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Full Length Research Paper

A Critical Analysis of the Function of Soil Nitrogen for the Boreal Forest Conifers

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The most crucial component for plant development and sustenance is thought to be nitrogen. Its availability and function for conifers in boreal forests are still up for discussion, though. Boreal conifers have changed their tactics to deal with the decreased amount of nitrogen available. Boreal conifer roots are linked to ECM fungi, which promote soil exploration and N nutrition, particularly in areas with a high proportion of organic N. While estimates of nitrate uptake are often lower, conifers typically absorb ammonium at amounts similar to simple organic N, which likely becomes more significant as organic matter builds up with stand age. Conifers may depend on internal N cycling to support the growth of new tissues in the spring, particularly slow-growing species. N promotes growth and wood development by increasing photosynthesis and leaf area, which mostly results in greater earlywood production and broader radial rings. The growth of boreal forests may be impacted by N-depositions and disturbances (such as fire and harvest) that change the soil N-cycle. The expansion of boreal forests over the past century is thought to have been caused by N depositions. High N-depositions and intensive harvesting may cause N to become less abundant than other elements (e.g. P, K, and B). Through a variety of intricate processes, such as altered fire return intervals, direct impacts of warmer soils on N mineralization, and the stimulation of plant growth, climate change should alter the balance between N stored in soils and in living and dead (such as wood) biomass. Future studies should aim to deepen our knowledge of the potential effects of shifting disturbance regimes, N-depositions, and climate. These studies should focus on the role of mosses in fixing nitrogen, canopy N uptake, and conifers' reactions to shifting microbial (symbiotic and non-symbiotic) communities.

Key words: Ammonium; boreal conifers; growth; N limitation; nitrate; N uptake.

OVERVIEW OF THE N CYCLE IN BOREAL FOREST SOILS

Low evapotranspiration and decomposition are characteristics of the world's boreal forests, which correlate to delayed nutrient cycles and organic matter accumulations during forest stand successions [1,2]. Together with P, N is a crucial component of plant nutrition and is needed in large quantities for all of the key metabolic functions of plants. In order to determine the role of this essential component for forest productivity and carbon sequestration, it is crucial to fully comprehend the features of the N cycle in the boreal forest. The growth of the forest is thought to be N limited, but broad variations in nutrient availability and elemental interaction are typically observed [3,4,5].

In terrestrial ecosystems, biological N fixation (e.g. by cyanobacteria associated with mosses and lichens) and atmospheric N depositions are the main channels of N input in forms suitable for plants; lightning-induced N fixation is far less significant (Table 1) [6,7,8]. Leaching of dissolved N species can result in N losses. Although nitrate leaches more readily than NH4+, DON comparatively outweighs mineral N in intact forests, with losses of a few kilograms per hectare year [9, 10]. Additionally, N is lost by denitrification (Table 1) and volatilization (particularly fast volatilization from wildfire, whereas ammonia volatilization at high pH values is marginal in the usual acidic soils of the boreal forest) [11,12]. The fire return interval plays a significant role in assessing the long-term effects of fireinduced N volatilization on the ecosystem's long-term N balance. Wildfires and broadcast burning may in fact constitute a significant punctual N output (hundreds of kg N per ha). Lastly, polyphenols and other resistant compounds in plant and microbial biomass or in the soil following precipitation can immobilize N [13,14,15,16,17].

Although inputs and outputs are significant flows to and from the nitrogen cycle, they pale in comparison to the vast amount of nitrogen contained in the boreal forest's soils. [47] Calculated N-accumulation in three northern Scandinavian forest stands shows that soils are the primary source of N in these untouched woods, with humus exhibiting amounts that are three to twenty-four times higher than those found in vegetation. Between 0.30 and 0.35 g N m-2 yr-1, or roughly 85% of the N intake to these forests, was calculated to be the rate of N accumulation in organic soil and plants. Therefore, soil organic matter, which is composed of around 50% C and 5% N, but only partially (often less than 5%) in accessible form, is an important component of the N cycle [11].

Plants cycle nitrogen, and the turnover of plant biomass—primarily leaves and fine roots—both above and below ground provides the necessary inputs to soils. Compared to the canopy litter, the turnover of roots, particularly the fine roots and related mycorrhizae, can return two to five times as much organic matter and six times as much nitrogen to the soil [48,49,50]. Because of their varying litter chemistry, different species may have an effect on the microbial composition of the soil and, consequently, nutrient cycles [38,51,52,53,54,55]. Because of the higher acid strength of the organic waste deposited beneath the conifers, Binkley and Hogberg [56] found that the pH of the soil was lower in Norway spruce plantations than in hardwood plantations.

Two distinct concepts regarding N nutrition existed until recently (Fig. 1). According to the first, inorganic nitrogen obtained from mineralization and N inputs was widely utilized by plants. The process that controls the availability of nitrogen for plants is known as mineralization, which is the breakdown of organic monomers by heterotrophic bacteria that release NH4+ (ammonification). After that, oxidizing microorganisms that produced NO2 quickly converted it to NO3- (nitrification), as well as NO and N2O, using NH4+ as an energy source (Fig. 1A). The second, more contemporary paradigm proposed that plants may access both the inorganic and organic source of N, with less focus on mineralization as a limiting process [16,57]. SOM may break down into smaller and more easily accessible organic molecules (amino acids, nucleic acids, and amino sugars) through depolymerization, which is the breakdown of soil organic matter carried out by microbes and plants through the release of exoenzymes (Fig.1B). When these organic substances mineralize, inorganic nitrogen (NH4+ and NO3-) is released, making it easier for microbes and plants to obtain [57].

