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Soil $\text{NH}_4^+/\text{NO}_3^-$ 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 cannot 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.

Many coniferous species (especially such late successional tree species as *Tsuga heterophylla*, *Pinus banksiana*, *Picea glauca*, *Pseudotsuga mezesii*, *Picea abies*, 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; and 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.

Keywords forest soil, ammonium, nitrate, coniferous trees, adaptation, physiological and biochemical mechanisms

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1 Introduction

The term "habitat" in modern ecology refers, in a broad sense, to the regional environment that some certain organisms

traditionally live in, and it also specifically represents the current location of an organism community or individual. In the latter sense, it emphasizes on the practical ecological environment (Cai and Shang, 1995). In natural ecosystems, the plant's habitat consists of the soil it lives in and the surrounding microclimate, which directly provides various environmental resources for the plant. The nutritional environment of the soil, from which the plant acquires mineral elements it needs, constitutes the nutrition habitat of the plant.

In the long-term process of evolution, plants are likely to be adapted physiologically and anatomically to the specific primitive nutrition habitat, and thus develop into sorted ecological communities with different nutritional genotypes or nutritional characteristics. For instance, the long-term exposure to the low phosphorous stress in the soil is likely to lead to adaptation mechanisms, such as, morphological mutation or specialization of root systems, a considerable increase in the amount of special exudates (e.g., organic acids and extra-cellular phosphatases) as well as the effective absorption of roots to low-concentration H_2PO_4^- (C_{\min} and K_m) in the soil (Wang et al., 1998; Zhang et al., 1998). For another example, plants (calcicoles) long adapted to lime soil possess both tolerance and avoidance to high concentrations of Ca^{2+} and develop specifically a ferrum-deficient mechanism—inducing plasma membranes to produce reductases or inducing roots to excrete phytosiderophores such as mugineic acid (Liao and Yan, 2003). Diverse nutrition efficiency models exist in plants due to their difference in the uptake, utilization and translocation to soil nutrition (Lynch, 1998). The so-called “fertilizer-preferred plants” and “barren-tolerant plants” are in fact the outcome of a long adaptation to soil fertility in the plant's primitive habitats.

As one of the necessary macroelements for plants, nitrogen is assimilated more than other elements during the plant growth and development, and becomes the main restrictor element to plant growth (Aerts and Chapin, 2000). Nitrogen exists in soil in a variety of forms, of which nitrate nitrogen (NO_3^-) and ammonium nitrogen (NH_4^+) are two major forms that can be absorbed by plants. The long adaptation of plants to nitrogen nutrition neither exhibits merely as the quantitative difference of soil fertility or nutritional requirements, nor be restricted to some special N-acquiring behaviours (such as organic nitrogen absorption by symbiotic nitrogen-fixation and mycorrhiza), more importantly, it rests on the preferential selection to the two nitrogen sources (NO_3^- and NH_4^+) (Gutschick et al., 1981; Turnbull et al., 1996; Plassard et al., 2000). Furthermore, this phenomenon is characterized exclusively by nitrogen rather than by other elements. A large number of cultivation experiments show that many plants have a preferential utilization of specific nitrogen form during the long-term evolution: some species assimilate more nitrogen and grow well in a NO_3^- -only or NO_3^- -dominated condition, exhibiting as NO_3^- -preferred species, with nitrophilous plants as representatives (Vessey et al., 1990; Stadler and Gebauer, 1992; Cui, 1998a; Zhang et al., 2000; Walch-Liu et al., 2000; Guo et al., 2002); on the other hand, some grow

