土壤中的氮以各种复杂的化学形态存在,其中可被植物吸收利用的主要是硝态氮(NO_3^-)和铵态氮(NH_4^+)。植物对氮营养环境的长期适应不仅表现为土壤肥力或养分需求的数量差异,也不仅限于获取氮素的某些特殊行为(如共生固氮和菌根对有机氮的吸收),更重要的还表现为对 NO_3^- 和 NH_4^+ 两种不同形态氮源的偏向选择性^[7~9],而且这是在其它营养元素方面所不具备的特征。大量栽培实验表明,很多植物在长期进化过程中形成了对不同形态氮素的偏向利用特性:有些种类在纯 NO_3^- 或 NO_3^- 占优势的氮营养环境中吸收氮素较多,生长较好,表现为喜硝性(nitrophilous 类植物即其典型代表)^[10~15];另一些植物

则在纯 NH_4^+ 或 NH_4^+ 优势环境中生长速度快, 生理反应较好, 表现出喜 NH_4^+ 性^[8, 16~24]。尽管植物吸收 NH_4^+ 和 NO_3^- 的特性受介质N 浓度、pH 值和温度等环境因子的影响^[21, 22, 25~29], 但对两种氮源的不同反应仍主要取决于种的特性^[30~33]。这种差异是植物对 NO_3^- 或 NH_4^+ 的相对吸收能力、由 NO_3^- 向 NH_4^+ 的还原能力、对 NH_4^+ 的同化能力以及与氮源形态有关的碳、氮整体代谢过程所决定的^[31, 34~38], 是植物营养特性的反映^[30, 39]。而植物产生上述氮代谢差异, 可能主要是对其原始营养生境(NO_3^- 优势生境或 NH_4^+ 优势生境) 长期生理适应的结果, 一般来说植物总是趋于偏好其自然生境中最丰富的氮源形态^[8, 31, 40]。本文从这一观点出发, 试图通过大量相关例证, 阐明原始森林土壤的 NH_4^+ / NO_3^- 生境特征及某些针叶树对这种特定氮营养生境的生态适应, 以期为温带退化森林生态系统恢复提供营养生态学理论依据。

1 原始森林土壤 NH_4^+ / NO_3^- 生境特征

1.1 低 NO_3^- 水平与硝化抑制

本文“原始森林土壤”是指未被干扰的成熟期森林土壤(soils of mature forest), 在大多数情况下它意味着某一地区长期稳定的森林群落(顶极群落 climax) 下的土壤。由于湿润气候和较强淋溶作用的长期影响, 大多数原始森林土壤都呈酸性或弱酸性反应。很多研究表明, 从北方针叶林至热带雨林, 酸性、弱酸性原始森林土壤中 NH_4^+ 的供应大都远高于 NO_3^- (表 1), 硝态氮相对和绝对的过低现象在原始针叶林或演替后期阶段的稳定系统中尤为明显。