The latter paradigm is favored in this research because to its adaptability; it permits the usage of organic N under specific conditions while maintaining the role of mineralization. Recent research showing that both mycorrhizal and nonmycorrhizal plants may absorb organic N supports this conclusion [58,59,60]. Furthermore, in old forest stands, lower soil pH and the buildup of organic matter with high polyphenol concentrations may limit N mineralization, particularly nitrification, as time since fire increases. Proteolysis, or the depolymerization of proteins, may become increasingly significant in these situations (Fig. 2; [2,52,61]). However, because of the low pH and temperature, the buildup of allelopathic chemicals based on phenol, and the anaerobic and moist circumstances that prevent nitrification, mineralization is still significant in the boreal forest [2,17,42,62]. A variety of N shapes can be seen in boreal environments with intricate terrain [63,64,65,66]. While NO3- tends to gain importance on the most productive forest ecosystems (e.g., toe-slopes, fine-textured fluvial terraces), after disturbances (e.g., producing forest gaps, with temperature, pH, and light conditions stimulating mineralization and nitrification), or in areas subject to high N depositions, NH4+ is typically the predominant inorganic form of N when soils extraction is carried out in mature conifer stands on less fertile sites [65,67,68]. Along a transect that represents a primary succession, the buildup of organic matter was found to increase the concentration of amino acids (Fig. 2, Table 2) [2,69]. [70] proposed various amino acid sources and sinks to account for a rise in secondary succession stands with age. The source of increased organic N inputs would be the depolymerization of the existing soil organic matter (SOM) as well as increased direct input through needle litter, root exudates, and root turnover, which are all associated with higher aboveground and belowground plant biomass in mature stands. There may be significant distinctions between primary and secondary succession, though, with the former experiencing significant species changes along with total changes in litter quality and microclimate, while the latter occasionally retains the same species composition (for example, black spruce and balsam fir establishing right after a disturbance and continuing to the next stand-replacing event), likely having a different impact on the N cycle [70,71]. Instead of dominating and being replaced, pioneer trees and shrubs may eventually disappear during secondary succession. To elucidate the distinctions between primary and secondary succession in the N cycle, more articles are undoubtedly required.

1.1 Hypotheses of N-Limitation

aor instance, during snowmelt, when low soil temperature, high water fluxes, and the extended period of tree dormancy limit N uptake, the distinct mobility of N forms, especially NO3-, can result in larger losses than NH4+ [3,30]. However, considering the powerful N sinks typically represented by soil and plants in this N-limited environment, significant NO3-losses are most likely uncommon in the boreal forest. While DON losses (which are typically higher than DIN losses in older, undisturbed stands) proportionally gain importance during the later phases of stand succession, when organic matter accumulates, important N losses (such as N volatilization by fire and nitrate leaching after fire or clearcut) may be related to disturbances, particularly when plant uptake is absent or reduced [10,76,77]. Depending on the fire severity and return interval, N losses in gaseous forms during fires can range from hundreds of kg N ha-1, however they are episodic and have varying effects on long-term N trends [53].

The decreased availability of N was also explained by the strong C-N bond found in soil organic matter and litter [53,78]. Protein-precipitating and recalcitrant C molecules (polyphenols and tannin) would chemically and physically preserve N, potentially delaying its breakdown. Additionally, several polyphenolic chemicals have been shown to have allelopathic actions that may prevent plants from mineralizing or absorbing nitrogen [15,17,79,80]. Furthermore, intense competition between plants and soil microbes may lead to N-limitation [81]. Therefore, a decrease in competition for nitrogen is typically credited with the improved growth of conifer seedlings following weed eradication [82].

It appears contradictory that N-limited late-successional boreal forests lack N-fixing plants, as higher rates of N-fixation are found in nature when there is a low N supply [83]. However, the availability of other nutrients (such as P, Mo, or Fe), the high energy cost of the symbiosis (high light demand), and other factors, such as herbivores' preferred grazing of N-fixing plants, may limit N-fixation [3,78,84].

Evaluating how growth responds to N additions is a simpler method of proving that trees have a nitrogen restriction. However, site-specific variables and ecosystem disruption can make it more difficult to interpret the data. Furthermore, the lack of a growth response does not rule out the notion of limitation because other potent N sinks may sequester the additional nutrient in another part of the ecosystem (such as soil, microbial immobilization, or uptake by other plants) [53,85]. Analyzing tissue (particularly foliar) concentrations to determine its required levels and ratios with other elements (e.g., N:P, [53,86]) are other methods to assess N restriction.

1.2 Aim of the Review

Significant reviews of the connections between mycorrhizal fungi and nutrient cycling, as well as inorganic and organic N nutrition, have been published [1, 53, 61]. However, a detailed analysis of the unique dynamics of the N cycle that take place in the boreal coniferous forests is necessary to appreciate its unique characteristics. This paper's objectives are to: (1) explain the significance of various soil nitrogen forms for boreal conifer nutrition and the uptake strategies built under low N availability; (2) briefly address the effects of current disturbances (such as fire and forest harvesting), increased N depositions, and climate change on the N cycle of the boreal conifer ecosystems; and (3) address the shortcomings of previous research and offer some suggestions for further studies. The act of absorbing, assimilating, and using nitrogen is referred to as N nutrition in this review. Unless otherwise noted, the coniferous boreal forest will be especially consideraed.

2. STRATEGIES FOR N-UPTAKE

Trees must absorb N before it can be assimilated and used. Particularly active locations for nutrient uptake and exchange with mycorrhizal fungus are fine roots. Ruess et al. [50] calculated that almost all first-order fine roots (i.e., the most distant, smallest diameter, fine roots) in interior Alaskan white spruce exhibited mycorrhizal connections. These fungus have the ability to directly interact with other soil microbes and are crucial in improving N nutrition. Therefore, when examining the role of N in tree growth, it is necessary to take into account the role of mycorrhizae in N-nutrition as well as the methods of uptake for the various types of N.

2.1 Mechanisms of N-Uptake

The equilibrium between influx and efflux determines a nutrient's net absorption, which is a concentration-dependent process controlled by plasma-membrane transporters [61]. Active transport is necessary for NO3-uptake, and ATP provides the energy [42]. Similar to K, NH4+ is absorbed through channels that are controlled by the negative cell membrane potential, which causes the rhizosphere to become more acidic [42]. Non-mycorrhized white spruce seedlings cultivated in hydroponics may absorb NH4+ at absorption rates 20 times higher than those of NO3- [87]. Low NO3-uptake capability in spruce was observed by Grenon et al. [88], indicating that NO3-may be a significant nutritional source for soil microorganisms. NO3-uptake and assimilation require 10–15 times more ATP than NH4+ [89,90]. According to Meyer et al. [91], the C costs for NH4+ and simple organic N assimilation are half of those for NO3-: 0.17 kg C/kg of NH4+ or Norganic vs. 0.34 kg C/kg of NO3-.

In contrast to NO3-, NH4+ efflux most likely occurs via an active antiport, and the significant energy cost involved is commonly cited as one of the reasons why many species that are not acclimated to soils with excess NH4+ experience ammonium toxicity [72,87]. The buildup of amino acids in plant tissues is another characteristic of NH4+ toxicity. Britto and Kronzucker [72] hypothesized that NH4+ toxicity could result from a high NH4+ influx and an excessive efflux to preserve the electrochemical balance of the cells due to the competitive exclusion of K+ by NH4+ and the overexpression of K+ channels at high external NH4+ concentrations. Furthermore, it has been noted that NH4+ toxicity is linked to decreased leaf moisture and water potentials and is particularly noticeable at high light intensities [42,72].

