Review Paper

Role of soil nitrogen for the conifers of the boreal forest: a critical review

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ABSTRACT

Nitrogen is considered the most important element in plant nutrition and growth. However its role and availability for boreal forest conifers is still debated. Boreal conifers have adapted strategies to cope with the reduced availability of N (especially organic N). ECM fungi, associated with boreal conifer roots, increase soil exploration and N nutrition, especially where organic N predominates. In conifers of the boreal forest, NH4+ is the preferred form of inorganic N taken up, while organic N may be taken up at rates comparable to or greater than NH4+ and tends to predominate in late-successional boreal forest soils. Conifers, especially slow growing species, may rely on internal N cycling to sustain the development of new tissues in spring. N increases photosynthesis and leaf area and thus increases growth and wood formation, leading to wider radial rings mostly because of increased earlywood production. N-depositions and disturbances (e.g. fire and harvest) may alter the soil N-cycle and affect boreal forest growth. N depositions are considered responsible for the increase in boreal forest growth during the last century. Intensive harvest and high N-depositions may shift limitation from N to another element (e.g. P, K, and B). The majority of the studies support the hypothesis that the growth of the boreal forest is limited by the availability of N. Nonetheless, there is evidence that N limitation becomes more severe in the late-successional stages of stand development, when low rates of decomposition an d mineralization cause an accumulation of organic matter on the soil.

Keywords ammonium; boreal conifers; growth; N limitation; nitrate; N uptake

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1. OVERVIEW OF THE N CYCLE IN BOREAL FOREST SOILS

The boreal forests of the world are characterized by low evapotranspiration and decomposition rates, corresponding to slow nutrient cycles and accumulations of organic matter during the forest stand successions ([1],[2]). N is an essential element for plant nutrition and, together with P, is copiously required for all essential metabolic processes of the plants. The growth of the boreal forest is considered N limited, but wide ranges are generally observed in nutrient availability and interaction between elements ([3],[4], [5]), so it is important to thoroughly understand the characteristics of the N cycle in the boreal forest in order to identify the role of this fundamental element for forest productivity and C sequestration.

The major pathways of N input in forms available for plants in terrestrial ecosystems are biological N fixation and atmospheric N depositions, while N fixation through lightning is much less important (Table 1) ([6], [7], [8]). N losses may occur through leaching of dissolved N species. Nitrate is preferentially leached as compared to NH_4^+ but in unperturbed forests, DON could represent the major part of leaching losses ([9], [10]). Losses of N can also occur through volatilization (especially rapid volatilization through wildfire, while ammonia volatilization at high pH values is marginal in the typical acidic soils of the boreal forest), and denitrification (Table 1) ([11], [12])). Moreover, N can be immobilized with polyphenols and other recalcitrant substances in microbial and plant biomass or in the soil after precipitation ([13], [14], [15], [16], [17]).

Table 1 Characteristics of the soil N cycle in the boreal forest

INPUT	**Biological N fixation**	**N-deposition**	**OUTPUT**	**Leaching**	**Volatilization**	**Denitrification**
Characteristic	Energy intensive (symbiosis favored) N-fixers have high requirements for P, Fe and Mo Positive relation with evapotranspiration Favored where N supply is reduced Negative relation with N-depositions (e.g. for N-fixation in mosses)	Probably low in remote and undisturbed areas Mainly as NH_4^+ and NO_3^-, through precipitations Greater in southern boreal forest, near polluted areas Probably greater in northern Europe than in Canada		Flushes of NO_3^- associated with high water content (e.g. during snowmelt), especially in coarse-textured soils Higher potential for losses through Dissolved Organic Nitrogen (DON) with increasing organic matter accumulation Increased N losses following disturbances (insect outbreaks, harvesting and wildfires)	N losses through wildfire may be locally important Ammonia volatilization is insignificant in the boreal forest	Favored by limited availability of O_2, high NO_3^- concentrations, high soil moisture, availability of soil carbohydrates, warm temperatures Low in the boreal forest (since low NO_3^- concentrations) Increase after freeze/thaw and wet/dry cycles
Estimate	N-fixation in mosses: 1-2 kg ha^{-1} yr^{-1} (comparable to low atmospheric N depositions 2-3 kg ha^{-1} yr^{-1})	Pristine watershed in eastern Canada: 1.7 kg ha^{-1} yr^{-1} as N-NO_3; 1.2 kg ha^{-1} yr^{-1} as N-NH_4; Total Dissolved Nitrogen (TDN) fluxes as deposition 3.1 kg ha^{-1} yr^{-1} North-eastern North America: from <4 kg N ha^{-1} yr^{-1} in isolated zones to 10-12 kg N ha^{-1} yr^{-1} in polluted areas In eastern Canada (Quebec) N depositions, 2-11 kg ha^{-1} yr^{-1}, on average 5.8 ± 1.8 kg ha^{-1} yr^{-1}		Pristine watershed in eastern Canada: 0.25 kg ha^{-1} yr^{-1} exported via stream output N-NO_3; 0.05 kg ha^{-1} yr^{-1} exported via stream output N-NH_4; Total Dissolved Nitrogen (TDN) stream export 0.9 kg ha^{-1} yr^{-1}; DON represent 67% of TDN in stream export		0.11 kg ha^{-1} yr^{-1} for coniferous forests (but no information for the boreal forest)
Source	[3], [6], [18], [19], [20], [21], [22], [23], [24]	[25], [26], [27], [28], [29], [30]		[31], [32], [28]	[6], [11], [12], [33], [34], [35], [36]	[37], [38], [39], [40], [41]

Even if inputs and outputs are important fluxes to and from the N cycle, they represent small amounts compared to the large pool stored in the soils of the boreal forest. [42] estimated N-accumulation in three northern Scandinavian forests stands demonstrating that, in these undisturbed forests, soils are the main reservoir of N, with humus showing contents from 3 to 24 times higher than those observed in vegetation. Rates of N accumulation in organic soil and vegetation were estimated to range between 0.30 and 0.35 g N m-2 yr-1, corresponding to about 85% of the N input to these forests. Consequently, a key element of the N cycle is soil organic matter, which is constituted by c.a. 50% of C and 5% of N, only partially (usually less than 5%) in available form ([11]).

N is cycled through plants and the relevant inputs to soils come from the turnover of below- and above-ground plant biomass, mostly leaves and fine roots. The turnover of roots, especially the fine roots and associated mycorrhizae, can return two to five times more organic matter and six times more N to the soil than the canopy litter ([43], [44], [45]). Different species may have an impact on the microbial composition of the soil and thus nutrient cycles through their different litter chemistry ([33], [46], [47], [48], [49], [50], [51]) reported lower soil pH in Norway spruce plantations than in plantations with hardwoods, because of the greater acid strength of the organic matter accumulated under the conifers.

There are two different paradigms concerning N nutrition (Fig. 1). The first one asserts that plants prevalently use the inorganic N derived from N-inputs and mineralization. Mineralization, i.e. the breakdown of organic monomers performed by heterotrophic microbes releasing NH4+ (ammonification), is considered the step regulating the availability of N for plants. NH4+ is then used as energy source by oxidizing microbes producing NO2- readily converted to NO3- (nitrification) and also NO and N2O (Fig. 1A). The second, more recent paradigm places less emphasis on the mineralization as a limiting process and suggests that plants can access both the inorganic and organic pool of N ([16], [52]). Through depolymerization (i.e. soil organic matter breakdown operated by microorganisms and plants through the release of exoenzymes) (Fig.1B), SOM may be decomposed in smaller and more readily available organic compounds (amino acids, nucleic acids, amino sugars). These organic compounds can be mineralized releasing inorganic N (NH4+ and NO3-), which is more easily available for plants and microorganisms ([52]).

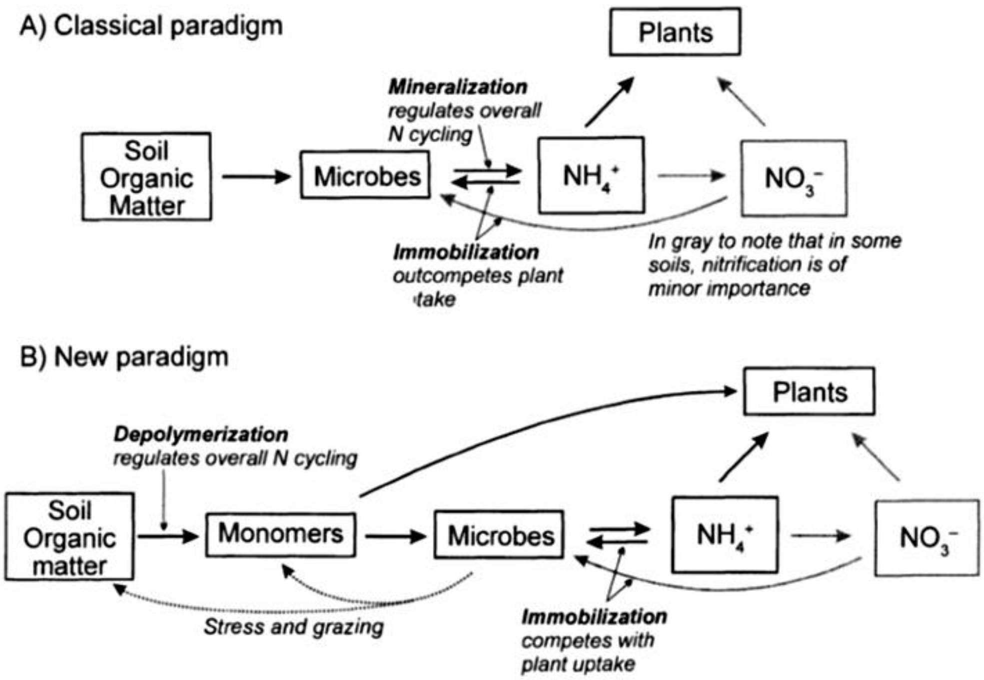

Fig. 1. The changing paradigm of the soil N cycle. (A) The dominant paradigm of N cycling up through the middle 1990s. (B) The paradigm as it developed in the late 1990s (from [52])