表 1 一些原始森林土壤的 NH_4^+ / NO_3^- 状况和净氮矿化(M in) /硝化(N it) 速率

Table 1 NH_4^+ / NO_3^- status and net nitrogen mineralization (M in) /nitrification (N it) rates of some undisturbed forest soils									
地点 Site	林型 Forest type	土壤 Soil							资料来源 A dapted from
		类型 Classification	深度 Depth (cm)	pH	NH_4^+ -N ($\mu\text{g/g}$)	NO_3^- -N ($\mu\text{g/g}$)	M in ($\mu\text{g/g}$)	N it ($\mu\text{g/g}$)	
美国怀俄明 Wyoming, U SA	美国黄松 Lodgepole pine	Typic Cryoboralfs	0~ 10	5.00	0.59	0.04	0.69 ¹⁾	0.04	[41]
美国印第安纳 Indiana, U SA	槭类Maple	Typic Dystrochrept	FF ²⁾ 0~ 15	5.7 5.8	90 4.5	11.9 2.4	550 ³⁾ 26	450 24	[42]
		Typic Dystrochrept	FF 0~ 15	5.2 3.8	97 2.1	4.2 0.4	500 17	220 3	
	栎类Oak	Typic Dystrochrept	FF 0~ 15	5.2 3.8	97 2.1	4.2 0.4	500 17	220 3	[42]
		Typic Dystrochrept	FF 0~ 15	5.2 3.8	97 2.1	4.2 0.4	500 17	220 3	
美国新英格兰 New England, U SA	硬阔 Northern hardwoods	Aquic Fragiorthod	FF 0~ 15 15~ 30	4.0 4.1 4.3	81 12.5 5.6	7.0 2.8 1.4	950 110 —	120 80 —	[42]
		Typic Udistamment	FF 0~ 15 15~ 30	4.0 4.5 4.9	10.7 0.2 1.1	0.2 0.1 0.2	420 60 —	trace 30 —	
	美国黄松 Ponderosa pine	Typic Ustorthent	FF 0~ 10	6.4 6.8	28 2.1	1.4 0.1	50 5	trace trace	[42]
		Typic Ustorthent	FF 0~ 10	5.4 5.8	70 7.0	2.8 0.1	200 12	20 5	
		Dystic Cryochrept	FF 0~ 20	5.2 4.7	56 9.8	0.7 0.2	80 20	trace trace	
		Typic Ustorthent	FF 0~ 10	5.4 5.8	70 7.0	2.8 0.1	200 12	20 5	
美国西北部 Pacific Northwest, U SA	花旗松 Douglas-fir	Typic Ustorthent	FF 0~ 15	5.1 4.6	37 2.2	1.1 0.1	80 10	5 2	[42]
		Typic Ustorthent	FF 0~ 15	5.1 4.6	37 2.2	1.1 0.1	80 10	5 2	
	银枫 Silver fir	Typic Ustorthent	FF 0~ 15	3.4 4.0	38 4.4	0.5 0.1	30 3	trace trace	[42]
		Typic Ustorthent	FF 0~ 15	3.4 4.0	38 4.4	0.5 0.1	30 3	trace trace	
美国新墨西哥 New Mexico, U SA	美国黄松 Ponderosa pine	—	0~ 15	5.0	1.39	0.19	—	—	[43]
	针叶混交林 Mixed conifer	—	0~ 15	5.1	2.65	0.23	—	—	
	山杨Aspen	—	0~ 15	5.1	4.41	0.24	—	—	
	云冷杉Spruce-fir	—	0~ 15	4.6	1.32	0.25	—	—	
美国俄勒冈 Oregon, U SA	北美西部圆柏 Western juniper	—	0~ 15	5.9	1.32	0.50	—	—	[43]
	铁杉Hemlock	—	0~ 15	4.8	0.97	0.18	—	—	
	铁杉-云杉 Hemlock-Spruce	—	0~ 15	3.8	4.53	0.08	—	—	
	铁杉和云杉 Hemlock and Spruce	—	0~ 15	3.8	4.53	0.08	—	—	
美国纽约州 New York, U SA	铁杉和云杉 Hemlock and Spruce	frigid Typic Haploorthods	0~ 5 5~ 15	3.5 ⁴⁾ 2.8	6.0 ⁵⁾ 6.3	0.0 < 0.1	— —	— —	[46] [44]

续表 1

	湿地针叶林	—	0~5	3.4	2.39	0.27	0.118 ⁽⁶⁾	0.000	
	Wetland Conifer		5~15	3.2	2.06	0.00	0.076	0.069	
加拿大BC省 British Columbia, Canada	北方针叶林	Podzols	FF	—	150 ⁽⁷⁾	<5	—	—	[45]
	Boreal coniferous forest		0~10	—	10	<1	—	—	
瑞典北部 Northern Sweden	欧洲赤松	Typic or Entic Haplocryods	表土 Top soil	3.5	20.2 ⁽⁸⁾	0.06	-0.1	-0.02	[46]
加拿大安大略 Ontario, Canada	针叶混交林	Podzols	0~10	3.7	1200 ⁽⁹⁾	70	334 ⁽¹⁰⁾	37	[47]
	Conifer mixed		10~20	4.8	—	—	90	6	
中国长白山 Changbai Mountain, China	阔叶红松林	暗棕壤	0~5(FF)	6.8	488.0	9.4	—	—	[48, 49]
	Korean pine-broadleaved	Dark Brown	5~11	5.4	62.2	0.6	—	—	
	forest	Forest Soil	11~25	5.6	54.4	0.4	—	—	
中国长白山 Changbai Mountain, China	阔叶红松林	暗棕壤	0~10	6.7	—	—	1.3 ⁽¹¹⁾	0.62	[50]
	Korean pine-broadleaved	Dark Brown							
	forest	Forest Soil							
	云冷杉林	山地棕针土	0~10	5.8	—	—	1.1	0.35	
	Spruce-fir forest	Mountain							
		Brown							
中国大兴安岭 Great Xingan Mountain, China	落叶松林	棕色针叶林土	A层	4.9	15.6	2.3	—	—	[51]
	Larch forest	Brown	A horizon						
		Coniferous							
中国西双版纳 Xishuangbanna, China	季雨林	砖红壤	0~10	3.75	19.75	4.71	6.55	16.28	[52, 53]
	Tropical Seasonal Rainforest	Latoil							