According to Kronzucker et al. [92], early-successional species (trembling aspen and Douglas fir) and late-successional species (white spruce) may be less sensitive to NH4+ excesses due to their greater ability to regulate NH4+ fluxes through the plasma membrane. Additionally, in contrast to white spruce and jack pine seedlings, early successional deciduous species (like aspen) grown in hydroponics shown a good capacity to absorb NO3- concurrently with NH4+ [93]. In contrast to NO3-, all studied species exhibited greater affinities and rates of uptake with NH4+ [93,94]. This pattern was validated by Min et al. [95], who found that lodgepole pine had 16 times the NH4+ uptake of NO3-, whereas trembling aspen only had 2-3 times the uptake. Similarly, 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, and glycine), rates of uptake of amino acids and NH4+ were 7-8 times higher than those of NO3-. However, at a high proportion of NH4+ in the fertilizer, seedling growth and mortality were observed at a high proportion of NH4+, likely due to NH4+ toxicity [96]. According to Min et al. [95], lodgepole pine and Douglas fir showed comparable NH4+ utilization to aspen, but a reduced capacity to utilize NO3- with lower levels of nitrate reductase activity and translocation to shoot. Therefore, they put out the theory that species distribution in temperate and boreal ecosystems may be influenced by the availability of various types of nitrogen, which may be linked to niche separation among species.

Given the buildup of phenolic compounds that may lessen the mineralization of soil organic matter, amino acids and organic nitrogen may become more significant in plant nutrition over time in comparison to inorganic nitrogen forms [2,11,67,70,97]. In addition to their ability to absorb amino acids, plants can form mycorrhizal relationships that improve the nutrition of organic nitrogen [58,98,99,100]. According to a recent lab study, many nonmycorrhizal species can absorb complete proteins and amino acids, but they have restricted growth potential when exposed to N sources that only include organic N [59]. In a field trial, Norway spruce and common bilberry showed a greater uptake of NH4+ and amino acids than NO3-, whereas wavy hair-grass demonstrated the reverse effect [98]. Amino acid absorption was comparable to or greater than that of NH4+ in a different Scots pine experiment, although NO3-uptake was minimal [100]. Accordingly, the rate of NO3-uptake in Scots pine and black spruce is often lower than that of NH4+ and amino acids [96,100].

2.1.1 N-canopies and depositions N uptake: yet another crucial route?

N enters ecosystems by N-depositions (dry, wet, and gaseous), in addition to N fixation (e.g. by cyanobacteria associated with mosses, which are particularly important in less polluted places) and the breakdown of organic matter. The canopy may retain a significant portion of the atmospheric inorganic N deposition, especially for NH4+ [31,101]. Generally speaking, canopies do not retain organic nitrogen; nevertheless, they do retain inorganic nitrogen at a rate of 1–12 kg N ha–1 year–1, or 50–70% of the nitrogen delivered at the study sites by [102]. According to Houle et al. [31], who measured the difference between throughfall and bulk precipitation, the uptake of NH4+ in a coniferous boreal forest (spruce and fir) was 75% of incoming wet NH4+ deposition during the growing season and was significantly higher than that of a deciduous canopy, which is consistent with earlier studies [103]. For both canopies, the intake of NO3- and NH4+ was particularly noticeable in October, whereas a net release was noted in January. Epiphytic lichens successfully eliminated NO3- and NH4+ from melting snow after an overnight incubation [31]. Lichens may contribute significantly to canopy N intake and are frequently seen in large quantities on the branches of coniferous forests [31,104]. As a result, the N intake of trees themselves—which is determined by subtracting the total throughfall flux from wet deposition—is most likely overstated. [31, 85, 105]. In fact, the overall reactivity for both outflow and influx in a balsam fir experiment was in ascending order: twigs, fresh needles, old needles, and lichens [104]. Using a scanning electron microscope to examine balsam fir tissues revealed that twigs had more bacterial and fungal coverage than needles.

Older ones were more covered between needles than younger ones. Therefore, it is hypothesized that the three main factors influencing ion loss or uptake in the balsam fir canopy are needle age, the extent of micro-epiphyte cover, and the richness of lichen cover [104].

Sparks [106] emphasized the significance of taking into account foliar and soil mechanisms of N incorporation into biota independently in a review on direct foliar uptake of N. With canopy uptake of reactive N ranging from 0 to 50% of plant N demand, the mechanisms of foliar uptake remain unclear and estimates vary widely. Comparing throughfall under real canopies and fake plastic trees, Ignatova and Dambrine [101] calculated that over 4 kg ha-1 of inorganic N were absorbed by the canopies of the various stands in 8.5 months, which accounted for 10–30% of the foliage's annual N requirements. Nevertheless, following two years of N addition to the canopy, less than 5% of the label was recovered in living foliage and wood in a recent labeling experiment using 15N [107]. Twig and branch elements contained most of the label. The authors were unable to determine whether canopy N retention was caused by actual uptake or physico-chemical interactions with plant surfaces for these materials, and they were unable to differentiate between bark and wood [107]. They came to the conclusion that the majority of the nitrogen was short-term maintained on the surfaces, branches, and main stem bark of plants, with little incorporated into woody substance and minimal impact on the sequestration of carbon.

In low productivity sites, like as some spruce and spruce-fir sites, canopy "uptake" can be almost equal to foliar increment, in contrast to more productive sites where it only makes up a small portion of the foliar increment and stand requirement [32]. Nonetheless, internal retranslocation (resorption) and root uptake continue to provide the majority of the tree's nitrogen needs. Furthermore, it seems that spruce-fir canopies with large biomass of epiphytic lichens absorb the most inorganic N. Although forest canopies release organic nitrogen, this release is typically less than the quantity of inorganic nitrogen absorbed, resulting in a generally higher consumption of total nitrogen [32]. Once more, though, it is challenging to distinguish between physico-chemical interactions with canopy surfaces and/or uptake by epiphytes vs uptake by trees. Wintertime typically sees no detectable canopy uptake [108], highlighting the biological origin of this process. In fact, the physiological conditions of the trees and epiphytes during these months—low photosynthesis, slower development, and a lower seasonal demand for nitrogen—may be the cause of this. A significant part of the old-growth canopy, epiphytic lichens and mosses undoubtedly influence the nitrogen flux in the throughfall, with stands with an abundance of epiphytes absorbing more inorganic N [108].