In this paper the latter paradigm is adopted because of its flexibility: it does not refute the role of mineralization but, at the same time, allows the use of organic N in certain circumstances. This decision is supported by recent findings demonstrating that mycorrhizal and nonmycorrhizal plants can take up organic N ([53], [54], [55]). Moreover, in late successional mature boreal forests, increased soil acidity and the accumulation of organic matter with high concentrations of polyphenols favors proteolysis (i.e. depolymerization of proteins) rather than mineralization (Fig. 2; [2], [47], [56]). However, mineralization remains important in the boreal forest, since the low pH and temperature, the accumulation of phenolic-based allelopathic compounds, the wet and anaerobic conditions that inhibit nitrification, favor the formation and/or accumulation of NH4+ ([2], [17], [37], [57]). As a result, when soils extraction are carried out, NH4+ is the predominant inorganic form of N in the boreal forest, while NO3- tends to be present in very limited quantities (Fig. 2). However, the latter could be more abundant after disturbances or in areas subject to high N depositions. Also concentration of amino acid increases with stand succession following the accumulation of organic matter (Fig. 2, Table 2) ([2], [58]).

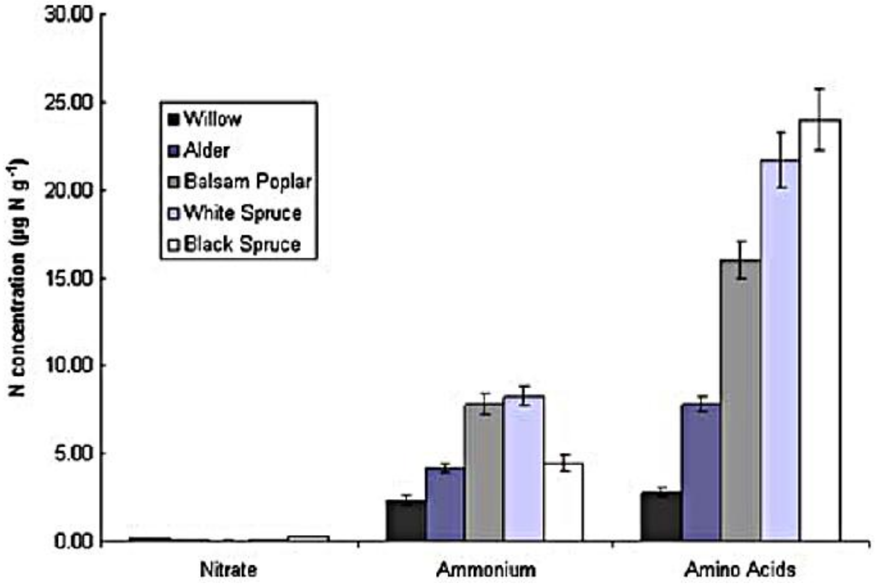

Fig. 2. Concentrations of soil nitrate, ammonium and free amino acids across a primary successional sequence on the Tanana River, interior Alaska. Values are seasonal average concentrations from monthly measurements in June-October. Mean ±SE, n=3 (from [2])

Table 2. Characteristics and estimates of the different N forms in boreal soils

	Organic N		**Inorganic N**	
N forms	Greatest concentrations in the organic surface horizons	*(of which) Amino acids* Major component of simple organic N pool: Glu, Asn, Gln, Asp, Ala and His	NH_4^+	NO_3^-
Characteristic	Quantitatively the most important in undisturbed northern ecosystems Constituted by monomeric (e.g. amino acids) and polymeric organic compounds containing N	At acid and subacid pH reduced mobility of basic amino acids (such as L-Arg and L-Lys) compared to neutral amino acids (e.g. Gly and L-Ala)	Less mobile than NO_3^- (readily adsorbed to the cation exchange sites in the soil) Reduced leaching losses compared to NO_3^-	Mobile (due to soil overall negative charge) Easily lost through leaching Mostly delivered to roots through diffusion and mass flow, guided by the transpirational water stream
Estimate	*DON* 16-32 kg ha^{-1} (about an order of magnitude greater than DIN) Soluble proteins (0.5 mg g^{-1} soil, corresponding to c. 0.08 mg protein N g^{-1} soil)	Concentrations in the bulk soil solution: Range 0.1-50 mM	*DIN* $NH_4^+NO_3^-$, 0.9-1.5 kg ha^{-1} Concentrations (in forest floor soil solution): average 2 mM; Range 0.4-4 mM Diffusion coefficients: 10- to 100-fold less than NO3- Mean residence time in the FH horizon 0.30-0.86 days	Diffusion coefficient is ca. 1×10^{-10} m^2 s^{-1} Mean residence time in the FH horizon 0.23-0.75 days
Source	[1], [2], [16], [18], [33], [37], [47], [56], [58]		[2], [37], [56], [57], [59]	

1.1. Hypotheses of N-limitation

Historically, growth in the northern temperate and boreal forests has been considered essentially N-limited, as N-addition often resulted in increases in productivity ([5], [60], [61], [62]). Vitousek and Howarth

[3] proposed that N-limitation may occur through biogeochemical mechanisms (increased losses and immobilization) and limitation to N-fixation (decreased inputs).

The mobility of N, in particular NO3-, can lead to great losses, for example during snowmelt, when low soil temperature, high water fluxes, and the long period of tree dormancy limit N uptake ([3], [25]). However, in the boreal forest, high NO3- losses are rare or limited to particular situations such as after disturbances, while DON losses (which are generally greater than DIN losses) proportionally gain importance during the later phases of stand succession, when organic matter accumulates ([10], [63], [64]). Also, N losses occur in gaseous forms in areas where fires are frequent ([48]).

The strong C-N bond of litter and soil organic matter was also proposed to explain the lower availability of N ([48], [65]). N would be chemically and physically protected by protein-precipitating and recalcitrant C compounds (polyphenols and tannin), which could slow down its decomposition. Besides, allelopathic effects of certain polyphenolic compounds have been described, which may inhibit N mineralization or N uptake by plants ([15], [17], [66], [67]). Moreover, N-limitation could result from strong competition between soil microorganisms and plants ([68]). So the increased growth of conifer seedlings after weed control is usually attributed to a reduced competition for N ([69]).

In nature, higher rates of N-fixation are observed with low N supply, thus it seems paradoxical that N-limited late-successional boreal forests do not contain N-fixing trees ([70]). However N-fixation may be constrained by the availability of other nutrients (as P, Mo or Fe), by the high energy cost of the symbiosis (high requirement for light) and other mechanisms including the preferential grazing of N-fixing plants by herbivores ([3], [65], [71]).

The more straightforward way to demonstrate the existence of N limitation of trees is to evaluate the response of growth to N additions. However disturbance of the ecosystem and site-specific conditions can complicate the interpretation of the results. Moreover, the absence of a growth response does not reject the hypothesis of limitation, since the added nutrient could be immobilized in another component of the ecosystem (e.g. soil or microbial immobilization or uptake by other plants) ([48]). Other approaches to evaluate limitation in N are the analyses of tissue (especially foliar) concentrations to calculate its critical levels and ratios with other elements (e.g. N:P, [48], [72]).

1.2. Aim of the review

Important reviews have been published on inorganic and organic N nutrition and on the relationships between mycorrhizal fungi and nutrient cycling ([1], [48], [56]). Nevertheless, for its particular features, a specific examination is required concerning the distinctive dynamics of the N cycle occurring in the boreal ecosystems. The aims of this paper are (1) to describe the importance of the different soil N forms in the nutrition of boreal conifers and the strategies of uptake developed under low N availability; (2) to define the main N uses; (3) to identify the impact of the recent increases in N depositions on the boreal ecosystems; (4) to discuss the limitations of the past studies and provide some recommendations for future investigations.

In this review, N nutrition is defined as the process of uptake, assimilation and use of N and, unless otherwise indicated, the coniferous boreal forest will be taken specifically into account.

2. N-UPTAKE AND NUTRITION

Before its assimilation and use, N has to be taken up by trees. Fine roots are especially active sites of nutrient uptake and exchange with mycorrhizal fungi. In white spruce of interior Alaska, Ruess et al. [45] estimated that nearly every first-order fine root (i.e. the most distal, smallest diameter, fine roots) presented mycorrhizal associations. These fungi play an important role in enhancing N nutrition and can directly interact with other soil microorganisms. So, the influence of mycorrhizae in N-nutrition and the mechanisms of uptake for the different N forms need to be taken into consideration when analyzing the role of N in tree growth.