(1) 室内培养 1 个月测定值 M in. and N it. determined with Lab incubations for one month; (2) FF: 森林枯枝落叶层 Forest floor; (3) 室内培养 4 周测定值 Determined with Lab incubations for 4 weeks; (4) pH (CaCl₂); (5) kg/hm²; (6) 埋袋法培养 40d 测定值(kg/(hm²·d)) Determined with buried polyethylene bag technique incubated for about 40 days(kg/(hm²·d)); (7) 埋袋法培养 6 周测定值 Determined with buried polyethylene bag technique incubated for about 6 weeks; (8) NH_4^+/N 和 NO_3^-/N 用离子交换树脂法 NH_4^+/N 和 NO_3^-/N determined with ionic resins(μg per capsule), M in. 和 N it. 用埋袋法培养 1 个月测定($\mu\text{g}/(\text{g} \cdot \text{d})$) M in. and N it. determined with buried polyethylene bag technique incubated for about 1 month($\mu\text{g}/(\text{g} \cdot \text{d})$); (9) mg/m²; (10) 年净矿化/硝化量 Annual net N mineralization/nitrification; (11) 室内 25℃培养 30d 测定(kg/(hm²·d)) Determined with Lab incubations at 25℃ for 30 days(kg/(hm²·d))

尽管 NO_3^- 可能因不易被胶体吸附(易流失)而在许多土壤中会低于 NH_4^+ , 但森林土壤过低的 NO_3^- 水平往往与过低的净硝化速率(net nitrification rate)有关^[42, 54~56], 表 1 中的一些实例也反映出这一趋势。在室内或野外培养实验中, 森林土壤常表现出较弱的硝化潜力(nitrification potential)和较长的硝化滞后期(Lag in nitrification)^[55, 57]。因此, 大多数人认为酸性森林土壤中存在不同程度的硝化抑制。对于森林土壤的硝化抑制机理, 国内外研究者先后提出下面一些解释:

(1) 一般认为自养硝化菌(auto trophic nitrifiers)是不耐酸的, 所以森林土壤固有的低 pH 值常常抑制了硝化作用^[53, 55, 56, 58~62]。

(2) 低 NH_4^+ 可给性限制了 NO_3^- 生成, 因为自养硝化菌与异养微生物和植物竞争有效氮源(NH_4^+)时处于劣势^[42, 63~67]。在成熟森林生态系统中, 净氮化速率一般处于一定的较低水平, 使土壤 NH_4^+ 主要通过有效的封闭式循环(Closed N cycle)进入植被和微生物养分库^[68], 结果便导致 NH_4^+ 源缺乏和硝化抑制^[69, 70]。另一方面, 处于演替晚期阶段的森林凋落物(尤其针叶凋落物)大都具有较高的 C/N 值, 并含有较高的木素、单宁或游离酚类物质。在这种情况下, 不仅有机质的分解速率会较低, 土壤和凋落物层中 NH_4^+ 或活性有机氮的异养微生物固定或化学固定(与多元酚形成难被微生物利用的稳定复合物或腐殖质)也都较强烈, 从而大大降低了氮的矿化(尤其净矿化)速率^[71~79], 因此也就缺乏足够的可被硝化菌利用的 NH_4^+ 源。