The connection between N depositions and N fixation at the moss level is intriguing to emphasize. According to some research, early in a fire forest succession, N fixation by moss-associated microorganisms typically declines when N deposition rises or when N availability increases [27,109]. The development of a thick carpet of mosses during secondary succession typically begins when the canopy closes and intensifies over time following disturbance. Since the buildup of polyphenols and the decline in the ratio of mineral N to DON in late-successional stands may gradually diminish soil N availability, the N fixed at the level of these mosses may constitute an important potential input of N [19,97]. Despite mosses' capacity to hold moisture, seedlings placed in these feather moss layers establish and grow poorly, most likely as a result of mosses' slow rate of litter decomposition and their potent ability to absorb available nutrients [97]. While N fixation is downregulated, bryophytes may consume some of the N that arrives through depositions, restricting uptake by woody plants [18]. However, certain moss species exhibit decreased biomass and may even go extinct at high N levels.

We advise interested readers to refer to other, more focused research on canopy uptake because of the uncertainty surrounding this process and the fact that our critical evaluation focuses on the significance of soil N for the conifers in the boreal forest.

2.2 Roots and Competition for N

The size, distribution, and structure of the root system are influenced by soil N. When nitrogen is limited, starch builds up in the leaves of Norway spruce and silver birch, and more photosynthates are sent to the roots, enabling the root system to grow in size [42,110]. It is thought that the ratio of N to C in roots and shoots affects the processes related to C fixation or the development of new tissues and establishes how resources are distributed between aboveground and belowground components [110,111]. The timing and duration of root growth are influenced by variables such as soil temperature, moisture content, and nutrient availability, whereas microsite circumstances, development patterns, and growing season duration regulate root longevity [112].

SOM depolymerization and mineralization are two important ways that soil microbes control the availability of nutrients. The other soil microorganisms, with the exception of symbionts (like mycorrhizae), are frequently C-limited, which leads to intense competition for energy sources. This is particularly true when the buildup of recalcitrant organic compounds (high lignin:N ratio, high content of polyphenols, tannins, and lignin) limits the availability of labile C substrates [17,54,113,114,115,116]. Through a priming effect, the rhizosphere's enhanced labile C supply can significantly increase microbial activity [11,38,113]. However, the availability of mineral nutrients like N and P might also limit microbes [62,114].

According to certain isotopic tracer investigations, plants are less effective than microorganisms at absorbing both organic and inorganic nitrogen in the short term (one to a few days), but they gradually accumulate more of the tracer over longer time periods (weeks or months) [61]. Long-term factors include microbial turnover, mycorrhizal and microorganism competition, the longevity of tree tissues with high sink potential, and effective nutrient conservation techniques [117,118].

Competition with other plants has an impact on conifers' nutrition in addition to competition with microorganisms. The considerable benefits of weed suppression on the survival and growth of boreal conifer seedlings, which result in higher foliar concentrations of N and other nutrients, may be explained by less competition [93,119]. There are various methods in which plants might compete. Sheep laurel, for instance, might reduce the nutrition of black spruce by sequestering soil nitrogen through the production of tannin-protein complexes that are difficult for the spruce to reach [80]. The height and biomass of seedlings growing distant from sheep laurel were positively connected with foliar N concentrations in black spruce, according to Yamasaki et al. [79], who suggested that this pattern cannot be explained by decreased mineralization alone. They suggested that there are four ways in which sheep laurel might influence black spruce growth: (4) higher susceptibility to root infections as a result of the diminished mycorrhization; (2) direct allelopathic effects on black spruce; (3) allelopathic impacts on mycorrhizal development or maintenance; and (4) competition for resources. Although the results are still inconclusive, several writers have proposed that polyphenols may impede microbial activity and hence diminish N mineralization [14,19,97].

2.3 Mycorrhizal Associations and N Nutrition

The two mycorrhizal fungal groups that are most common in boreal forests are ECM, which is linked to conifers, and ERM, which is linked to ericaceous shrubs that grow in heathlands and the forest understory. Arbuscular mycorrhizae, which are linked to grasses, are found in more fertile microsites or following disturbances [65,120,121]. Mycorrhizal fungi are thought to be crucial for plant nutrition, particularly in situations where nitrogen is in short supply. There is a relationship between the abundance of various N forms, mycorrhizal connections, and their host species. A number of studies [63,64,65] found that a change from inorganic to organic N forms in soils was correlated with a change in vegetation and productivity along a brief transect in a Fennoscandian boreal forest. In the tall-herb type, NO3- was as prevalent as NH4+ and plants absorbed almost equal amounts of the two mineral ions. Specifically, NH4+ rose in the Norway spruce/short-herb type. Along the gradient of soil N concentration, productivity rose, and changes in the mycorrhizal community were linked to changes in the plant community. For example, the Scots pine/dwarf-shrub type was dominated by ECM and ERM, whereas the tall-herb type was dominated by arbuscular mycorrhizal fungi [63,64]. With high and low ratios linked to bacteria and fungi, respectively, the C:N ratio and pH appear to be reliable indicators of alterations in the composition of microbial communities. In certain Scots pine stands in Sweden, there has also been a negative link found between the C:N ratio and the rates of N mineralization [114,122,123].

ECM is efficient at absorbing NH4+, and low levels of this ion in the soil solution of some boreal forests may be caused in part by mycorrhizal roots' quick uptake [89]. When Norway spruce roots colonized by ECM were removed from a section of soil (using plastic tubes), for instance, Nilsson and Wallander [124] found that the contents of NH4+ and NO3- were higher in the removed section. Soil respiration was decreased by about 50% after a few weeks and microbial biomass by one-third after one to three months in a major tree-girdling experiment with Scots pine that was carried out by chopping off the phloem and cambial tissues surrounding the stem [123,125]. The 45% decline in a fungal biomarker linked to ECM, as shown by phospholipid fatty acid analysis, indicated that the loss of ECM fungus was the primary cause of the decline in microbial biomass. Furthermore, the conifers linked to ECM fungus were effective competitors for nitrogen, as seen by the increased N content and growth of dwarf shrubs following tree-girdling [123]. These results unequivocally show the unique significance of ECM connections in boreal forest soils.