2.1. Mechanisms of N-uptake

The net uptake of a nutrient results from the balance between influx and efflux and is a process dependent on concentration and regulated by plasma-membrane transporters ([56]). NO3- uptake requires active transport and the energy is supplied by ATP through an H+-ATPase channel to maintain a proton gradient across the plasma membrane ([37]). NO3- is able to rapidly induce the expression of NO3- transporters at very low concentrations (< 10 μM), resulting in higher NO3- fluxes after a few hours, in some herbaceous plants, or several days, in conifers ([73]). However, high NO3- fluxes are not sustained for long, since feedback downregulation may result from the accumulation of N-metabolism endproducts as amino acids ([73]). NO3- efflux seems to be a passive process, probably through anion channels, but knowledge is still scarce ([11], [56]). The uptake of NH4+, like that of K, occurs through channels mediated by the negative cell membrane potential, producing an acidification of the rhizosphere ([37]). The rates of NH4+ uptake by nonmycorrhized white spruce seedlings growing in hydroponics could be 20 times greater than that of NO3- ([74]). Grenon et al. [75] reported low NO3- uptake capacity in spruce suggesting that NO3- may be an important nutrient form for soil microbes. Compared to NH4+, NO3- uptake and assimilation require 10-15 additional ATP ([76], [77]). Meyer et al. [78] estimates that C costs for the assimilation of NH4+ and simple organic N are half those for NO3-: 0.17 kg C/kg of NH4+ or of Norg vs 0.34 kg C/kg of NO3. NH4+ nutrition negatively affects the NO3- uptake, probably reducing the expression of NO3- transporters ([11], [37]). The efflux to influx ratio, related to the net uptake of nutrients, is positively correlated with the external concentrations ([79], [80]). Since efflux increases with increasing external concentrations, so the rate of NH4+ uptake is reduced at high soil and cytosolic NH4+ concentrations ([80]).

Contrary to NO3-, NH4+ efflux probably takes place through an active antiport, and the associated high energy cost is sometimes considered to be one of the causes of NH4+ toxicity in many species that are not adapted to soils with excess NH4+ ([74], [59]). Other features of NH4+ toxicity are the accumulation of amino acids in plant tissues. Britto and Kronzucker [59] speculated that the competitive exclusion of K+ by NH4+ and the over-expression of K+ channels at high external NH4+ concentrations could cause a high NH4+ influx, and consequently an excessive efflux to maintain the electrochemical balance of the cells, leading to NH4+ toxicity. Moreover, it has been observed that NH4+ toxicity is more pronounced at high light intensities and associated with reduced leaf moisture and water potentials ([37], [59]).

Kronzucker et al. [81] proposed that sensitivity to excesses of NH4+ may decrease between early- (trembling aspen and Douglas fir) and late-successional (white spruce) species because of the increased efficiency in controlling NH4+ fluxes through the plasmamembrane. Moreover, early successional deciduous species (e.g. aspen) cultivated in hydroponics showed a good capacity of absorbing NO3- concurrently with NH4+, contrary to white spruce and jack pine seedlings ([82]). However, all the species tested showed higher affinities and rates of uptake with NH4+ compared to NO3- ([82], [83]). Min et al. [79] confirmed this pattern, observing that, compared to NO3-, NH4+ uptake was 16-fold higher in lodgepole pine, while only 2-3-fold higher in trembling aspen. Similarly, rates of uptake of amino acids and NH4+ were 7-8 times higher than those of NO3- in a 100-day greenhouse experiment with potted seedlings of Norway spruce and Scots pine supplied with three concentrations of N (1, 3 and 10 mM of total N) in various forms and mixtures (NO3-, NH4+, arginine, glycine), but reductions in growth and mortality of seedlings were observed at a high proportion of NH4+ in the fertilizer, probably because of NH4+ toxicity ([84]). Min et al. [79] observed that, compared to aspen, lodgepole pine and Douglas-fir had similar NH4+ utilization but lower capacity of utilizing NO3- with lower translocation to shoot and lower levels of nitrate reductase activity. So they proposed the hypothesis that the availability of different N forms may be implicated in niche separation among species, thus influencing the species distribution in temperate and boreal ecosystems.

Compared to inorganic N forms, amino acids and organic N could gain importance in plant nutrition during the late successional phases of the boreal forest, given their increased concentration in the soil ([2], [11]). Conifers possess the capacity to take up amino acids and present mycorrhizal associations that enhance the nutrition of organic N ([53], [85], [86], [87]). A recent laboratory study showed that some nonmycorrhizal species can take up intact amino acids and proteins, but their ability to grow under N sources consisting of solely organic N was limited ([54]). In a field experiment, the uptake of NH4+ and amino acids was larger than that of NO3- for Norway spruce and common bilberry, while wavy hair-grass showed opposite results ([85]). In another experiment with Scots pine, amino acid uptake was similar to or larger than that of NH4+, while NO3- uptake was low ([87]). So, in black spruce and Scots pine the rate of NO3- uptake is lower than that observed for NH4+ and amino acids ([84], [87]).

2.1.1. Canopy N uptake, another important pathway?

Apart from the N fixation and decomposition of organic matter, N enters ecosystems through N-depositions (dry, wet and gaseous). An important part of the atmospheric inorganic N deposition may be retained within the canopy, particularly for NH4+ ([26], [88]). Canopies typically do not retain organic N, but they do retain inorganic N at a rate of 1-12 kg N ha-1 year-1, or 50-70% of deposited N ([89]). Measuring the difference between throughfall and bulk precipitation, Houle et al. [26] estimated that for a coniferous boreal forest (spruce and fir) the uptake of NH4+ was significantly higher than that of a deciduous canopy, in agreement with previous studies ([90]), and reached 75% of incoming wet NH4+ deposition during the growing season. The uptake of NO3- and NH4+ was especially pronounced in October, for both canopies, while in January a net release was observed. In an overnight incubation of melting snow, epiphytic lichens effectively removed NO3- and NH4+ ([26]). Lichens are often present in significant amounts on the branches of coniferous stands and they may be responsible for a significant part of canopy N uptake ([26], [91]). Because of this, there is a strong probability that the N uptake of trees themselves (calculated as the difference between total throughfall flux and wet deposition) is overestimated. ([26]). Indeed, in an experiment with balsam fir, the overall reactivity for both efflux and influx was in increasing order new needles, old needles, twigs and, finally, lichens ([91]). An observation of balsam fir tissues with a scanning electron microscope showed that bacterial and fungal coverage on twigs was greater than on needles and, between needles, older ones were more covered than younger ones. So, needle age, degree of microepiphyte cover and abundance of lichen cover are postulated as the three principal variables controlling ion loss or uptake in the canopy of balsam fir ([91]).

In a review on direct foliar uptake of N, Sparks [92] underlined the importance of considering foliar and soil pathways of N incorporation into biota separately. The mechanisms of foliar uptake are still unclear and estimates vary a lot with canopy uptake of reactive N varying between 0-50% of plant N demand. Ignatova and Dambrine [88], comparing throughfall under fake plastic trees and true canopies, estimated that in 8.5 months more than 4 kg ha-1 of inorganic N were taken up by the canopies of the different stands and that this represented between 10-30% contribution to annual requirement of N by foliage. However, in a recent labelling experiment with 15N, less than 5% of the label was recovered in live foliage and wood after 2 years of N addition to the canopy ([93]). The majority of the label was in or on twig and branch materials. For these materials the authors weren't able to distinguish between bark and wood and to establish if canopy N retention was due to physico-chemical interactions with plant surfaces or real uptake ([93]). They concluded that in the short term most of the N was retained on plant surfaces, branches and main-stem bark, with little being assimilated into woody material and little effect upon C sequestration. Unlike more productive sites, where canopy "uptake" represents only a small fraction of the foliar increment and stand requirement, in low productivity sites, like spruce and spruce-fir sites, canopy "uptake" can be nearly equal to foliar increment ([27]). However, most of tree N requirement is still being met by root uptake and internal retranslocation (resorption). Moreover inorganic N uptake appears to be greatest in spruce-fir canopies with high epiphytic lichen biomass. Organic N is released from forest canopies, but the amount of release is generally less than the amount of inorganic N uptake so that total N is generally consumed ([27]). However, again, it is difficult to differentiate between uptake by epiphytes vs uptake by trees and/or physico-chemical interactions with canopy surfaces. No measurable canopy uptake is usually observed during winter months ([94]), thus pointing out the biological nature of this phenomenon. Indeed, this may be a function of the physiological state of the trees and epiphytes during these months-low photosynthesis, reduced growth and limited seasonal demand for N. Epiphytic lichens and mosses are a major component within the old-growth canopy and they definitely affect the flux of nutrients in the throughfall, with greater uptake of inorganic N in stands where epiphytes are abundant ([94]). Given the uncertainties linked to canopy N uptake and that the focus of this critical review on the importance of soil N for the conifers of the boreal forest, we suggest interested readers to consult other more specific reviews on canopy uptake.