然而最近却有研究表明, 瑞典北方针叶林土壤的硝化作用并非受限于 NH_4^+ 源, 因为当加入易矿化有机氮(甘氨酸)后 NH_4^+ 大量积累, 而 NO_3^- 并没有显著增加, 推测演替晚期阶段硝化作用的限制因素可能是缺乏适当的环境条件或存在较高浓度硝化抑制成分(游离酚类)^[46]。

(3) 树干淋洗或凋落物分解释放的化感物质(如单宁或多元酚类)抑制硝化微生物活性^[80~85],而且这种抑制在演替过程中逐渐加强^[80]。这一观点虽由来已久,但也一直存在不同看法^[64,86~89]。近来有研究表明,一些高分子多元酚(higher molecular weight proanthocyanidins)抑制微生物活性^[79],而低分子酚类物质(low molecular weight phenolics)除了直接对硝化微生物产生抑制外,更可能作为异养微生物的有效碳源而被利用^[90,91]。正如在(2)中刚提到的,较高浓度的游离酚可以促进矿质氮的生物固定或导致活性氮被结合到多元酚复合物中^[92],因而会对硝化作用产生间接抑制。

(4) 温带、寒温带原始林或北方针叶林下土壤冷湿,不利于氮矿化和硝化作用进行^[35,51,58,93,94]。而且,硝化作用对冷湿条件的反应可能比氨化作用更敏感^[95],因而会导致 NH_4^+ 相对“积累”。

1.2 微生物对 NO_3^- 的强烈吸收固定——另类全新观点

与矿化和硝化有关的森林土壤氮转化过程十分复杂,许多问题尚不完全清楚。关于原始森林土壤的硝化作用近来有另一种截然不同的观点。 ^{15}N 同位素稀释实验(^{15}N isotope-dilution technique)表明,原始针叶林土壤微生物养分库内的硝酸盐周转率比先前预想的高很多^[96];在许多这样的森林土壤中总硝化速率(gross nitrification rate)都相当高,而微生物对 NO_3^- 的同化作用却又异常强烈,几乎能消耗掉所产生的所有 NO_3^- ,因此净硝化速率远不能反映土壤的总硝化速率^[43,96]。换言之,某些原始森林土壤过低的 NO_3^- 水平可能主要是由于微生物强烈的同化作用,而非如前所述的“硝化抑制”。

无论哪种原因导致森林土壤的低 NO_3^- 水平,起码有一点是可以肯定的:酸性、弱酸性的原始森林土壤为森林植物提供了以 NH_4^+ 占优势的氮营养生境,这与多数荒地土壤和农田土壤中 NO_3^- 供应占优势的情况完全不同^[55,97,98]。

2 某些针叶树种的适应特点——喜铵性

森林树种对其长期所处的营养生境往往有着深刻的改造与适应。尤其是某些在演替晚期阶段或顶极阶段占优势的针叶树种,如加州铁杉(*Tsuga heterophylla*)、北美短叶松(*Pinus banksiana*)、花旗松(*Pseudotsuga m e z iesii*)、白云杉(*P icea glauca*)、挪威云杉(*P icea abies*)和海岸松(*P inus pinaster*)等,其有关特性在北美、北欧和澳洲国家颇受关注。这些针叶树的凋落物分解特点和硝化抑制成分往往造就了典型的酸性及 NH_4^+ 占绝对优势的土壤环境,有机质分解释放的氮素养分一般只停留在 NH_4^+ 形态^[58,80,81,93,99~101];由于硝化抑制或微生物对 NO_3^- 的强烈固定,土壤中 NO_3^- 的浓度往往极低^[97]。从进化的角度看,这些树种对 NH_4^+ 应该有着较高的吸收和利用效率,而对 NO_3^- 的高效吸收利用似乎就是冗余的。事实上,顶极群落的长期稳定性使得它们在各自的原始生境中对 NH_4^+ 产生了充分适应(complete adaptation),以至于对非还原态氮(NO_3^-)的吸收与利用能力严重下降^[17,35,97,102,103]。这样,就会在栽培实验中表现出强烈的铵偏向选择,且只在 NH_4^+ 占优势的营养环境中生长良好(表2)。