faster in pure NH_4^+ or NH_4^+ -predominant soils, appearing as NH_4^+ -preferred species (Van den Driessche, 1971; Ingestad, 1979; Finlay et al., 1989; Turnbull et al., 1996; Marschner et al., 1991; Miller et al., 1991; Peuke and Tischner, 1991; Garnett and Smethurst, 1999; Majerowicz et al., 2000; Cui, 2001). Despite that some environmental factors, such as nitrogen level in media, pH value and temperature, have certain impacts on plant's assimilation to NH_4^+ and NO_3^- (Clarkson, 1985; Bloom, 1988; Jones et al., 1991; Peuke and Tischner, 1991; Serna, 1992; Jones and Dighton, 1993; Garnett and Smethurst, 1999), its response to the two nitrogen sources depends largely on the plant species itself (Falkengren-Grerup, 1995; Claussen and Lenz, 1999; Malagoli et al., 2000; Warren and Adams, 2002). The difference of plant's preference to nitrogen sources is jointly decided by plant's affinity to NH_4^+ or NO_3^- , the reducing ability from NO_3^- to NH_4^+ , the assimilability to NH_4^+ as well as the metabolic process of carbon and nitrogen regarding nitrogen forms (Lavoie et al., 1992; Raven et al., 1992; Bedell et al., 1999; Claussen and Lenz, 1999; Bijlsma et al., 2000; Bijlsma and Lambers, 2000), and it reflects plant nutrition speciality (Falkengren-Grerup, 1995; Wang et al., 1999). The difference of nitrogen metabolism might stem from the long-range physiological adaptation to the primitive nutrition habitats (NH_4^+ - or NO_3^- -dominated habitats), for plants generally prefer the most abundant nitrogen source in natural habitats (Stewart et al., 1989; Turnbull et al., 1996; Claussen and Lenz, 1999). Starting from this point of view, this study tries to elaborate the soil $\text{NH}_4^+/\text{NO}_3^-$ habitat characteristics in primary forests and the ecological adaptation of some conifers to specific nitrogen habitats for the purpose of providing a theoretical basis to the restoration of temperate degenerated forest ecosystems.

2 Soil $\text{NH}_4^+/\text{NO}_3^-$ habitat characteristics in primary forests

2.1 Low NO_3^- level and nitrification inhibition

The primary forest soils mentioned in this study refer to undisturbed soils in mature forests, which implies in most cases the soils in a stable forest community (climax community) for a long term. Due to the impacts of humid climates and eluviation over a long period, most primary forest soils present acidic or faintly acidic features. Many previous researches showed that the provision of NH_4^+ in acidic or lightly acidic soils of primary forests is much higher than that of NO_3^- , either in north coniferous forests or in south tropic rain forests (Table 1), and that the relatively or absolutely low NO_3^- level is remarkable, especially in primary coniferous forests or in the stable ecosystems of late successional stage.

Despite that NO_3^- is not easy to be absorbed by soil colloids and thus results in a lower content than NH_4^+ , the excessively low level of NO_3^- is correlated rather with net nitrification rate (Vitousek et al., 1982; Gosz and White,

Table 1 $\text{NH}_4^+/\text{NO}_3^-$ status and net nitrogen mineralization (Min)/nitrification (Nit) rates of some undisturbed forest soils