2.2. Roots and competition for N

Soil N affects size, structure and distribution of the root system. In Norway spruce and silver birch, starch accumulates in leaves when N is limiting, and additional amounts of photosynthates are translocated to the roots, thus allowing an increase of the size of the root system ([37], [95]). It is assumed that, in roots and shoots, the balance between N and C influences the processes associated with C fixation or formation of new tissues and determines the allocation of resources between belowground and aboveground components ([95], [96]). Factors like soil temperature, moisture and nutrient availability play a role in the timing and duration of root growth, while root longevity is controlled by microsite conditions, patterns of development and length of the growing season ([97]). In a long-term experiment with mature Norway spruce trees in northern Sweden, fine root longevity was reduced in either heated or fertilized plots, but the reduction was lower in the combined treatment ([98]).

According to Aerts and Chapin [48], mass flow and diffusion in poor soils of the tundra supplies less than 1% of N to the roots. So, the root proliferation for acquiring limiting resources that could be available in localized soil patches gains importance ([99], [100]). Because of its higher mobility, NO3- can leach from patches where organic matter is decomposed and mineralized and diffuse to the root surface, acting like a signal for root proliferation ([11], [52], [100]). The recently-discovered sensory proteins for NO3- are probably responsible for repression of root growth at high levels of NO3- and for root elongation in response to NO3- under NO3- deficiency ([11], [37], [100]).

Soil microorganisms play a key role in regulating the availability of nutrients through SOM depolymerization and mineralization. Except for symbionts (e.g. mycorrhizae), the other soil microorganisms are often C-limited resulting in a strong competition for energy sources, especially when availability of labile C substrates is limited by the accumulation of recalcitrant organic compounds (high lignin:N ratio, high content of polyphenols, tannins and lignin) ([17], [49], [101], [102], [103], [104]). The increased availability of labile C in the rhizosphere can strongly stimulate microbial activity through a priming effect ([11], [33], [101]). However, microorganisms can also be limited by the availability of mineral nutrients as N and P ([57], [102]).

Some experiments with isotopic tracers have found that plants are inferior to microbes in the uptake of inorganic and organic N in the short term (one to several days), but they acquire more and more of the tracer over longer periods (weeks or months) ([56]). Various elements are important in the long term, including microbial turnover, competition between mycorrhizae and microorganisms, lifespan of the tree tissues with great sink potential and strategies of effective nutrient conservation ([105], [106]).

Apart from the competition with microbes, the nutrition of conifers is also influenced by the competition with other plants. A reduced competition could explain the strong positive effects of weed-suppression on survival and growth of boreal conifer seedlings, leading to higher foliar concentrations of N and other nutrients ([82], [107]). Plants can compete in different ways. For example, sheep laurel is able to sequester soil N through the formation of tannin-protein complexes that are not easily accessible to black spruce, thus reducing its nutrition ([67]). Yamasaki et al. [66] observed that foliar N concentrations in black spruce were positively correlated with the height and biomass of seedlings growing away from sheep laurel, and proposed that the reduced mineralization alone is unable to explain this pattern. They proposed that sheep laurel could affect the growth of black spruce through four different mechanisms: (1) competition for nutrients; (2) direct allelopathic effects on black spruce, 3) allelopathic effects on mycorrhizal formation or maintenance, 4) increased susceptibility to root pathogens, as a consequence of the decreased mycorrhization. Some authors have suggested that polyphenols may inhibit microbial activity and thus reduce N mineralization, but results are still not definitive ([14], [18]).

2.3. Mycorrhizal associations and N nutrition

Boreal forests are characterized by the prevalence of two groups of mycorrhizal fungi: ECM, associated with conifers, and ERM, associated with the ericaceous shrubs that spread in heathlands and forest understory ([108], [109]). These fungi are considered to play an important role in plant nutrition, especially when N is scarce. The abundance of different N forms and mycorrhizal associations and their host species are related. Along a short transect, Giesler et al. [110] and Nordin et al. [111] observed that the change in forest types was associated with a shift from inorganic to organic N forms in soils from a Scots pine/dwarf-shrub type. In particular, NH4+ increased in the Norway spruce/short-herb type, and finally in the tall-herb type NO3- was as abundant as NH4+ and plants took up nearly equal amounts of the two mineral ions. The productivity increased along the gradient of concentration of soil N and the change in plant community was associated with changes in the mycorrhizal community, from a dominance of ECM and ERM in the Scot pine/dwarf-shrub type to a prevalence of arbuscular mycorrhizal fungi in the tall-herb type ([110], [111]). C:N ratio and pH seem to be good predictors of changes in microbial community structure, with high and low ratios associated with fungi and bacteria, respectively. A negative correlation has also been reported between C:N ratio and N mineralization rates in some Scots pine stands in Sweden ([102], [112], [113]).

ECM are effective in the uptake of NH4+ and low concentrations of this ion in the soil solution of some boreal forests may be in part a consequence of a rapid uptake by mycorrhizal roots ([76]). For example, Nilsson and Wallander [114] excluded roots of Norway spruce colonized by ECM from a portion of soil (through plastic tubes), and observed that NH4+ and NO3- concentrations were higher in the portion where roots were excluded. However, the characteristic that probably confers the most competitive advantage to the mycorrhizae is the ability to access organic N ([1], [109]). Indeed, uptake and transport of amino acids and intact peptides by seedlings of conifers colonized by mycorrhizae have been observed both in the lab and field (e.g. [53], [87], [115]). However these potential advantages for plant uptake come at the cost of supporting the fungal partner. Estimates of C transfer to the mycorrhizal mycelium are between 14 and 30% of the C assimilated, with values attaining 0.8 t C ha-1 yr-1 ([44], [78]). In Northern Sweden, in a large tree-girdling experiment with Scots pine realized by killing trees by means of cutting the phloem and cambial tissues around the stem, soil respiration was reduced by ca. 50% after a few weeks and microbial biomass by one third after 1-3 months ([113], [116]). Analyzing phospholipid fatty acid, the 45% decrease in a fungal biomarker associated with ECM suggested that the decrease in microbial biomass was mainly due to loss of ECM fungi. Moreover, the higher N content and growth of dwarf shrubs after tree-girdling revealed that the conifers associated with ECM fungi were efficient competitors for N ([113]). These findings clearly demonstrate the peculiar importance of ECM associations in soils of the boreal forest.

A strategy that could reduce the competitive pressure and enhance conifer nutrition is the spatial separation and use of different N sources by saprotrophic fungi and plants associated with ECM and ERM ([117]). Lindahl et al. [104] observed a vertical separation between saprotrophic and mycorrhizal fungi in the upper organic layers. It has been hypothesized that ERM and ECM fungi (not being C-limited, contrary to saprotrophs) could continue the degradation of energy-depleted substrates (decreased C:N ratio in the L-layer, after the initial exploitation by saprotrophs), as they descend in the FH layer ([1]). So, according to Lindahl et al. [104], the observed increase in C:N ratio, after the initial decomposition, indicates a selective removal of N by mycorrhizae supplied with root-derived C. This hypothesis is supported by an increase in δ15N (due to different isotopic fractionation) in the horizons dominated by ECM fungi ([38], [104]).

Compared with ERM and saprotrophic fungi, ECM show a reduced capacity to take up N from protein-polyphenol complex ([14]). Considering different δ15N as an indication of niche separation and access to different N pools, Schulze et al. [117] suggested that ECM of white spruce would use NH4+, NO3- and organic N from litter, while ERM of Vaccinium spp. would break down more complex slowly-decomposing organic matter. Read et al. [1] proposed that proximity, achieved through an extensive colonization of organic horizons containing important quantities of N and P (especially the FH layer), is an effective strategy to gain access to these nutrients before the formation of the polyphenol complexes that reduce the availability of N for the trees associated with ECM. In the organic horizons, microbial biomass and mesofauna could also be an important source of uncomplexed organic N, as nutrients become available with microbial turnover or through direct predation of certain mesofauna (e.g. nematodes; [105], [115]).

Recently, Paul et al. [19] have observed the association of N-fixing bacteria with the ECM Suillus tomentosus on lodgepole pine in tubercules growing inside rotting wood, possibly acting as a reservoir for moisture during periods of drought. They also report that N-fixation was higher in young stands and during the dry summers (10-15% of the values observed in alder). Moreover, associations between N-fixing bacteria and mycorrhizae were observed in Douglas fir ([20]). Given the relevance of these findings for the N-limited boreal forests, it could be interesting to explore if the presence is limited to the youngest stands or if they are also associated with adult and older trees.

Recent studies pointed out that N-fixation by algae living on mosses can equal inputs from atmospheric N depositions, especially in the late-successional stages of forest development at sites with low N depositions ([21], [22], [118]). Mycorrhizal fungi are able to efficiently colonize dead and senescing bryophytes, but it is not clear to what extent they are able to mobilize both N and P from living tissues of mosses ([119], [120]). So, the role of these widespread mosses and their interactions with mycorrhizal fungi in providing an additional supply of N to the boreal forest deserves further investigation ([21], [23], [121]).