ECM exhibits a decreased ability to absorb nitrogen from the protein-polyphenol combination in comparison to ERM and saprotrophic fungi [14]. According to Schulze et al. [126], ECM of white spruce would consume NH4+, NO3-, and organic N from litter, while ERM of Vaccinium spp. would break down more complicated slowly-decomposing organic matter. This is because differing 15N is a sign of niche separation and access to separate N pools. According to Read et al. [1], proximity—achieved by colonizing large areas of organic horizons that contain significant amounts of N and P, particularly the FH layer—is a useful tactic to obtain these nutrients prior to the development of polyphenol complexes that lower the amount of N available for the trees connected to the extracellular matrix. Microbial biomass and mesofauna may also be a significant source of uncomplexed organic nitrogen in the organic horizons. This is because certain mesofauna, such as worms, can directly prey on them or microbial turnover can release nutrients.

In tubercules growing inside rotting wood, Paul et al. [21] have recently identified the interaction of N-fixing bacteria with the ECM Suillus tomentosus on lodgepole pine, potentially serving as a moisture storage space during dry spells. Additionally, they note that during the dry summers and in young stands, N-fixation was higher (10–15% of the levels seen in alder). Furthermore, in Douglas fir, relationships between mycorrhizae and N-fixing bacteria were noted [25]. It could be worthwhile to investigate if the presence is restricted to the youngest stands or if it is also linked to adult and older trees, considering the significance of these discoveries for the N-limited boreal forests.

Particularly in the late-successional stages of forest formation in places with low N depositions, recent studies have shown that N-fixation by algae that live on mosses can match inputs from atmospheric N depositions [26,27,109]. The extent to which mycorrhizal fungi can mobilize both N and P from living moss tissues is unclear, but they can effectively colonize dead and senescing bryophytes [128,129]. Therefore, more research is necessary to determine how these common mosses and their interactions with mycorrhizal fungi contribute to the boreal forest's extra N supply [26,28,130].

2.4 Key-Concepts of N Uptake

Boreal conifers have developed coping mechanisms to deal with the scarcity of nitrogen. There are still many unknowns surrounding the topic, making it impossible to assess the true significance of these processes, even though canopy N intake may contribute to N nutrition in conifers, particularly in low productive areas. When competing for N resources, the rooting system's plasticity—the ability to explore and quickly colonize fertile patches—becomes crucial, and root proliferation to enhance interception appears to take precedence over diffusion in the soil solution due to the decreased mobility (low diffusion coefficients, see Table 2) of some soil N forms, particularly the heavier organic ones. Trees benefit from ECM because of its large absorbent surface, enhanced soil micropore exploration and colonization of fertile patches, broader enzymatic capabilities than plant roots alone, and better access to a wide range of nutrient sources. While estimates of nitrate uptake are generally lower in boreal conifer seedlings but relatively greater in grasses and broadleaves, conifers typically absorb ammonium at amounts similar to simple organic N, which likely becomes more significant as organic matter accumulates with stand age.

3. N METABOLISM AND USES

Following assimilation, N is moved to organs and tissues where, depending on the needs of the plant, it is either stored or used for various purposes. Both xylem and phloem are involved in the transport of amino acids [42]. In order to support shoot elongation, bud burst, and needle growth, the protein and amino acid reserves in the stem, roots, and older leaves are quickly remobilized in the spring [131,132]. According to certain studies conducted on conifer seedlings, needle development mostly depends on nitrogen from pre-existing shoots, and N retranslocation is independent of the current N supply [131,133,134,135]. Nonetheless, certain species-to-species variances have been noted. For instance, Sorbus aucuparia remobilized half of the stored nitrogen before more nitrogen was absorbed by roots, whereas Scots pine and silver birch maintained their first stages of leaf growth simultaneously through root uptake and remobilization. The significance of internal nutrient reserves was once again demonstrated by the higher height and biomass growth of black spruce seedlings that received a high nutritional treatment prior to plantation [136]. According to estimates, between 30 and 60 percent of the nitrogen in the new leaves of some adult conifers may come via internal cycling [133].

Photosynthetic capacity and N concentration in leaves are strongly positively correlated; the latter varies with P availability and across biomes, with the arctic and boreal ecosystems having the highest slope and lowest intercept at the lowest N:P ratio [137]. In addition to increasing photosynthetic capability, N fertilization promotes the growth of leaves [138]. Although the findings were not verified for heart-leaf paper birch, Evans et al. [139] noted that balsam fir stored nitrogen in the foliar tissues by increasing the N supply, even if this did not result in greater growth. Three-year N additions raised the foliar concentrations of N, Ca, Mg, and Mn in a mature black spruce site without influencing growth [77]. In response to nutrient stress, slow-growing species may use luxury consumption (and storage) during times when resources are more readily available (such as at the start of the growing season) to maintain appropriate internal concentrations of N and other nutrients [140,141]. In fact, black spruce growth was less inhibited by low N conditions than white spruce, but even though growth was comparable, the absorption rate was higher under high N conditions [141]. Black spruce was thought to have better adapted to limited nutrient availability as a result.

Reich et al. [142] found that broadleaf species had high rates of N uptake, but conifers had low rates in a greenhouse experiment with boreal tree species. The rates of N intake in the examined species interacted with light availability and were correlated with relative growth rates. The impact of higher soil fertility was less noticeable in low light [143]. Since N is involved in cell lignification [147], promotes photosynthesis [148], and influences growth rate (in height and diameter, for example [149,150]), it is also expected to have an impact on the characteristics of wood [144,145,146]. In fact, radial growth increases following N-fertilization are reported in numerous research [144,151]. Wood structure is also impacted by fertilization. Increased earlywood proportions in Norway spruce frequently lead to increases in ring width because earlywood typically has a lower density than latewood, which lowers wood density [144].

3.1 Key-Concepts of N Metabolism and Uses

Before being utilized in plant metabolism, nitrogen that is absorbed from the soil is often converted into organic nitrogen molecules, primarily amino acids. After assimilation, N is either kept as a reserve or delivered to the growing organs to support growth. Increases in N availability lead to higher net photosynthesis and the creation of more leaves since N is a crucial component of photosynthetic proteins and enzymes. Relative growth and N intake are positively correlated, and biomass production is increased by N fertilization. Growth is somewhat independent of the current N supply in the soil, especially at the start of the growing season, because boreal conifers, especially the slow-growing species, appear to rely heavily on the stored N and its internal cycle.