Site	Forest type	Soil							References
		Classification	Depth /cm	pH	$\text{NH}_4^+\text{-N}$ /($\mu\text{g}\cdot\text{g}^{-1}$)	$\text{NO}_3^-\text{-N}$ /($\mu\text{g}\cdot\text{g}^{-1}$)	Min. /($\mu\text{g}\cdot\text{g}^{-1}$)	Nit. /($\mu\text{g}\cdot\text{g}^{-1}$)	
Wyoming, USA	Lodgepole pine	Typic Cryoboralfs	0–10	5.0	0.59	0.04	0.69 ¹⁾	0.04	Giardina and Rhoades, 2001
Indiana, USA	Maple	Typic	FF ²⁾	5.7	90	11.9	550 ³⁾	450	Vitousek et al., 1982
		Dystrochrept	0–15	5.8	4.5	2.4	26	24	
New England, USA	Northern hardwoods	Typic	FF	5.2	97	4.2	500	220	Vitousek et al., 1982
		Dystrochrept	0–15	3.8	2.1	0.4	17	3	
		Aquic	FF	4.0	81	7.0	950	120	
		Fragiorthod	0–15	4.1	12.5	2.8	110	80	
New Mexico, USA	Ponderosa pine	Typic Ustrothent	15–30	4.3	5.6	1.4	–	–	Vitousek et al., 1982
			FF	4.0	10.7	0.2	420	Trace	
			0–15	4.5	0.2	0.1	60	30	
			15–30	4.9	1.1	0.2	–	–	
New Mexico, USA	Mixed conifer	Typic Udorthent	FF	6.4	28	1.4	50	Trace	Vitousek et al., 1982
			0–10	6.8	2.1	0.1	5	Trace	
			FF	5.4	70	2.8	200	20	
			0–10	5.8	7.0	0.1	12	5	
Pacific Northwest, USA	Douglas–fir	Dystric Cryochrept	FF	5.2	56	0.7	80	Trace	Vitousek et al., 1982
			0–20	4.7	9.8	0.2	20	Trace	
			FF	5.1	37	1.1	80	5	
			0–15	4.6	2.2	0.1	10	2	
New Mexico, USA	Silver fir	–	FF	3.4	38	0.5	30	Trace	Stark and Hart, 1997
			0–15	4.0	4.4	0.1	3	Trace	
			0–15	5.0	1.39	0.19	–	–	
			0–15	5.1	2.65	0.23	–	–	
Oregon, USA	Aspen	–	0–15	5.1	4.41	0.24	–	–	Stark and Hart, 1997
			0–15	4.6	1.32	0.25	–	–	
			0–15	5.9	1.32	0.50	–	–	
			0–15	4.8	0.97	0.18	–	–	
New York, USA	Hemlock and spruce	Frigid typic Haplorthods	0–15	3.8	4.53	0.08	–	–	DeLuca et al., 2002; Ohri et al., 1999
			0–5	3.5 ⁴⁾	6.0 ⁵⁾	0	–	–	
			5–15	2.8	6.3	<0.1	–	–	
			0–5	3.4	2.39	0.27	0.118 ⁶⁾	0	
British Columbia, Canada	Boreal coniferous forest	Podzols	5–15	3.2	2.06	0	0.076	0.069	Prescott et al., 2003
			FF	–	150 ⁷⁾	<5	–	–	
			0–10	–	10	<1	–	–	
			0–10	–	10	<1	–	–	
Northern Sweden	Scots pine	Typic or entic Haplocryods	Top soil	3.5	20.2 ⁸⁾	0.06	–0.1	–0.02	DeLuca et al., 2002
			0–10	3.7	1,200 ⁹⁾	70	334 ¹⁰⁾	37	
Ontario, Canada	Conifer–mixed	Podzols	10–20	4.8	–	–	90	6	Devito et al., 1999
			0–5 (FF)	6.8	488.0	9.4	–	–	
Changbai Mountain, China	Korean pine–broadleaf forest	Dark brown forest soil	5–11	5.4	62.2	0.6	–	–	Li, 1995a, 1995b
			11–25	5.6	54.4	0.4	–	–	
			0–10	6.7	–	–	1.3 ¹¹⁾	0.62	
Changbai Mountain, China	Korean pine–broadleaf forest	Dark brown forest soil	0–10	5.8	–	–	1.1	0.35	Zhou and Ouyang, 2001
			Spruce–fir forest	Mountain brown coniferous forest soil	0–10	5.8	–	–	
Great Xing'an Mountain, China	Larch forest	Brown coniferous forest soil	A horizon	4.9	15.6	2.3	–	–	Cui, 1998b
Xishuangbanna, China	Tropical seasonal rainforest	Latosol	0–10	3.75	19.75	4.71	6.55	16.28	Sha and Cao, 1999; Sha et al., 2000

1) Min. and Nit. were determined with lab incubations for one month; 2) FF: forest floor; 3) Determined with lab incubation for 4 weeks; 4) pH (CaCl₂); 5) kg/hm²; 6) Determined with buried polyethylene bag technique incubated for about 40 days (kg/(hm²·day)); 7) Determined with buried polyethylene bag technique incubated for about 6 weeks; 8) $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ determined with ionic resins ($\mu\text{g}/(\text{g}\cdot\text{day})$), Min. and Nit. determined with buried polyethylene bag technique incubated for about one month ($\mu\text{g}/(\text{g}\cdot\text{day})$); 9) mg/m²; 10) Annual net N mineralization/nitrification; 11) Determined with lab incubations at 25°C for 30 days (kg/(hm²·day)).

1986; Donaldson and Henderson, 1990; Johnson, 1992). The examples in Table 1 also illustrate this tendency. In the indoor or field incubation, forest soils often exhibit a weak nitrification potential and a long lag in nitrification (Donaldson

and Henderson, 1990; Cui and Zheng, 1998). Therefore, most researchers consider that there exists nitrification inhibition in acidic forest soils. Scholars outside China brought about following explanations regarding its mechanisms:

1) The autotrophic nitrifiers are generally considered not acid-tolerant, so the inherent low pH value in forest soils often inhibits the nitrification (Berg, 1986; Binkley and Hart, 1989; Donaldson and Henderson, 1990; Johnson, 1992; Mo and Kong, 1997; Evans et al., 1998; Sha et al., 2000; Li et al., 2001).