2.4. Key-concepts of N uptake

The boreal conifers have adapted strategies to cope with the limited availability of N. Even if canopy N uptake may contribute, especially in low productive sites, to N nutrition in conifers, a lot of uncertainties remain on the subject, not allowing evaluating the real importance of these mechanisms. In response to the reduced mobility (low diffusion coefficients, see table 2) of certain soil N forms, especially of the organic ones in the late-successional phases of stand development, root proliferation to increase interception seems to gain importance over diffusion in the soil solution and the plasticity (capacity of exploration and rapid colonization of fertile patches) of the rooting system become important when competing for N resources. ECM confer an advantage to trees through the extensive absorbing surface, the increased exploration of the soil micropores and colonization of fertile patches, the wider enzymatic capabilities compared to plant roots and the improved access to a wide variety of sources of nutrients. NH4+ is the preferred inorganic form taken up, at a level comparable to simple organic N, which grows in importance as organic matter accumulates during the stand development.

3. N METABOLISM AND USES

3.1. N assimilation

After uptake by trees, NO3- is reduced to NH4+ and then assimilated into amino acids in roots rather than in leaves, contrary to herbaceous species ([79]). Indeed, NH4+ is rarely transported in this form to the shoot, so only small amounts of NH4+ are usually found in xylem ([79], [122]). This results in complex patterns of allocation: in an experiment with Scots pine, more 15NO3- than amino acid and 15NH4+was transported to the needles, even if NO3- uptake was the smallest one, resulting in similar amount of N allocated to the shoots between the three N forms ([87]).

NH4+ is assimilated into amino acids through the glutamine synthetase/glutamate-2-oxoglutarate aminotransferase (GS/GOGAT) system ([79], [123]). NH4+ can derive from both root uptake and amino acid catabolism. Other enzymes are important in N assimilation and metabolism and are closely intertwined with C metabolism. Asparagine synthase (AS) and glutamate dehydrogenase (GDH) are among the most studied enzymes of the N metabolism. GDH has a high affinity for NH4+ (ca. 5.8 mM) and is considered to be implicated in NH4+ detoxification, since its expression is higher at elevated NH4+ concentrations ([37]). In young pines, the accumulation of asparagine could support the establishment of the secondary vascular system ([124]). Even if N is not present in lignin, amino acids are implicated in its biosynthesis: through the deamination of phenylalanine (or tyrosine), the phenylalanine ammonia-lyase (PAL) supplies the phenylpropane used as skeleton for lignin formation, releasing NH4+ that is successively reassimilated via the GS/GOGAT pathway ([124]). Moreover, the catabolism of glycine and serine generates the methyl groups used by the cells in lignification and releases NH4+ that is readily reassimilated ([124]).

Amino acid transporters are expressed in several tissues and developmental stages but with different functions: uptake in roots, redistribution in leaves, loading, transport and storage in xylem and phloem ([37], [56]). The metabolism of glycine after uptake is the better known, since this amino acid has often been used in experiments to study the uptake of organic N by boreal species ([53], [84], [86], [87]). Once absorbed by roots, glycine is rapidly transformed to serine, and then glutamine, glutamate and alanine, and is transported to the shoots ([56], [87], [123]).

3.2. Transport, storage and internal cycling of N

After assimilation, N is transported towards organs and tissues where it is stored or used for different functions, depending on plant requirements. Transport of amino acids occurs both in xylem and phloem ([37]). The most common amino acids extracted from the conducting system of conifers are glutamine, asparagine, glutamate and aspartate ([125]). Under elevated N-fertilization, arginine and asparagine tend to replace glutamine as the dominant compound, probably acting as N transport and storage ([95], [125], [126], [127]). Glutamine is considered more efficient than arginine for transport, since it is directly involved in NH4+ assimilation through the GS/GOGAT pathway, and thus does not require additional energy to be synthesized. Being slightly negatively charged or uncharged at normal xylem sap pH, glutamine is not retained by cell-wall material of the xylem ([125]). So, when N availability is low or adequate, glutamine is probably the major compound for the transport of organic N. Arginine and asparagine may also accumulate in needles of conifers in response to low P supply, nutrient imbalance or stress ([126], [128]).

Many studies on boreal conifers have noticed that trees show a pronounced seasonal variation in nutrients, and the relative abundance of amino acids varies according to tree growth ([129], [130]). During the growing season, there is often a decrease in nutrients in needles older than the current year, probably explained by a translocation to the developing needles ([129], [130]). In fact, during winter N is stored mainly in roots and current-year needles, ([126], [131]). Together with arginine, asparagine is a major storage of N during winter, even if high concentrations of butyric acid and proline have been observed in Scots pine and white spruce ([122], [126], [131]). The reserves of proteins and amino acids in stem, roots and older leaves are rapidly remobilized in spring to sustain shoot elongation, bud burst and development of needles ([126], [131]). Glutamine and glutamate concentrations are high in spring and summer, probably due to their role in transporting N ([126], [131]). Replenishment of needle N takes place during autumn and winter, even when soil temperature and inorganic N concentration are low, and show an inter-annual variability dependent on the weather conditions ([129], [130]). Seedlings growing at low N supply show more N storage in roots, compared to those grown at high N supply ([129]). However compared to silver birch and European rowan, Scots pine stores more N in needles, which makes it more sensitive to artificial defoliation of 1-yr old needles ([132]).

Some experiments in conifer seedlings have found that N retranslocation is independent of current N supply and that needle development relies mostly on N from pre-existing shoots ([126], [129], [133], [134]). However, some differences between species have been observed. For example, the first phases of leaf growth of Scots pine and silver birch were sustained concurrently by root uptake and remobilization, while Sorbus aucuparia remobilized half the N from storage before any N was taken up by roots ([132]). Seedlings can show both predetermined and free growth ([129]). High N supply can contribute to the replenishment of N of preexisting shoots, which become depleted as N is remobilized, sustaining a second flush of growth ([126], [129], [133]). Black spruce seedlings receiving a high nutrient fertilization before plantation showed greater height and biomass growth than unfertilized seedlings ([135]), pointing again to the importance of internal nutrient reserves. It has been estimated that in some mature conifers, the internal cycling may provide between 30 and 60% of the N contained in the new foliage ([129]).

3.3. N, photosynthesis and growth

After being transported to green tissues, N is also used to build proteins of the photosynthetic apparatus. So increases in Rubisco and chlorophyll a/b protein complex are observed with increasing availability of N ([136], [137]). It has been reported that in various evergreen conifers, the allocation of N within the photosynthetic apparatus is quantitatively suboptimal with respect to photosynthesis with over-investment in Rubisco ([128], [136], [138]). Consequently, some authors have proposed that Rubisco may act as N store during winter ([128], [138], [139]).

A strong positive relationship is observed between N concentration in leaves and photosynthetic capacity, the latter varying with P availability and across biomes with the highest slope and lowest intercept at the lowest N:P ratio, corresponding to the arctic and boreal ecosystems ([140]). The slope of the photosynthesis-leaf N relationship is less steep in evergreen conifers than in deciduous broadleaves. Some authors have proposed that conifers may be less efficient in the allocation of N between different components of the photosynthetic apparatus or that the lower efficiency of photosynthesis per unit N may arise from the diffusional limitation due to the different leaf structure between conifers and angiosperms ([136], [138]), [139]

N fertilization increases the photosynthetic capacity but also stimulates foliage production ([141]). Fertilized Norway spruce showed greater leaf area index than the control ([98]). Moreover, it has been observed that stand-level water use efficiency (WUE) increases in response to N fertilization ([142], [143]). However, results are inconclusive on this last point. For example, N-fertilization in Douglas fir resulted in significantly greater rates of photosynthesis and transpiration of shoots but WUE similar to that of the control ([143]).

Evans et al. [144] observed that by increasing N supply, balsam fir accumulated N in the foliar tissues even if this did not translate into increased growth, but the results were not confirmed for heart-leaf paper birch. In a mature black spruce site, 3-year-long N additions increased N, Ca, Mg and Mn foliar concentrations without affecting growth ([64]). It has been suggested that slow growing species could respond to nutrient stress by adopting strategies to maintain adequate internal concentrations of N and other nutrients through luxury consumption (and storage) during the periods when resources are more available (e.g. at the beginning of the growing season) ([127], [145]). Indeed, compared to white spruce, growth of black spruce was less reduced in response to low N conditions, while the absorption rate was higher at high N conditions, even if growth was similar ([145]). This was interpreted as a better adaptation of black spruce to low nutrient availability.

In a greenhouse experiment with boreal tree species, Reich et al. [146] measured low rates of N uptake in conifers, while broadleaf species showed high rates of N uptake (Fig. 3). In the species tested, the rates of N uptake were related to the relative growth rates (Fig. 4). When foliar mass was taken into account, the relative growth rate was also in relation to the photosynthetic rate (Fig. 4), with the lowest values being observed in conifers ([146]). In the same study, a positive relation was also reported between N concentration in leaves and mass-based photosynthetic rate, confirming the biochemical role of proteins in photosynthesis.