3 适应的生理生化机制

针叶树种往往表现出“喜铵性”和相应程度的“厌硝性”,其主要生理生化机制可能在于下列几方面:

(1) 氮同化酶 植物对某种氮营养环境产生适应的一个重要先决条件可能在于催化 NO_3^- 还原和 NH_4^+ 同化的酶类^[31,106]。首先,硝酸还原酶(NR)作为硝酸盐同化的起始酶和限速酶,其活性与植物同化 NO_3^- 的能力密切相关。树木的NR活性可分布在根部和叶部,喜 NH_4^+ 的针叶树通常根中的NR活性较高,而叶中的NR活性较低^[32,107~109]。即使经过 NO_3^- 的诱导,多数情况下也是根中的NR活性增加,而叶中的变化不大^[102];而且,达到其最大 NO_3^- 吸收速率所需的诱导时间也很长^[97]。所以这些针叶树往往不能有效地利用 NO_3^- ,不能把 NO_3^- 作为主要氮源。

另一方面, NH_4^+ (或 NH_3)同化是高等植物氮同化的共有步骤。喜 NH_4^+ 的针叶树根部和叶部通常都具有较高的将游离 NH_4^+ 转化为谷氨酸的谷氨酰胺合成酶(GS)和谷氨酸合成酶(GOGAT),有的还具有较高的直接将 NH_4^+ 合成为谷氨酸的谷氨酸脱氢酶(GDH)活性^[102,107,110,111]。当这些针叶树吸收大量的 NH_4^+ 进入体内后,这些酶可以将 NH_4^+ 迅速转化成氨基酸,同时避免了 NH_4^+ 毒害发生。尽管GDH一般不是氮同化的主要酶(Primary N assimilating enzyme),但在有外源 NH_4^+ 加入或 NH_4^+ 浓度较高时,GDH的活性会显著增强^[36,102,110,112]。

(2) 解毒作用与高耐铵性 很多植物在介质或体内 NH_4^+ 度较高时会发生“铵毒害”^[113]。进入植物体内的 NH_4^+ 离子必须被迅速同化以避免其对组织的毒害作用^[114~116]。 NH_4^+ 主要在根部通过GS/GOGAT途径同化为谷氨酰胺和谷氨酸(即所谓“解毒作用”),以免将 NH_4^+ 直接输送到更敏感的茎、叶部位^[31,117]。

然而越来越多的研究表明,一些喜 NH_4^+ 针叶树不仅具有上述较强的同化“解毒功能”,还具有相对较强的耐铵能力。在供应 NH_4^+ 氮源的情况下,即使体内(细根、叶等)积累了较高浓度的游离 NH_4^+ 也不出现明显的毒害迹象^[33,35,97,118]。有人认为,这些树种的体内可能具有 NH_4^+ 的贮存库,它们主要通过贮存作用消除或降低 NH_4^+ 的潜在毒害^[119]。

(3) 根对 NH_4^+ / NO_3^- 离子的相对吸收及 NO_3^- 吸收的反馈控制 相对于 NH_4^+ 而言,有的针叶树(如北美短叶松)根系对 NO_3^- 的吸收速率低下,在 NO_3^- 环境中氮的吸收环节(而不是对 NO_3^- 的还原能力)成为限制生长的瓶颈^[35]。据认为,白云杉根系对 NO_3^- 的吸收速率明显低于 NH_4^+ ,可能是因为原生质膜上相应的 NO_3^- 载体蛋白数量较少,而非载体对两种形态氮的亲