2) The low NH_4^+ provision restricts the production of NO_3^- , for the autotrophic nitrifiers and heterotrophic microbes become poor competitors for effective nitrogen sources ($\text{NH}_4^+\text{-N}$) compared with plants (Johnson and Edwards, 1979; Lamb, 1980; Adams and Attiwill, 1982; Vitousek et al., 1982; Johnson and Ball, 1990; Attiwill et al., 1996). In mature forest ecosystems, net ammonification rate commonly remains at a low level, making soil NH_4^+ flow into vegetation and microbial nutrition pool mainly through an effective closed N cycle (Cole, 1981), thus causing a deficiency of NH_4^+ source and nitrification restriction (Vitousek, 1981; Robertson, 1982). On the other hand, forest litter in a late successional stage (especially coniferous litter) mostly presents high C/N ratio and contains more lignin, tannin and free phenols. In this case, the decomposing rate of organic matters would slow down, and heterotrophic microbial fixation or chemical fixation (forming steady complexation or humic matter with proanthocyanidins difficult to utilize by microbes) of NH_4^+ or active organic N in soils and litter would become intense, thus reducing considerably the net mineralization (especially net mineralization) rate (Mortland and Wolcott, 1965; Nommik and Vahtras, 1982; Berg et al., 1984; Berg and McClaugherty, 1987; Schimel and Firestone, 1989a, 1989b; Northup, 1995, 1998; Schimel, 1998), and then NH_4^+ source available for nitrifiers would be insufficient.

Nevertheless, the recent researches indicate that the soil nitrification in coniferous forests of northern Sweden is not rather inhibited by NH_4^+ source. It was found that, with an addition of easily mineralized organic nitrogen (glycin), there is a marked upbuilding of NH_4^+ , rather than an obvious increase in NO_3^- content. So it is deduced that the limiting factor to the nitrification in the late successional stage might stem from the lack of favourable environment or the existence of high content of nitrification restricting components (free phenols) (DeLuca et al., 2002).

3) Allelopathic compounds (tannins and polyphenols) released through trunk eluviation or litter decomposition inhibits the activity of nitrifiers (Rice and Pancholy, 1972, 1973; Lodhi and Killingbeck, 1978; Baldwin et al., 1983; Olson and Reiners, 1983; White, 1986), and such inhibition would become more intense along with the succession (Rice and Pancholy, 1972). Accompanying the long recognized viewpoint, there are some different opinions (Lamb, 1980; Robertson and Vitousek, 1981; Cooper, 1986; Bremner and McCarthy, 1988; Brais, 1995). Recent studies showed that some higher molecular weight proanthocyanidins restrain microbial activities (Schime, 1998), but low molecular weight phenolics, on the other hand, are more likely to be utilized as efficient nitrogen sources for heterotrophic microbes except for their direct restriction to nitrifiers (Schimel and Granstrm,

1996; Souto et al., 2000). As stated in 2), a high concentration of free phenols could promote the biological fixation of mineral nitrogen or make active nitrogen be integrated into polyphenols (Bradley et al., 2000), and thus indirectly inhibits the nitrification.

4) The chilly and humid soils in temperate and cold temperate primary forests or north coniferous forests are not conducive to the mineralization and nitrification of nitrogen (Berg, 1986; Pastor and Post, 1986; Lavoie et al., 1992; Cui, 1994, 1998b). In addition, the response of nitrification to chilly and humid conditions might be more sensitive than that of ammonification (Ineson et al., 1998), which hence leads to a relative NH_4^+ accumulation.

2.2 Microbes' intense uptake and fixation to NO_3^- —a distinctly novel viewpoint

The translocation process of nitrogen in forest soils in regard to mineralization and nitrification is quite complex and lots of issues remain unclear yet. A completely new point of view is put forward recently regarding soil nitrogen nitrification. The ^{15}N isotope-dilution technique shows a much faster turnover rate of nitrates than prediction in the microbial nutrition pool of primary coniferous forest soils (Davidson et al., 1992); in such type of forest soils, the gross nitrification rate is considerably high, yet the microbe's assimilation to NO_3^- is extremely intense, almost depleting all produced NO_3^- , so the net nitrification rate can hardly reflect the gross one (Stark et al., 1997; Davidson et al., 1992). In other words, the excessively low NO_3^- levels in some primary forest soils might be attributed mainly to the intense assimilation of microbes, rather than to the nitrification inhibition as stated above.