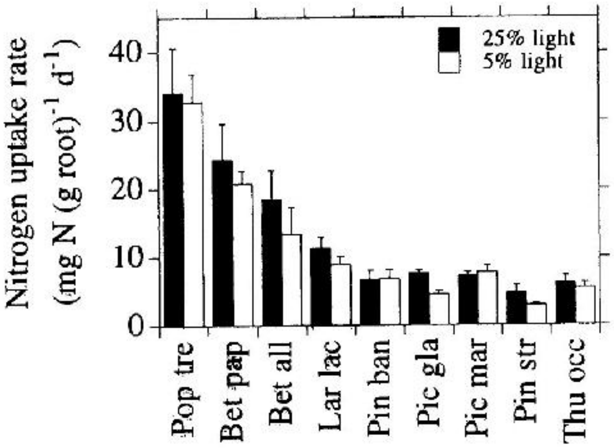

Fig. 3. Nitrogen (N) uptake rates (± one standard error) on root mass basis for nine boreal species grown at either 5 or 25% of full sunlight (from [146]). [Pop tre = Populus tremuloides; Bet pap = Betula papyrifera; Bet all = Betula allegheniensis; Lar lac = Larix laricina; Pin ban = Pinus banksiana; Pic gla = Picea glauca; Pic mar = Picea mariana; Pin str = Pinus strobus; Thu occ = Thuja occidentalis]

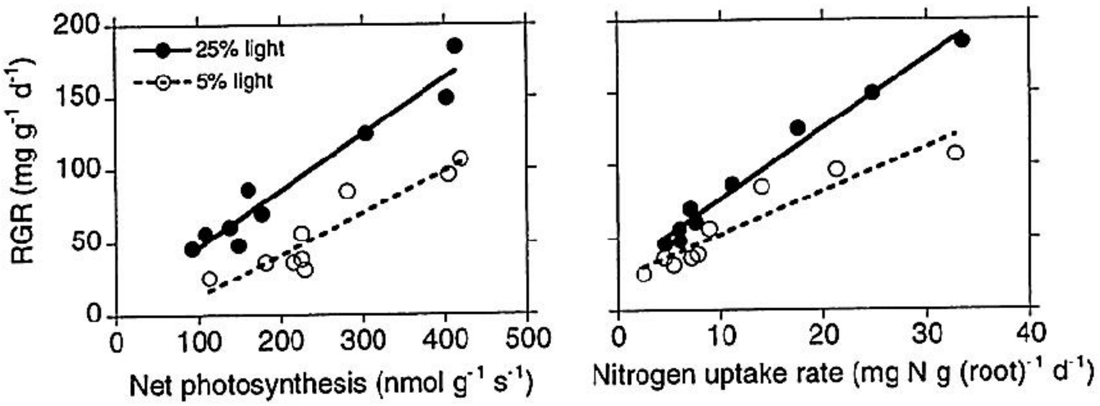

Fig. 4. Correlations between relative growth rate (RGR, mg g-1 day-1) and mass-based A_{sat} (nmol g-1 s-1) and N uptake rate [mg N (g root)-1 day-1] for seedlings of nine boreal species grown at either 5 or 25% of full sunlight. (from [146])

3.4. N and wood

Wood properties are likely to be influenced by N ([147], [148], [149]) as N is implicated in cell lignification ([124]), stimulates photosynthesis ([150]), and affects growth rate (in height and diameter, e.g. [151], [152]). Indeed, many studies report increases in radial growth after N-fertilization ([147], [153]). Fertilization also affects wood structure: in Norway spruce increases in ring-width are often the result of increased proportions of earlywood; since earlywood has usually lower density than latewood, wood density decreases ([147]) (Fig. 5). N-addition can generate shorter tracheids in wood, as observed in a 70-yr-old stand of lodgepole pine in western Canada, with the greatest reduction in the high-N treatment ([154]). Wood density decreased with fertilization, but only in the first five years following N-enrichment, and this decline coincided with greater growth in volume ([154]). Decreases in tracheid length and density produce softer tree rings and have consequences for mechanical properties ([149]). So, Meyer et al. [149] observed that the Norway spruces broken by windstorm showed a higher concentration of N in wood. However, the responses could vary with site because of the different soil and N-availability ([149], [152]).

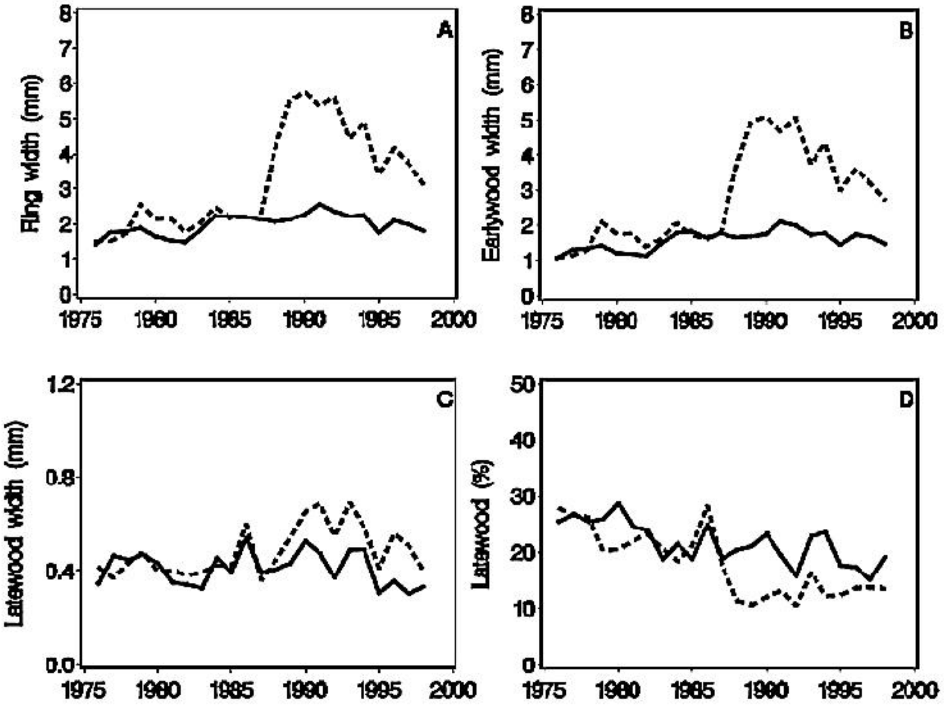

Fig. 5. Mean ring (A), earlywood (B), and latewood (C) width, as well as the proportion of latewood (D) of control trees (solid line) and fertilized trees (broken line) at breast height (from [147])

Changes in wood chemistry have also been observed with fertilization, with greater concentrations of lignin in fertilized Norway spruce ([153]). Soluble sugars, sterols and dehydroabietic acid have also been observed to increase in the same way ([153]). However, the effects can vary between sites: in a northern site where fertilization resulted in increased height and diameter, the ratios lignin:N and C:N decreased, while in the southern site where growth was unaffected, extractives increased ([152]). This can have implications on wood decomposition and industrial utilization.

3.5. Key-concepts of N metabolism and uses

N taken up from the soil is generally assimilated into organic N compounds (mainly amino acids) before it can be used in plant metabolism. Following assimilation, N is transported towards the developing organs to sustain growth or stored in the form of reserve. N is an important constituent of photosynthetic proteins and enzymes, so increases in N-availability result in increased net photosynthesis and foliage production. There is a positive relation between N uptake and relative growth and N fertilization increases biomass production. Boreal conifers, especially the slow growing species, seem to rely much on the stored N and its internal cycling, so growth is partially independent of current N supply in the soil, especially at the beginning of the growing season.

4. N-DEPOSITIONS AND BOREAL FORESTS: A BRIEF ACCOUNT

N-cycle and plant nutrition have been greatly altered in the last two hundred years by anthropogenic N depositions ([6], [155], [156]). In boreal and temperate forests, considered N-limited ecosystems, N addition through wet and dry depositions are very likely responsible of increased forest growth and C sequestration observed in the 20th century ([156], [157], [158]). Magnani et al. [158] showed that the increase in C sequestration in the last century was mainly determined by the additional input of N induced by human activities. Even if the estimates proposed by Magnani et al. [158] are among the highest, a recent review on the subject confirmed the stimulating effect of N-deposition on forest growth ([62]). De Vries et al. [62] reported positive forest growth under low to moderate N additions, with increase in site productivity for Scots pine and Norway spruce between 1 and 4% in response to a fertilizing effect of N deposition of 1 kg of N ha-1 year-1. On the basis of a wide European growth dataset, the response of trees was between approximately 20 and 40 kg C/kg N ([62]). Tree C sequestration was 3-4 times higher than soil organic carbon sequestration, pointing at the role of wood as an important C sink, due to its high C:N ratio ([62], [158]).

It has been proposed that in areas exposed to high N-depositions, tree growth may shift from limitation in N to limitation in other nutrients, as base cations (Ca, Mg, K) or P ([51], [159], [160], [161]). Addition of NPK fertilizers, increased the response of C-sequestration to N alone at N rich sites (soil C:N ratio below 25), possibly pointing out a limitation of P and K for tree growth ([62]). In a survey on the response of Swedish forests to increased N depositions, Binkley and Hogberg [51] reported that growth increased by about 30% from the 1950s to 1990s, and only stands that received heavy N fertilizations responded to fertilization with P or base cations or trace amounts of boron. However Houle and Moore [64] found no response to N-additions in a balsam fir and black spruce dominated site of eastern Canada where N depositions were low (5.7 kg ha-1 yr-1) but concentrations of foliar N were already high in the control trees (1.5% of dry weight). They proposed that this could be due to the high retention by other components of the ecosystem (e.g. soil immobilization) or, alternatively, to a limitation by other nutrients.