力有差异^[97]。

表 2 一些针叶树种对 NH₄⁺/NO₃⁻ 氮源的反应

Table 2 Response of some conifer species to ammonium (NH ₄ ⁺)/nitrate(NO ₃ ⁻) nitrogen		
树种 Forest species	对 NH ₄ ⁺ /NO ₃ ⁻ 的反应 Response to NH ₄ ⁺ /NO ₃ ⁻	资料来源 Reference
加州铁杉 <i>Tsuga heterophylla</i>	在N 浓度相同的单一氮源中, 幼苗吸收NH ₄ ⁺ 速率是NO ₃ ⁻ 的 3.2 倍; 在 50 : 50 的混合氮源中, 吸收 NH ₄ ⁺ 的数量是NO ₃ ⁻ 的 2.1 倍。In NH ₄ ⁺ or NO ₃ ⁻ only treatment of equimolar solution, NH ₄ ⁺ was taken up at 3.2 times the rate of NO ₃ ⁻ . In NH ₄ ⁺ + NO ₃ ⁻ (50: 50) treatment, NH ₄ ⁺ uptake was 2.1 times as much as NO ₃ ⁻ uptake	[102]
北美短叶松 <i>Pinus banksiana</i>	在遮荫与不遮荫情况下, 以相同浓度的NH ₄ ⁺ 或NO ₃ ⁻ 单一氮源栽培幼苗, 12 周后, NH ₄ ⁺ 处理苗株积累的氮量是NO ₃ ⁻ 处理的 2.1~ 2.4 倍, 前者地上生物量为后者的 1.5~ 2.6 倍。Seedlings were grown (in a shaded or unshaded light regime) with either NH ₄ ⁺ or NO ₃ ⁻ as the sole nitrogen source in a 12-week culture. Total nitrogen accumulation and shoot biomass of ammonium-fed plants were 2.1~ 2.4 and 1.5~ 2.6 times greater, respectively, than that of nitrate-fed plants	[35]
白云杉 <i>Picea glauca</i>	苗木经过充分的硝态氮诱导后, 植入摩尔浓度相等的NH ₄ ⁺ 或NO ₃ ⁻ 溶液中短期培养。每 g 鲜根对NH ₄ ⁺ 的吸收量可达NO ₃ ⁻ 吸收量的 20 倍, 细胞质的NH ₄ ⁺ 浓度达NO ₃ ⁻ 浓度 10 倍。After induced with NO ₃ ⁻ , seedlings were transplanted in NH ₄ ⁺ or NO ₃ ⁻ solutions for a short-time culture. Uptake of NH ₄ ⁺ (per gram of fresh roots) was up to 20 times greater than that of NO ₃ ⁻ from equimolar solution, cytoplasmic concentration of NH ₄ ⁺ was up to 10 times greater than that of NO ₃ ⁻ , and physiological processing of NO ₃ ⁻ was much less than that of NH ₄ ⁺ .	[97]
欧洲赤松和欧洲落叶松 <i>Pinus sylvestris</i> and <i>Larix decidua</i>	同时供应NH ₄ ⁺ 和NO ₃ ⁻ 的条件下, 对NH ₄ ⁺ 的吸收速率明显高于NO ₃ ⁻ , 约可高出 6 倍。Absorbing NH ₄ ⁺ preferentially over NO ₃ ⁻ when supplied with NH ₄ ⁺ + NO ₃ ⁻ nitrogen sources, with NH ₄ ⁺ net uptake rate about 6 times higher than NO ₃ ⁻ uptake rate	[32]
花旗松 <i>Pseudotsuga menziesii</i>	在供应NH ₄ ⁺ 氮源时, 苗株生物量, 相对生长速率(RGR) 及侧根数皆达到最高。Whole-seedling biomass, relative growth rate (RGR), and number of lateral roots, were greatest in seedlings grown with NH ₄ ⁺ .	[36]
	在混合氮源中优先吸收NH ₄ ⁺ , NH ₄ ⁺ 营养优于NO ₃ ⁻ 营养。Absorbing NH ₄ ⁺ prior to NO ₃ ⁻ in mixed nitrogen sources, NH ₄ ⁺ nutrition superior to NO ₃ ⁻ nutrition	[104, 105]
挪威云杉 <i>Picea abies</i>	吸收的NH ₄ ⁺ 多于NO ₃ ⁻ , 在NH ₄ ⁺ 条件下生长较好。Absorbed more nitrogen in NH ₄ ⁺ than in NO ₃ ⁻ , growing better when supplied with NH ₄ ⁺ .	[17, 19]
海岸松 <i>Pinus pinaster</i>	在较高浓度下供应NH ₄ ⁺ 或NH ₄ ⁺ + NO ₃ ⁻ 混合氮源的苗株干重比供应NO ₃ ⁻ 单一氮源者约高 3 倍。Dry mass of seedlings supplied with NH ₄ ⁺ or NH ₄ ⁺ + NO ₃ ⁻ nitrogen at higher concentrations was approximately threefold greater than seedlings supplied with NO ₃ ⁻ alone	[33]
多种针叶树 Many conifers	对NO ₃ ⁻ 的吸收利用能力低下, 适于NH ₄ ⁺ 营养环境。Lower ability to use NO ₃ ⁻ , be more adapted to NH ₄ ⁺ nutrition	[16]