No matter what causes the low NO_3^- level, we can be certain of one point that acidic and lightly acidic soils in primary forests provide plants a NH_4^+ -dominant nutrition habitat, which is essentially different from the NO_3^- -predominance in most wastelands or farmlands (Donaldson and Henderson, 1990; Kronzucker et al., 1997; Glass and Siddiqi, 1999).

3 Adaptation characteristics of some conifers— NH_4^+ -preference

Forest tree species sometimes have a substantial alteration and adaptation to their nutrition habitats, especially for conifers at the late successional stage or in the climax communities, such as *Tsuga heterophylla*, *Pinus banksiana*, *Pseudotsuga mezesii*, *Picea glauca*, *Picea abies* and *Pinus pinaster*, which have attracted much attention in North America, Northern Europe and Australia. The litter decomposing characteristics and nitrification inhibitors of these species often lead to a typical and NH_4^+ -dominated soil regime, and the nitrogen released by organic matter's decomposition often presents merely in the form of NH_4^+ (Rice and Pancholy, 1972, 1973; Vogt and Edmonds, 1982; Turner and Franz, 1985; Berg, 1986; Pastor and Post, 1986; Rashid and Scheafer,

1988); the concentration of NO_3^- is often extremely low due to the nitrification inhibition and the intense fixation of microbes to NO_3^- (Kronzucker et al., 1997). From the aspect of evolution, these tree species should possess a high uptake and utilization efficiency to NH_4^+ , and the assimilation and utilization to NO_3^- seem almost redundant. In fact, the long-term stability of climax communities causes the complete adaptation of the tree species to NH_4^+ in their own primitive habitats, which as a result severely reduces their uptake and utilization to NO_3^- (Ingestad, 1979; Lavoie et al., 1992; Knoepp et al., 1993; Kronzucker et al., 1996, 1997). In this way, a remarkable NH_4^+ -preference will occur in the incubation experiment and the plants grow well only in the NH_4^+ -dominant conditions (Table 2).

4 Physiological and biochemical mechanisms regarding the adaptation

The NH_4^+ -preferred and NO_3^- -repellent to a corresponding extent in conifers might be attributed to the physiological and biochemical mechanisms as follows:

4.1 Nitrogen assimilating enzymes

An important prerequisite of plant's adaptation to a certain nitrogen environment might be the enzymes catalyzing the reduction of NO_3^- and the assimilation of NH_4^+ (Lee and Steward, 1976; Claussen and Lenz, 1999).

Firstly, as the starting enzyme and restriction enzyme for nitrates, nitrate reductase (NR) activity is closely correlated with a plant's NO_3^- -assimilating ability. NR activity of trees might be distributed in roots and leaves: for NH_4^+ -preferred conifers, it is often higher in roots and lower in leaves (Margolis et al., 1988; Seith et al., 1994; Vézina et al., 1988;

Malagoli et al., 1988). Even though induced by NO_3^- , NR activity increased only in roots and changed little in leaves (Knoepp et al., 1993); in addition, the induction time till the culmination of NO_3^- uptake rate will be quite long (Kronzucker et al., 1997). Accordingly, these conifers cannot effectively utilize NO_3^- or depend on NO_3^- as their major nitrogen sources.

Secondly, NH_4^+ (or NH_3) assimilation is a process that higher plants share commonly. The roots and leaves of NH_4^+ -preferred conifers always contain a high amount of glutamine synthetase (GS) and glutamate synthetase (GOGAT) which transform free NH_4^+ into glutamic acid, and some species are found to have high level of glutamate dehydrogenase (GDH) activity which directly synthesizes NH_4^+ into glutamic acid (Srivastata and Singht, 1987; Vézina et al., 1988; Vollbrecht et al., 1989; Knoepp et al., 1993). After the uptake of a large amount of NH_4^+ into plants, these enzymes can immediately transform NH_4^+ into amino acids and avoid the harm brought by excessive NH_4^+ . Though GDH is not the primary N assimilating enzyme, its activity will markedly improve with the addition of exogenous NH_4^+ or in the presence of high-level NH_4^+ (Oaks and Hirel, 1985; Srivastata and Singht, 1987; Knoepp et al., 1993; Bedell et al., 1999).