In an experiment combining heating and fertilization, stem growth of Norway spruce increased by 84 and 25% in heated and in heated plus fertilized plots, respectively ([162]). In various experiments, the lower fertilizer applications or lower N depositions were always more efficient in stimulating growth than greater ones ([60], [156]). C accumulation in response to N addition was 25 kg C/kg N and 11 kg C/kg N added for tree and soil, respectively. The application of NPK fertilization improved tree C accumulation to 38 kg C/kg N, suggesting the occurrence of co-limitation by P and K in these sites. Comparing the sites from northern and southern Sweden, higher N-depositions in the southern Norway spruce stands were estimated to be responsible for an increase of 2.0 kg m-2 and 1.3 kg m-2 of C in tree and in soil organic carbon, respectively ([60]). In a 40-yr old Norway spruce stand, long-term N-addition resulted in 10-fold additional carbon storage (3.0 Mg C ha-1 yr-1) compared to the effect on the humus layer (0.3 Mg C ha-1 yr-1). Even if production and litterfall were increased, no increase was observed in soil heterotrophic activity, suggesting a possible negative effect of N on SOM decomposition ([163]). In fact, some studies have found that moderate or high N additions (>5-10 kg N ha-1 yr-1) inhibit the decomposition of low quality litter with a repression of the lignolytic enzymes of decomposing fungi ([33], [164]).

The presence of mycorrhizal fungi usually decreases with N depositions ([165], [166]). This may be the consequence of direct changes in the soil conditions or in belowground/aboveground allocation by trees. In a Norway spruce stand, fine root mortality increased by 191% in fertilized plots ([98]). However, root longevity was lower in either heated or fertilized plots than in the combined treatment, underlining the existence of an interaction between temperature and fertilization ([98]). Other studies employing N-fertilization found contrasting results on the diversity of fungal species ([167], [168], [169]). The observed contrasting results could be related to the different host species and their fungal partners, the quantity of N added (i.e. high N loads may be deleterious), the form of N added (e.g. organic N may increase ECM; see [167]) and the composition of the microbial community. Moreover, there are reports that some mycorrhizal species may be well adapted to soils with high rates of N mineralization and the optimum N concentration could evidently differ between the fungal species ([165], [168], [169]).

5. LIMITATIONS AND KEY-FINDINGS OF PAST STUDIES

5.1. Different N forms and plant nutrition

There is evidence that in boreal soils, NO3- levels are always very low while NH4+ and organic N usually represent the majority of the N pool, with an increase in the ratio of organic to inorganic N according with the organic matter accumulation ([2]). NO3- was thus not considered an important source of N for plants of the boreal forest. However, the rate of flux through the different N pools could be more important than their size ([63]). Moreover in experiments with lysimeters, which represent concentrations in the soil solution rather than total nitrogen present in the soil (soil extractions), NO3- is usually well represented ([31]). So these conclusions, about different soil N forms, have to be taken with caution because we don't know yet which measure better represent available N for plant growth. Hydroponics experiments do not take into account the mobility of the different N forms in the soil, and thus fail to quantify the real availability and plant preference for these forms. Nonetheless, various experiments performed in conifers have confirmed that uptake of NO3- is slower than that of NH4+ and amino acid, thus excluding the importance of NO3- as a primary source of N for conifer nutrition ([53], [87]). Instead, NO3- probably acts as a signal to trigger the proliferation of roots towards fertile patches of soil ([52]).

5.2. Mycorrhizal fungi and N nutrition

ECM fungi enhance conifer nutrition through several mechanisms. One of the most important and controversial issues is their ability to use organic N. Jones et al. [63] proposed that DON is abundant in boreal soils because it has a reduced availability for plant and microbial nutrition, and thus accumulates. Moreover, if the trees associated with ECM were able to use this N source, why should N-limitation persist? The answer may be in the cost required by mycorrhizal associations for the use of organic N ([170]). For breaking-down organic matter in order to absorb low molecular weight organic compounds, mycorrhizal fungi and plants have to release exoenzymes ([171]). Since N is required to produce enzymes, the return on investment may be low if organic N decomposition is inhibited ([170]). This might explain why productivity is lower than that measured in soils where inorganic N is more abundant ([110], [111]). Polyphenols and other recalcitrant substances may reduce the ability of ECM exoenzymes to breakdown organic matter ([14]). However, it is still unclear to what extent polyphenols directly reduce the uptake by ECM trees ([18], [66]). Bending and Read [14] report that polyphenols may inhibit ECM when they are in solution, but not when they are precipitated with proteins.

It should be stressed that early studies have often been conducted in greenhouses and in vitro, sometimes using hydroponics or agar-cultures ([14], [56]). Moreover, the majority of the field experiments use seedlings, so it is difficult to correctly evaluate how these results can be scaled up to adult or mature trees. For example, root exudates (substances released in the rooting zone) vary with species and age, underlining the problem of extrapolating results from studies on seedlings to older plants ([44]). Besides, in a natural forest, the competition with the surrounding vegetation (e.g. ericaceous species) and other microbial communities adds complexity to the interpretation of results. The chemical composition of root exudates also varies in the presence of microorganisms (e.g. mycorrhizae) that can cycle them through their metabolism ([44]). As pointed out by Nasholm and Persson [106], a major problem in studying the competition between plants and soil microorganisms is to distinguish among the different microorganisms in the field (e.g. mycorrhizae vs. other microorganisms), thus short-term studies can underestimate N acquisition by trees. However, recently, the analysis of phospholipid fatty acids (with biomarkers for ECM, saprotrophic and bacterial communities) has been used profitably to distinguish between the different microbial groups ([113]).

Many experiments testing the importance of different N forms in the field have often added N at unrealistic rates, thus impeding an evaluation of the effective nutrition in natural conditions, but rather simulating a saturating condition ([56]). Some experiments have observed that growth may be reduced at high concentrations of certain amino acids, especially for those compounds that are generally present at low endogenous concentrations in plants ([56]). Given that the uptake of organic N differs between amino acids, the widespread use of glycine in many studies is subject to criticism, since this amino acid can be rare in boreal soils (3% of total free amino acid concentration) while alanine or glutamine could be used as substitutes ([58], [87]). Finally, experiments focus essentially on uptake, so the contribution of the organic N taken up, to the total N plant, is not known ([56], [63]). Jones et al. [63] report that, in some grass species, the contribution of the organic N could be low, but it should be noted that, contrary to arbuscular mycorrhizal fungi associated with grasses, ECM always show greater capacities to use organic N ([170]).

Some doubts still remain concerning the regulation of exchanges and transfer of nutrients between ECM and their hosts ([170]). The studies with excised roots do not account for the effect of exudation and transfer of C to the mycorrhizae. These should be the key elements in defining N dynamics in the soil and could affect N uptake and transfer ([113]). In both lab and field studies, mycorrhizal plants are depleted in δ15N, while mycorrhizal fungi are enriched relative to the supplied N sources or soil N ([172]), suggesting that N taken up by mycorrhizae is “selectively filtered” (i.e. metabolized) by the fungi before being transferred to the host tree. Moreover, a delay could occur between mycorrhizal uptake and transfer to the host, so mycorrhizal fungi may store N and make it temporarily unavailable to the partner ([173]).

Future studies with dual labeled amino acids (i.e. with both C and N isotopes) and labeled inorganic N could allow a better understanding of the uptake and metabolism of these compounds ([56]). By using small amounts of highly enriched tracers in long-term studies it should be possible to study uptake and assimilation at more realistic concentrations and to characterize how the partitioning of N varies with time according to plant requirements. Finally, it will be important to better quantify how much of total plant N is represented by the labeled N compounds taken up.

5.3. N uses in conifers

Some studies report that uptake and assimilation of NH4+ are less energy-expensive compared to those of NO3- ([63]). However, NO3- is transported without the toxicity problems of NH4+. Thus, NH4+ has to be assimilated in the organic compounds before it can be transported to those organs where N is needed and, together with amino acids, its translocation is slower than that of NO3- ([87]). This may explain the importance of internal N stores in conifers, which may rely less on current N supply in the soil for the formation of new tissues in spring ([126]). Moreover, many boreal conifers, especially the slow growing species of the late-successional phases of stand development, show luxury consumption of N and may use the stored N to sustain growth during periods of reduced N supply ([127]). This can be seen as a strategy for nutrient conservation in poor soils where N is not readily available. Various traits of conifers (low tissue N, long leaf lifespan, high concentrations of phenols and other defense compounds) are also interpreted as strategies for nutrient conservation and adaptations to nutrient-poor environments ([174], [175], [176]).

Reich et al. [176] proposed that the adaptation to the nutrient-poor environments typical of conifer species of native habitats have generated a series of correlated leaf traits, a "syndrome" of slow growing species. This may have implications for competition and forest succession, since these traits are also involved in the low responsiveness of conifers to environmental changes when compared to deciduous species ([174]). One of the trade-offs of longer leaf lifespan could be lower photosynthesis, probably due to diffusional constraints and storage of N in Rubisco ([138], [177]). Slow growing species may be more adapted to conditions typical of late successions while fast-growing species, with their higher photosynthesis rates, usually have higher rates of nutrient uptake that cannot be sustained where nutrient availability is limited ([146]). On the contrary, where resources are not limiting, slow growing species may be less competitive and thus be excluded.