4. Natural and anthropogenic elements influencing the N-cycle

4.1 N-Depositions and Boreal Forests: a Brief Account

Over the past 200 years, anthropogenic N depositions have significantly changed the N-cycle and plant nutrition [6,152,153]. This extra input is caused by nitrogen pollution from burning fossil fuels, which typically results in pH changes in precipitation, higher S depositions, and, over time, may alter the amount and makeup of the soil's N pool and other nutrients (e.g., increased loss of base cations, due to the acidification of the soil by acid rain). Increased forest growth and carbon sequestration in the 20th century are most likely the result of N addition through wet and dry depositions in temperate and boreal forests, which are thought to be N-limited ecosystems [153,154,155]. Magnani et al. [155] demonstrated that the extra N intake brought on by human activity was the primary cause of the rise in C sequestration over the past century. A recent study of the topic verified that N-deposition stimulates forest development [75], even though the estimations put forth by Magnani et al. [155] are among the highest. In response to a fertilizing effect of N deposition of 1 kg of N ha-1 year-1, De Vries et al. [75] observed favorable forest growth under modest to moderate N additions, with increases in site productivity for Norway spruce and Scots pine ranging from 1 to 4%.

According to certain theories, tree growth in regions with significant N depositions may change from N limitation to other nutrient limitation, such as base cations (Ca, Mg, K) or P

[56,156,157,158]. At N-rich sites (soil C:N ratio ≤ 25), the addition of NPK fertilizers improved the response of C-sequestration to N alone, potentially indicating a limitation of P and K for tree growth [75]. Only stands that got significant N fertilizations responded to fertilization with P or base cations or trace levels of boron, according to a survey by Binkley and Hogberg [56] on how Swedish forests responded to increasing N depositions. Growth increased by roughly 30% during the 1950s and 1990s. However, Houle and Moore [77] discovered no reaction to N-additions in a site in eastern Canada that was dominated by black spruce and balsam fir. The site had low N depositions (5.7 kg ha-1 yr-1), but the control trees already had high foliar N concentrations (1.5% of dry weight). They suggested that this might be the result of a limitation by other nutrients or, on the other hand, a high retention by other ecosystem components (such as soil immobilization). Strong N sinks may exist in these arctic coniferous forests, as evidenced by the fact that no discernible changes in soil N or tree growth were seen in a balsam fir and a black spruce stand following three years of simulated increased N-depositions [85,105].

Norway spruce stem growth rose by 84 and 25% in heated and heated plus fertilized plots, respectively, in a heating and fertilization combination experiment [159]. Lower N depositions or fertilizer treatments were consistently more effective in promoting growth than higher ones in a variety of tests [73,153]. For trees and soil, the corresponding C buildup in response to N addition was 25 kg C/kg N and 11 kg C/kg N, respectively. NPK fertilization increased tree C accumulation to 38 kg C/kg N, indicating that P and K co-limitation occurs in these locations. Higher N-depositions in the southern Norway spruce stands were thought to be the cause of an increase of 2.0 kg m-2 in tree and 1.3 kg m-2 in soil organic carbon, respectively, when comparing the sites from northern and southern Sweden [73]. Long-term N-addition increased carbon storage in a 40-year-old Norway spruce stand by a factor of 10 (3.0 Mg C ha-1 yr-1) in comparison to the impact on the humus layer (0.3 Mg C ha-1 yr-1). No increase in soil heterotrophic activity was seen even with increased production and litterfall, indicating that N may have a detrimental influence on SOM decomposition [160]. According to certain research, moderate or high N additions (>5–10 kg N ha-1 yr–1) actually prevent low-quality litter from degrading by suppressing the lignolytic enzymes of decomposing fungi [38,161].

With N depositions, mycorrhizal fungal populations often decline [162,163]. This could result from direct modifications to the soil or from the distribution of trees aboveground and belowground. Fertilized plots in a Norway spruce stand showed a 191% increase in fine root mortality [164]. The diversity of fungal species was the subject of conflicting findings in other N-fertilization investigations [165,166,167]. For instance, Rossi et al. [167] observed that their high N treatment (+30 kg N ha-1 yr-1, or ten times the current N deposition) increased the number of morpho-types, viable root tips, and root tips exhibiting ectomycorrhizae. Following eight years of ammonium nitrate addition in a natural black spruce stand of the Canadian boreal forest, to the control (no N added). The observed disparate outcomes may be due to the various host species and their fungal partners, the amount of N added (high N loads may be harmful), the type of N added (for example, organic N may increase extracellular matrix; [165]), the makeup of the microbial community, and the reaction of the plants to N addition (for example, enhanced C fixation and photosynthetic availability for the fungal partner would result from positive N fertilization effects on tree growth in N poor sites [167,168]. Furthermore, some mycorrhizal species may be well suited to soils with high rates of nitrogen mineralization, and it is possible that different fungal species have different ideal N concentrations [162,166,167].

4.2 Forest Harvesting, Fire and Climate Change: the Impact of Different Anthropic and Natural Disturbances on the N Cycle

The N cycle is impacted by disturbances, albeit the consequences might vary depending on the kind and intensity of the disturbance. Studies have looked into the effects of wildfires, which are likely the most frequent natural and anthropogenic disturbances in boreal forests, and forest management practices including clearcutting and variable-retention harvesting. A recent meta-analysis found that following clearcut, there were no changes in the concentration of inorganic nitrogen in the soil, ammonification, or N mineralization rates, but there were increases in soil nitrogen concentrations as nitrate, N concentration in leachates, nitrification rates, and pH [68]. Compared to deciduous stands, the effects of clearcutting were delayed in coniferous stands, but they remained for a number of years. In some experiments, when about the same number of trees were removed, gap creation—the removal of a group of trees—produced greater changes in nitrates than single-tree selection [68,169].

Found that the type of forest floor or soil had a bigger impact on nitrate concentrations than variations in the gaps' environmental circumstances, and that the rates of litter and forest floor decomposition in gaps of all sizes were comparable to or slower than those of uncut forests. [170] found that young wildfire-burned stands had substantially less soil organic N, while mature and young clearcut stands had comparable levels of soil N. Additionally, they found that the most noticeable distinction between the disturbance types was for net nitrification. They came to the conclusion that, because nitrate and ammonium have different mobility, the differences between clearcutting and wildfres can have significant effects on plant nutrition and leaching losses after disturbance. [171] came to the conclusion that fire had no discernible impact on the amount or concentration of soil N in any of the studies they "screened" for their meta-analysis. They also came to the conclusion that only the top few millimeters of the soil are primarily affected by fire.

Increases in mineral N production and concentration following disturbances are typically brief (ranging from a few months to a few years) and fast [67,170,171]. Increases in N availability are frequently followed by a fall after an initial "spike" after fire [67]. [70], examining chronosequences from 4 to 60 years following stand-destroying fire, found that the concentration of amino acids increased and that the mineral N trended parabolically with stand age, declining after a high concentration and then rising again. Similar to this, N mineralization rates in jack pine forests dropped to low levels 14 years after fire and then rose again for 70 years, possibly as a result of growing soil organic matter reserves [172]. Other research, however, indicated that net N mineralization rates might decrease as stands age [19,71]. The direction (increase or decrease) of N availability late in secondary succession may be influenced by climate, according to Vitousek et al. [71], who claimed that there is not enough data to determine which pattern is more prevalent.