4.2 Detoxification and high NH_4^+ -tolerance

To many plants, "ammonium toxicity" will occur in the conditions of high NH_4^+ -level medium or inside the plants (Gerendás et al., 1997). The NH_4^+ flowing into plants have to be assimilated immediately to avoid its toxicity to plant issues (Mehrer and Mohr, 1989; Magalhaes et al., 1992; Pearson and Stewart, 1993). NH_4^+ is assimilated and transformed into glutamine and glutamic acid (the so-called detoxification) mainly in roots through the way of GS/GOGAT, thus preventing a direct transportation of NH_4^+ to stems or leaves which

Table 2 Response of some conifers to ammonium (NH_4^+)/nitrate (NO_3^-) nitrogen

Forest species	Response to $\text{NH}_4^+/\text{NO}_3^-$	Reference
<i>Tsuga heterophylla</i>	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 $\text{NH}_4^+ + \text{NO}_3^-$ (50:50) treatment, NH_4^+ uptake was 2.1 times as much as NO_3^- uptake.	Knoepp et al., 1993
<i>Pinus banksiana</i>	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.	Lavoie et al., 1992
<i>Picea glauca</i>	After being 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^+ .	Kronzucker et al., 1997
<i>Pinus sylvestris</i> and <i>Larix decidua</i>	Absorbing NH_4^+ preferentially over NO_3^- when supplied with $\text{NH}_4^+ + \text{NO}_3^-$ nitrogen sources, with NH_4^+ net uptake rate about 6 times higher than NO_3^- uptake rate.	Malagoli et al., 2000
<i>Pseudotsuga mezesii</i>	Whole-seedling biomass, relative growth rate (RGR), and number of lateral roots, were greatest in seedlings grown with NH_4^+ . Absorbing NH_4^+ prior to NO_3^- in mixed nitrogen sources, NH_4^+ nutrition superior to NO_3^- nutrition.	Bedell et al., 1999
<i>Picea abies</i>	Absorbed more nitrogen in NH_4^+ than in NO_3^- , growing better when supplied with NH_4^+ .	Van den Driessche and Dangerfield, 1975; Olsthoorn et al., 1991
<i>Pinus pinaster</i>	Dry mass of seedlings supplied with NH_4^+ or $\text{NH}_4^+ + \text{NO}_3^-$ nitrogen at higher concentrations was approximately threefold greater than seedlings supplied with NO_3^- alone.	Ingestad, 1979; Marschner et al., 1991
Many conifers	Lower ability to use NO_3^- , be more adapted to NH_4^+ nutrition.	Warren and Adams, 2002
		Van den Driessche, 1971

are more sensitive to it (Barker and Mills, 1980; Claussen and Lenz, 1999).

Increasing numbers of studies, however, indicate that some NH_4^+ -preferred conifers possess both powerful “detoxification function” and high NH_4^+ -tolerance as well. Given enough NH_4^+ supply, an obvious NH_4^+ -harm cannot be detected even if there is a high accumulation of NH_4^+ in shoots and leaves (Flaig and Mohr, 1992; Lavoie et al., 1992; Kronzucker et al., 1997; Warren and Adams, 2002). Some scholars attributed this to a possible NH_4^+ pool in these conifers to diminish or reduce the potential NH_4^+ harm (Vollbrecht and Kasemir, 1992).

4.3 Root's relative uptake to $\text{NH}_4^+/\text{NO}_3^-$ and feedback control over NO_3^-

The root system of some conifers (like *Pinus banksiana*) has a rather lower uptake capacity to NO_3^- compared with that to NH_4^+ , and the uptake to nitrogen in a NO_3^- environment (rather than the reduction capacity to NO_3^-) becomes the bottleneck that inhibits the plant growth (Lavoie et al., 1992). The marked lower uptake rate of *Picea glauca* root systems to NO_3^- than to NH_4^+ was thought to be caused more by the few NO_3^- -vector proteins in plasma membranes than by the difference of vector's affinity to the two nitrogen forms (Kronzucker et al., 1997).