N is also implicated in the biosynthesis of lignin and the changes in photosynthesis and growth following N additions may affect wood properties ([147], [149]). However it is not clear how N supplies vary at stand level and determine differences among groups of trees under otherwise common environmental conditions ([149]), even if, at a broader scale, a positive relationship exists between mineralization and productivity ([111], [150]).

5.4. Disturbance and N-depositions: implications for N-nutrition

Fertilization tests have found that the majority of N is retained by the soil rather than vegetation, confirming that boreal soils are strong sinks for N. The capacity of N retention in soils depends on the history of the past depositions and disturbances (e.g. fire frequency and intensity), soil chemistry (e.g. C:N ratio) and physical properties (e.g. texture) ([4]). The accumulation of organic matter, which has a high exchange capacity at low pH, can increase NH4+ retention. Following N-depositions, NO3- leaching has been observed especially in systems approaching saturation (which are currently rare in boreal forests) or during winter, when N uptake is reduced ([26], [178], [179]). Apart from the excessive quantity added, one of the problems of many N-addition experiments is the low frequency of applications. In nature, gradual changes and lower deposition levels are more common, so these unnaturally-high and punctual additions can alter the structure and competition of the microbial community ([113], [116]). Nonetheless, these experiments are a realistic approximation of the situation following disturbances (especially in more polluted areas), and their results should be interpreted and applied in this sense. Usually, N-additions have stimulated aboveground rather than belowground growth, indicating that, at high N availability, trees invest fewer resources for soil exploration and N uptake ([95], [96]). Future efforts should be directed towards reducing the quantities and increasing the frequency of N-additions, using highly enriched isotopic tracers and taking into account the specific effects of the different N forms in plant nutrition.

The clear responses to N fertilization have confirmed that N-limitation is widespread in the boreal forest ([60], [62]). The changes in N cycle following fire may favor fast-growing species, resulting in a temporary release from N-limitation. Nonetheless, it is reasonable to expect that frequent fires, leading to continuous N losses, can reduce N availability. Moreover, wildfires and harvesting seem to affect differently the N cycle: for example even if harvesting and wildfires increased initial N losses, DON exports were higher in harvested areas compared to burnt areas, where inorganic and organic N exports were equally important ([32]). Other disturbances, like insect outbreaks, may also increase N losses and alter the N cycle (e.g. nitrification), thus affecting forest growth ([31]). Harvesting, especially that of whole trees, removes important quantities of certain nutrients, such as Ca, Mg and P, from the ecosystem, so shifting the growth limitation from N towards other elements, especially in stands chronically subject to high N depositions ([32], [160], [161], [180], [181],). It should be underlined that the occurrence of co-limitation is probably restricted to limited areas, where acidic depositions and harvesting have been intense for a long period of time ([51], [161]).

During stand development after a major disturbance, the forest become denser, the competition for N increases, and the availability of mobile forms (NO3-) is reduced, gradually leading trees to invest more resources for N scavenging and favoring the belowground allocation towards mycorrhizae, which are particularly adapted for this function ([1], [18]). N-limitation can also be related to the competition with ericaceous species and soil microorganisms, as demonstrated by weed-control and experiments excluding roots of competing plants that resulted in an improved nutrition of conifer seedlings ([68], [69]).

The reduced decomposition at high latitudes could be an effect of low temperatures on the forest floors when the canopy closes and organic matter insulation increases, the prevalence of low quality litter, low pH, and the particular microbial communities ([18], [23], [47]). The accumulation of organic matter, increased proportions of recalcitrant compounds, and increased soil acidity could affect the availability of mineral N. So, it is proposed that late-successional conifers have slow growth because they rely on less available organic N sources.

6. CONCLUDING REMARKS AND RESEARCH DIRECTIONS

The majority of the studies support the hypothesis that the growth of the boreal forest is limited by the availability of N. Nonetheless, there is evidence that N limitation becomes more severe in the late-successional stages of stand development, when low rates of decomposition and mineralization cause an accumulation of organic matter on the soil. Organic N is less available to conifers than inorganic N, which predominates after disturbances. Consequently, the late-successional conifers must rely more on organic N than the early-successional species.

Read and Perez-Moreno [109] proposed that the role of mycorrhizal associations gains importance for N nutrition moving from temperate towards boreal forest and tundra, with ERM especially important in tundra, where the decomposition of organic matter is extremely reduced due to the low temperatures. We refine their hypothesis, based on our conclusion that N limitation could vary over time according to the successional stages and the history of past disturbances (e.g. changes in N-depositions), and that the composition of soil microbial communities varies with N cycle (e.g. C:N ratio, pH and variability of N forms). We deduce that early-successional forests are less N limited since the disturbances, resetting the successional sequence, tends to increase mineralization and to release the N stored in the soils of the late-successional stages. Future studies should test this hypothesis using chronosequences or manipulating the N cycle and testing how competitive relations may change by measuring the increase in growth after fertilization performed at low rates and concentrations, simulating natural conditions.

As succession proceeds, species change according to changes in N cycle: the less available and less mobile forms of N are, the higher the dependence on symbiotic fungi for nutrition is. At the same time, the importance of the processes operated by bacteria decreases. Boreal conifers of the late-successional stages seem adapted to these conditions and show low rates of N uptake, associated with low rates of growth. Consequently, the majority of these late-successional species are classified as slow growing. However, a doubt arises that some young conifers may show rapid juvenile growth after a major disturbance that modified the nutrient cycles ([182]). We propose that the rate of growth, which is related to the nutrient uptake, the capacity to adjust growth to changes in availability of N and nutrients, and the presence of different species (conifers and broadleaves) may drastically alter the competitive relations between organisms and define the development of the ecosystem following disturbance.

Moreover, as succession proceeds, the importance of strategies to cope with the reduced N availability and with the space-time variability in N supply increases. So there is evidence that late-successional conifers rely greatly on their N reserves and their growth may be in the short term (e.g. few years) partially uncoupled from current N supply, possibly explaining the lack of growth response in certain slow-growing conifers after fertilization. This should be tested using isotopic tracing techniques and trying to follow isotopes through the ecosystem and within trees over several years following N addition.

The increase in anthropogenic N depositions in the last century seems to have alleviated N limitation and stimulated tree growth in certain region of the boreal forest. The increase in N depositions, coupled with climate change, may affect the N cycles, increasing the decomposition of soil organic matter and the availability of inorganic N, thus reducing N limitation in the long term, but also altering competitive relations among species. Fast-growing early-successional broadleaf species could be more responsive to these changes because of their closer relationship between N and photosynthesis and their higher rates of N uptake and growth, and could gain advantage over conifers. It is urgent to test this hypothesis through manipulative experiments that simulate scenarios of N enrichment coupled with climate warming to understand the potential responses of the boreal ecosystems and their consequent future evolution.

This paper focused the role of soil N in the nutrition of boreal conifers, but N depositions may also affect N nutrition and, as a result, impact soil N cycle through direct canopy uptake. This process is insufficiently understood (a brief account of current knowledge has been given in the text), so we suggest that future research should aim to verify and define its importance in respect to N uptake and study its impact on the microbial, and in particular mycorrhizal, communities of the boreal ecosystems. Finally it is important to point out that the review of the literature has showed that studies tend to be concentrated in certain areas. It is surprising the small number of studies available regarding Siberia and the Russian part of the boreal forest. We encourage researchers to publish (in English) more on this area, since the relative importance of different drivers of the N cycle may change in vast and less populated areas (e.g. N depositions, harvesting).

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DEFINITIONS, ACRONYMS, ABBREVIATIONS

DIN: dissolved inorganic nitrogen, the inorganic N in the soil solution, whose main components are NO3- and NH4+ ([56], [64])

DON: dissolved organic nitrogen, usually calculated by subtracting inorganic N (NH_4^+ and NO_3^-) from total dissolved N. ([28]. DON is a heterogeneous mixture of organic compounds that can be divided in two pools, one highly labile and another more recalcitrant. In boreal soils, free amino acids represent 10-20% of DON ([10]).

ECM: ectomycorrhizae, mycorrhizal fungi associated with trees forming sheathing mantles of fungal tissues over the exterior of the root surfaces and among the root cells ([1]).

ERM: ericoid mycorrhizae of fungi penetrating within the epidermal cells of roots. The mycelium does not extend widely beyond the individual roots but remains a few millimetres from the cortical cells ([108]).

L layer: litter layer of the organic soil horizon at the soil surface in forest floors, with slightly decomposed organic matter but still recognizable organic debris ([57], [183])

FH layers: fermentation-humification horizons on the top of the soil profile ([1]). Layers of the ectorganic soil horizon of forest floors with intermediate to high degree of organic matter decomposition. The original form of most plant and animal matter cannot be recognized with the naked eye ([57], [183]).

RUBISCO photosynthetic enzyme associated with C fixation; ribulose 1,5-bisphosphate carboxylase ([136])

SOM: Soil organic matter mainly composed of dead and chemically transformed material of biological origin as well as living microorganisms biomass, ([11])

Throughfall: Incident precipitation that had interacted with the forest canopy before reaching the forest floor ([26]).

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