Through direct effects on N mineralization through temperature and precipitation changes (e.g., soil moisture), indirect effects on species growth and composition, and effects on natural disturbance regimes, climate change may potentially have an impact on N cycles. Smithwick et al. [173] used model simulations to show that, in comparison to the current environment, future temperature scenarios would result in higher forest productivity and net N mineralization. Increases in N mineralization with rising soil temperatures were also noted by other syntheses and meta-analyses [55,174]. When fire return intervals and densities changed, soil organic matter C and N remained stable. For instance, [173] determined that fire return intervals would need to drastically decrease to affect long-term N and C storage at Yellowstone (USA) due to low aboveground N losses via combustion, the large soil N pool, and relatively quick recovery after fire. This was based on historical fire return intervals between 100 and 300 years and the fact that the N stocks were recovered less than 100 years after disturbance. Similarly, it was shown that 14 years following a forest fire was adequate to recover the pre-fire level of total N in soils in the sub-boreal spruce zone in the central interior British Columbia, Canada [175]. However, our ability to foresee is limited by intricate feedbacks and a lack of knowledge of several mechanisms and processes.

Chen et al. [176] proposed that Canada's boreal forests might see a 30% rise in Net Primary Production (NPP) as a result of climate change. It is unlikely that all boreal forests will show increased growth as a result of global change, according to a study that modeled the reaction of forest C dynamics in the boreal forest [177]. Depending on how the plant growth, decomposition, and disturbance regimes respond, the boreal forest may either become a source or a sink of carbon. In Canada, the area burned by wildfires each year will double, according to [178]. However, it is difficult and outside the purview of our review to fully examine how climate change affects the N cycle. At the forefront of current study is the integration of C-N feedbacks, while also accounting for natural and anthropogenic disturbance regimes, in models that forecast global change. As such, scientific endeavors in this area are encouraged.

5. LIMITATIONS AND KEY-FINDINGS OF PAST STUDIES

5.1 Different N Forms and Plant Nutrition

There is evidence that NO3- levels are frequently very low in boreal soils (with the exception of more fertile soils, certain topographical conditions, and the first years after disturbance), whereas NH4+ and organic N typically make up the majority of the N pool. This is the case late in the secondary succession, when the ratio of organic to inorganic N increases, when organic matter accumulates, or along a decreasing gradient of site productivity [2,66,97]. As a result, NO3- was not regarded as the primary supply of nitrogen for the conifers that make up most of the boreal forest. Nevertheless, their size may not be as significant as the flux rate through the various N pools [76]. Furthermore, NO3- is typically well represented in tests using lysimeters, which show concentrations in the soil solution (sometimes thought to be more readily available for plants) as opposed to the total amount of nitrogen contained in the soil (soil extractions) [36]. Since we are yet unsure of which metric best captures the amount of N accessible for plant growth, these conclusions about the various types of soil N must be interpreted cautiously. Experiments using hydroponics are unable to measure the true availability and plant preference for the various forms of nitrogen because they do not account for the movement of these forms in the soil. However, several studies conducted on conifers have demonstrated that NO3- uptake is slower than that of NH4+ and amino acids, which limits NO3-'s significance as a major source of nitrogen for conifer nutrition [58, 100]. Rather, NO3- most likely serves as a signal to encourage the growth of roots in the direction of fertile soil patches [57].

5.2 Mycorrhizal Fungi and N Nutrition

ECM fungus improve conifer nutrition in a number of ways. Their capacity to exploit organic materials is among the most significant and contentious topics. N. According to Jones et al. [76], DON is plentiful in boreal soils because it is less available for microbial and plant feeding, which causes it to accumulate. Furthermore, why should N-limitation continue if the trees connected to ECM might utilize this N source? The price that mycorrhizal associations demand for the usage of organic N may hold the key [179]. Exoenzymes must be released by mycorrhizal fungi and plants in order to break down organic matter and absorb low molecular weight organic molecules [180]. Inhibiting organic N breakdown may result in a negative return on investment because N is necessary for the production of enzymes [179]. This could be the reason for reduced production compared to soils with higher levels of inorganic N [63,64]. The breakdown of organic materials by ECM exoenzymes may be hindered by polyphenols and other resistant compounds [14]. The degree to which polyphenols directly lower absorption by ECM trees is still unknown, though [19,79]. Polyphenols may suppress extracellular matrix (ECM) when in solution, but not when precipitated with proteins, according to Bending and Read [14].

It should be emphasized that early research was frequently carried out in vitro and in greenhouses, occasionally with the aid of agar cultures or hydroponics [14,61]. Even while a significant variability in functional characteristics among ectomycorrhizal species has been noted, the role of ectomycorrhizae is essentially general, with little capacity to regulate the assembly of fungal species on a root system [181]. This is another possible problem with controlled experiments. Furthermore, it is challenging to accurately assess how these findings may be extrapolated to adult or mature trees with a vast network of ECM roots and significant internal nutrition storage because most field tests employ seedlings. The issue of extrapolating findings from research on seedlings to older plants is highlighted by the fact that root exudates, or chemicals secreted in the rooting zone, differ depending on the species and age of the plant [49]. Furthermore, the competition with other microbial communities and the surrounding vegetation (such as ericaceous species) in a natural forest complicates the interpretation of the data. The existence of microorganisms (such mycorrhizae) that can cycle them through their metabolism also affects the chemical makeup of root exudates [49]. Short-term studies can underestimate N acquisition by trees because, as noted by Nasholm and Persson [118], one of the main challenges in researching the competition between plants and soil microorganisms is differentiating between the various microorganisms in the field (e.g., mycorrhizae vs. other microorganisms). But lately, it has been profitable to differentiate between the various microbial groups by analyzing phospholipid fatty acids (with biomarkers for ECM, saprotrophic, and bacterial populations) [123].