However, the growth decline of NH_4^+ -preferred conifers supplied by sole NO_3^- -N cannot be simply explained by the low uptake rate to roots of NO_3^- , and the N metabolism might be the key factor (Warren and Adams, 2002). Firstly, plant's uptake of NO_3^- is controlled by the feedback of inherent “pool” and “flow” in the metabolism. Some inherent biochemical factors, like the concentration of carboxylates and amines in leaves and transporting fluids (especially the latter), control the uptake of NO_3^- and the transcription of genes coded by highly affinitive NO_3^- vectors (Cooper and Clarkson, 1989; Muller et al., 1996; Gessler et al., 1998; Forde and Clarkson, 1999; Vidmar et al., 2000). For some conifers, regardless of the decrease of N uptake when supplied with NO_3^- , the concentration of free amino acids, even NH_4^+ , in plants is on the contrary higher than corresponding NH_4^+ treatment (Lavoie et al. 1992; Warren and Adams, 2002). This implies that the concentration of major N-transporting substances like glutamine in phloem and xylem will accordingly improve (Warren and Adams, 2002), and it is just these substances that probably provide “feedback signals” to N-uptake sites in roots (Gessler et al., 1998; Weber et al., 1998; Forde and Clarkson, 1999). Therefore, the conifer's lower uptake rate to NO_3^- than to NH_4^+ might be the outcome of feedback regulation triggered by metabolic disorder and accumulation of free organic nitrogen after taking up NO_3^- .

Additionally, if supplied mainly with NO_3^- as the nitrogen source, the conifer's N metabolic disorder might be correlated with the metabolic deficiency of some microelements. The reduction of NO_3^- leads to an unbalance of OH^- , and

subsequently a substantial amount of organic acids will be synthesized to maintain the acid–base equilibrium (Raven and Smith, 1976; Warren and Adams, 2002); organic acids (anions) strongly chelate to metallic ions like Zn^{2+} , and excessive organic anions in roots might restrict the transportation of some microelements to canopy (Olykan and Adams, 1995). Warren and Adams (2002) found that, with high level NO_3^- as the sole nitrogen source, the Zn concentration in needles of *Pinus pinaster* seedlings approaches the critical point of deficiency, and typical Zn-deficient symptoms occur. Zn is one of the components of polymerase, participating in the transcription of protein synthesis; in addition, Zn has a close correlation with cell division. Plant meristems require a high concentration of Zn and other microelements to maintain their functions, so Zn deficiency or lack of other microelements will lead to a reduction of cell division, cell elongation and protein synthesis, and will result in the accumulation of “feedback substances” like amino acids and amides (Warren and Adams, 2002). In such case, the metabolic growth decline of NH_4^+ -preferred conifers, induced by the sole provision of NO_3^- as nitrogen source, will be inevitable.

4.4 Interconnection and equilibrium of nutrients

NH_4^+ and NO_3^- show difference in the absorption to other nutritional ions due to their electropolar discrepancy. Generally, NH_4^+ inhibits the uptake of K^+ , Ca^{2+} and Mg^{2+} , but improves the P uptake (H_2PO_4^- or HPO_4^{2-}), which is just the opposite to NO_3^- (Ingestad, 1979; Jia, 1990; Serna et al., 1992; Knoepp et al., 1993; Ruan et al., 2000). Accordingly, some scholars thought that tree species adapted to NH_4^+ might be more tolerant to nutrients short of positive ions (Knoepp et al., 1993), and a low requirement to Ca^{2+} and Mg^{2+} or low content of Ca^{2+} and Mg^{2+} in conifer tissues have been reported in many studies (Ryan et al., 1986; Xu and Li, 1989; Hemissari, 1990; Wang and Liu, 1991; Rathfon, 1993). On the other hand, the uptake of NH_4^+ will cause the acidification of soil (Rygiiewica et al., 1984; Olsthoorn et al., 1991), thus beneficial to the uptake of Al and Mg as well as insoluble P (Gahoonia, 1993; Majdi and Persson, 1995; Ruan et al., 2000). From the aspect either of ionic equilibrium or of rhizospheric effects, it seems that NO_3^- is not beneficial to the uptake of P. Currently, few evidence has been reported to predict what results will happen for the P nutrition of NH_4^+ -preferred conifers in a nitrate environment. The metabolic Zn deficiency induced by NO_3^- has raised academic concern as stated above.