然而, 喜NH₄⁺ 的针叶树以NO₃⁻ 为氮源时导致的生长下降往往并不能简单地从根系对NO₃⁻ 的吸收速率低来解释, 其中氮代谢因素可能是问题的关键^[33]。首先, 植物对NO₃⁻ 的吸收受其代谢过程所决定的内部“库”和“流”的反馈作用所控制。一些内部生化因子, 如叶和运输液中(尤其后者)羧化物和胺类组分的浓度, 控制着NO₃⁻ 的吸收以及高亲和力NO₃⁻ 载体编码基因的转录^[120~124]。某些针叶树在供应NO₃⁻ 时吸收的氮虽然减少, 但是体内的游离氨基酸甚至NH₄⁺ 的浓度反而显著高于相应的NH₄⁺ 处理^[33, 35], 这意味着韧皮部和木质部中主要氮运输化合物(如谷酰胺等)的浓度也会相应升高^[33], 而正是这类组分可能向根部氮吸收位置提供了“反馈信号”^[122, 123, 125]。因此, 针叶树对NO₃⁻ 的吸收速率低于对NH₄⁺ 的吸收, 可能就是吸收NO₃⁻ 后氮代谢失调和某些游离有机氮积累所引起的反馈调节的结果。

进一步讲, 针叶树以NO₃⁻ 为主要氮源时的氮代谢失调可能与微量元素代谢性缺乏有关。NO₃⁻ 还原导致OH⁻ 离子失衡, 为此植物体内会合成大量有机酸以维持酸碱平衡^[33, 126]; 而有机酸(阴离子)对Zn²⁺ 等金属离子有强烈的螯和作用, 根部过多的有机阴离子可能会阻碍一些微量元素向冠部运输^[127]。Warren 等发现, 以较高浓度供应NO₃⁻ 单一氮源时, 海岸松(*Pinus*

p. inaster) 幼苗针叶的 Zn 营养接近缺乏的临界浓度, 且出现典型的缺锌症状^[33]。锌是 RNA 聚合酶的成分, 它参与了蛋白质合成的转录过程; 锌还与细胞分裂有关。植物分生组织中一般都需要较高浓度的锌及其它微量元素, 所以缺锌(和其它微量元素) 会减少细胞分裂、细胞伸长及蛋白质合成, 并导致氨基酸或酰胺类“反馈物质”积累^[33]。在这种情况下, 喜 NH_4^+ 针叶树以 NO_3^- 为氮源导致的代谢性生长下降就不可避免。

(4) 养分关系与养分平衡 由于 NH_4^+ 和 NO_3^- 离子的电性差异, 二者对其它养分离子的吸收具有不同影响。通常 NH_4^+ 抑制 K^+ 、 Ca^{2+} 、 Mg^{2+} 等养分离子的吸收, 增加 $P(H_2PO_4^- \text{ 或 } HPO_4^{2-})$ 的吸收; 而 NO_3^- 的作用则相反^[17, 27, 102, 128, 129]。因此有人认为, 适应了 NH_4^+ 营养的树种可能对低阳离子养分具有更高的耐受力^[102], 而针叶树对 Ca 、 Mg 的低需求或组织中的低 Ca 、 Mg 现象也多有报道^[130~134]。另一方面, 树木吸收 NH_4^+ 后会导致根际土壤酸化^[104, 135], 因而有利于 Al 、 Mn 及难溶性 P 的吸收^[129, 136, 137]。无论从离子平衡还是从根际效应看, NO_3^- 似乎都不利于 P 的吸收。至于在硝态氮环境中喜铵性针叶树的磷营养是否会出现问题, 目前尚无确切证据。不过, 针叶树 NO_3^- 营养导致的代谢性缺锌已经引起关注, 这在上文已作了讨论。

(5) 光合作用 两种不同氮源导致的氮代谢差异和其他矿质营养差异必然会影响到植物的光合作用, 包括叶绿素含量与组成、Rubisco 含量与活性、 CO_2 气孔导度和叶肉导度、净光合速率和光合作用的水分利用率等^[31, 138, 139]。不过, 海岸松针叶的 Rubisco 含量和以单位叶质量计算的最大光合速率(A_{max}) 不受氮源形态的影响^[33], 多数喜铵针叶树光合作用指标对 NH_4^+ 、 NO_3^- 两种氮源的响应尚有待研究。

(6) 根部碳流失 当吸收 NO_3^- 后, 根的酸碱平衡和电荷平衡至少部分地靠 OH^- 或 HCO_3^- 的直接排放来维持, 而排出的 HCO_3^- 又主要源自苹果酸脱羧作用。因此, NO_3^- 营养会导致数量可观的有机和无机碳向根周围介质和菌根共生体中流失^[9, 140], 并可能在一定程度上导致生长下降^[33]。

除了上述生理、生化原因外, 还有一个值得注意的事实, 即多数在演替晚期阶段占优势的针叶树种具有耐荫性(尤其幼年期)。由于同化 NO_3^- 需要额外多消耗能量(由 NO_3^- 至 NH_4^+ 的还原过程), 而在光合能量获取方面对耐荫植物同化 NO_3^- 又是不利的, 这可能促使耐荫植物选择喜还原态氮(NH_4^+) 的进化策略^[7]。同时, 这也可以部分地解释为什么针叶树的 NR 活性大部分分布在根部, 而叶部的 NR 活性往往较低^[102]。有关雨林群落的研究也表明, 先锋树种(喜光) 具有高水平的 NR 活力, 叶硝酸盐同化占优势, 而低 NR 活性则一般是郁闭林树种的特性^[141]。实际上, 弱光或遮荫可以认为是土壤 NH_4^+ 优势生境之外导致耐荫针叶树喜铵性的另一耦合性长期环境因素。

4 结语

在酸性、弱酸性的原始森林土壤中, NH_4^+ 含量大都远高于 NO_3^- , 从而形成了以 NH_4^+ 占优势的“氮营养生境”。很多在演替晚期阶段占优势的针叶树种对其长期所处的 NH_4^+ 优势生境产生了充分适应, 表现为明显的“喜铵性”和“厌硝性”。国内外研究者提出了各种原始森林土壤矿质氮转化过程的控制机理和针叶树适应 NH_4^+ 营养生境的生理生化机制, 但对若干机理、机制问题的认识尚有待完善。

晚期演替针叶树种对 NH_4^+ 营养生境的固有适应性具有深刻的生态学和林学意义。首先, 这可能是顶极森林群落维持长期稳定的一个重要先决条件。然而, 最大的现实问题是原始针叶林或针阔混交林已大面积遭受采伐破坏, 干扰后土壤 NH_4^+ 氮库趋于大部分转化为 NO_3^- ^[35, 41, 42, 45, 51, 69, 97]。在 NO_3^- 增多的干扰立地上, 适于 NH_4^+ 营养的“原优势针叶树种”(幼苗) 将变成氮素养分资源的弱势竞争者(立地被更适于 NO_3^- 营养的先锋植物占据) 并由此导致其更新困难^[35, 97], 这一问题在退化森林生态系统恢复与重建过程中须予以充分考虑。另外, 在人工林培育(包括苗木培育) 过程中, 也应注意喜铵针叶树的氮营养特性。我国温带针阔混交林区、寒温带针叶林区及高海拔针叶林区都有大面积的退化森林生态系统和多个“顶极性”针叶树种, 因此系统地研究森林土壤氮营养生境特征和针叶树种的适应性问题在我国颇具现实意义。

揭示森林土壤矿质氮转化过程的控制机理和森林树种适应某一特征性氮营养生境的生理机制有助于从根本上解决上述生态学和林学问题, 所以该领域的基础性研究也将有着良好前景。

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