4.5 Photosynthesis

The difference of N metabolism and other mineral nutrients caused by the two nitrogen forms will surely influence plant photosynthesis, including the content and composition of chlorophyll, Rubisco content and activity, CO_2 stomatal conductance and mesophyll conductance, net photosynthetic rate, and water utilization efficiency (Claussen and Lenz,

1999; Xu, 2001; Wu et al., 2003). However, the nitrogen forms would not likely impact the Rubisco content and maximum photosynthetic rate (A_{\max}) on a leaf weight basis for *Pinus pinaster* (Warren and Adams, 2002), and the responses of photosynthetic indexes of most NH_4^+ -preferred conifers to the two nitrogen forms need further research.

4.6 Carbon loss in roots

The maintenance of the acid–base equilibrium and electric balance in roots depend at least partially on the direct release of OH^- or HCO_3^- , and the released HCO_3^- derives mainly from the decarboxylation of malic acids. Therefore, NO_3^- nutrition will cause a loss of a substantial amount of organic and inorganic carbon to the surrounding media and mycorrhizal symbiont (Vuorinen et al., 1995; Plassard et al., 2000), and probably lead to a growth decline to some extent (Warren and Adams, 2002).

Besides the physiological and biochemical mechanisms, there is another notable fact that most predominant coniferous species in the late successional stage are shade-tolerant, especially in their juvenility. The assimilation of NO_3^- requires some extra energy consumption (the reduction from NO_3^- to NH_4^+), and it is disadvantageous to shade-tolerant species in the acquisition of photosynthetic energy, which probably forces shade-tolerant species to choose NH_4^+ -preferred strategies during the evolution (Gutschick et al., 1981). This can partly explain why NR activity is mostly distributed in roots rather than in leaves (Knoepp et al., 1993). Some studies on rainforest communities also indicated that photophilous pioneer species often show a high NR activity and nitrate assimilation in leaves is predominant; and low levels of NR activity are often confined to closed forest tree species (Stewart et al., 1988). Actually, faint light or shade might be considered to be another long-term environmental factor, besides the NH_4^+ -dominated habitat, that causes the NH_4^+ -preference of shade-tolerant conifers.

5 Conclusions

In acidic or lightly acidic primary forest soils, the content of NH_4^+ is far higher than that of NO_3^- , which thus contributes to the formation of NH_4^+ -dominated nitrogen nutrition habitats. A large number of conifers predominant in their late successional stage have been completely adapted to their NH_4^+ -dominated habitats, characterized by an obvious NH_4^+ -preference and NO_3^- -repulsion. Researchers worldwide proposed various mechanisms concerning the control over transformation of mineralized nitrogen in primary forest soils as well as physiological and biochemical mechanisms regarding the adaptation of conifers to NH_4^+ nutrition habitats. But the understanding of these mechanisms is yet to be furthered.

The inherent adaptation of conifers, in their late successional stage, to NH_4^+ nutrition habitats is of ecological and

forestry significance. Firstly, it is probably one of the prerequisites to maintain the long-term stability for climax forest communities. Practically, the most severe problem, however, is the massive logging and destruction of primary coniferous forests or conifer–broadleaf mixture forests. After the damage, the soil NH_4^+ pool tends to transform largely into NO_3^- (Vitousek, 1981; Vitousek et al., 1982; Lavoie et al., 1992; Kronzucker et al., 1997; Cui, 1998b; Giardina and Rhoades, 2001; Prescott et al., 2003). In disturbed sites containing increasing amount of NO_3^- , the originally predominant conifers (seedlings) adapted to NH_4^+ nutrition will turn into poor competitors for nitrogen (the site will be inhabited by pioneer species which are more adapted to NO_3^-), which will result in more difficulties in regeneration (Lavoie et al., 1992; Kronzucker et al., 1997). This issue should be taken into serious consideration during the restoration and rehabilitation of degenerated forest ecosystems. Secondly, we should also take the nutritional features of NH_4^+ -preferred conifers into account in the plantation silviculture. Large areas of degenerated forest ecosystems and many climax coniferous species occur in the temperate conifer–broadleaf mixture forests, cold temperate coniferous forests and high altitude coniferous forests in China, which consequently poses much significance on studies of nutritional characteristics of nitrogen in primary forest soils as well as the adaptation of conifers.

It will be beneficial for us to settle principally the above issues if we discover mechanisms underlying the transformation of mineralized nitrogen in forest soils, as well as the physiological mechanisms in regard to the adaptation of forest tree species to a certain nitrogen nutrition habitat, and fundamental researches in this field also call for a promising future.

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