Numerous studies examining the significance of various kinds of nitrogen in the field have frequently introduced nitrogen at irrational rates, making it difficult to assess how well nutrition works in natural settings and instead replicating a saturated state [61,85,105]. High amounts of some amino acids have been shown in some trials to inhibit growth, particularly for those that are typically found in plants at low endogenous concentrations [61]. Since different amino acids absorb different amounts of organic nitrogen, the extensive use of glycine in many research has been criticized because it can be scarce in boreal soils (making approximately just 3% of the total concentration of free amino acids), whereas alanine or

Potential replacements include glutamine [69, 100]. Lastly, as research mostly concentrate on uptake, it is unknown how much organic N is absorbed in relation to the overall amount of N in the plant [61,76]. It should be highlighted that, in contrast to arbuscular mycorrhizal fungi associated with grasses, ECM always exhibit larger capacity to use organic N [179]. Jones et al. [76] report that the contribution of organic N may be limited in some grass species.

There are still some questions about how ECM and their hosts regulate nutrient transfers and exchanges [179]. The impact of exudation and C transfer to the mycorrhizae is not taken into consideration in the research involving removed roots. These activities could influence N uptake and transfer and could be important components in defining N dynamics in the soil [123]. Mycorrhizal plants are depleted in δ15N in both lab and field studies, whereas mycorrhizal fungi are enriched in relation to the supplied N sources or soil N [182]. This suggests that the fungi "selectively filter" (i.e., metabolize) the N that mycorrhizae take up before transferring it to the host tree. Furthermore, mycorrhizal fungi may store nitrogen and briefly prevent the partner from accessing it due to a potential delay in mycorrhizal uptake and transfer to the host [183].

The uptake and metabolism of these molecules may be better understood in future research using dual labeled amino acids (i.e., with both C and N isotopes) and labeled inorganic N [61]. It should be feasible to investigate absorption and assimilation at more realistic concentrations and describe how the partitioning of N changes over time in accordance with plant requirements by employing trace amounts of highly enriched tracers in long-term research. Lastly, it will be crucial to more accurately measure the proportion of total plant N that is represented by the tagged N compounds absorbed.

5.3 N Uses in Conifers

According to certain research, NH4+ absorption and assimilation use less energy than NO3- [76]. Nevertheless, NO3- is delivered without NH4+'s toxicity issues. Therefore, NH4+ must be absorbed by organic substances before it can be delivered to the organs that require nitrogen, and its translocation is slower than that of NO3- when combined with amino acids [100]. Given that conifers may be less dependent on the soil's present N supply for the development of new tissues in the spring, this could help to explain the significance of their internal N storage [131]. Furthermore, a lot of boreal conifers, particularly some slow-growing species, exhibit luxury N consumption and may use the stored N to continue growing or surviving when the availability of N is decreased [140]. In poor soils where N is not easily accessible, this could be considered a nutrient conservation tactic. Numerous characteristics of conifers, such as their extended leaf lifespan, low tissue N, and high phenol and other defensive chemical concentrations, are also thought to be adaptations to nutrient-poor environments and techniques for preserving nutrients [184,185,186].

According to Reich et al. [186], a "syndrome" of slow-growing species has been created by a series of associated leaf features brought about by adaptation to the nutrient-poor surroundings typical of conifer species in their native habitats. Given that these characteristics also contribute to conifers' lower response to environmental changes than deciduous species [184], this could have an impact on competition and forest succession. Lower photosynthesis may be one of the trade-offs of extended leaf lifespan, most likely as a result of Rubisco's N storage and diffusional restrictions [187,188]. While fast-growing species typically have greater rates of nitrogen intake that are unsustainable due to their higher photosynthetic rates, slow-growing species may be better suited to the circumstances typical of late successions.

where the availability of nutrients is restricted [142]. Conversely, slow-growing species might be less competitive and so rejected in environments where resources are not limited.

Wood characteristics may be impacted by changes in photosynthesis and growth after N additions, as N is also involved in the formation of lignin [144,146]. Even if there is a positive correlation between productivity and mineralization on a larger scale, it is unclear how stand-level variations in N supply affect differences across tree groups under otherwise similar environmental conditions [146]. According to a recent study by Coates et al. [189], the significance of soil fertility in sub-boreal forests on the radial growth of various tree species varied depending on the local neighborhood composition, species-specific competition, and context.

5.4 Disturbances, N-Depositions and Stand Development: Implications for N Cycling

Fertilization Boreal soils are powerful N sinks, as evidenced by fertilization studies that show the soil retains most of the N rather than vegetation. The history of previous depositions and disturbances (such as fire frequency and intensity), soil chemistry (such as the C:N ratio), and physical characteristics (such as texture) all affect a soil's ability to retain nitrogen [4]. NH_4^+ retention may be increased by the buildup of organic matter, which has a high exchange capacity at low pH. NO_3-leaching has been noted after N-depositions, particularly in systems that are getting close to saturation (which is uncommon in boreal forests at the moment) or in the winter, when N uptake is lower [31,190,191]. The low frequency of applications is one of the issues with many N-addition experiments, in addition to the excessive amount added. The structure and competitiveness of the microbial community can be changed by these artificially high and punctual additions because gradual alterations and lower deposition levels are more prevalent in nature [123,125]. However, the results of these tests should be interpreted and used in light of the fact that they represent a realistic approximation of the condition after disruptions (particularly in more polluted locations). N additions typically promote aboveground growth rather than belowground growth, suggesting that trees devote less energy to soil exploration and N uptake when N availability is high [110,111]. Using highly enriched isotopic tracers and considering the distinct impacts of the various types of N in plant nutrition, future work should focus on decreasing the amounts and increasing the frequency of N-additions.

N-limitation is pervasive in the boreal forest, as demonstrated by the obvious reactions to N fertilization [73, 75]. After a fire, the N cycle may shift in favor of species that develop quickly, temporarily relieving N-limitation. However, it makes sense to assume that regular fires, which result in ongoing N losses, could lower N availability. Furthermore, it appears that harvesting and wildfires had distinct effects on the N cycle. For instance, DON exports were larger in harvested regions than in burnt areas, where inorganic and organic N exports were equally significant, even though harvesting and wildfires increased initial N losses [37]. Forest growth may be impacted by additional disturbances, such as insect outbreaks, which can further increase N losses and change the N cycle (e.g., nitrification) [36]. Particularly in stands that are regularly exposed to high N depositions, harvesting, particularly of entire trees, removes significant amounts of specific nutrients, such as Ca, Mg, and P, from the environment, moving the growth constraint from N towards other elements [37,157,158,192,193]. It should be emphasized that co-limitation is most likely limited to a few locations where harvesting and acidic depositions have been severe for an extended length of time [56,158].

Trees gradually devote more resources to N scavenging and favor the belowground allocation towards mycorrhizae, which are especially adapted for this function [1,19]. This occurs during stand development following a major disturbance, when the forest becomes denser, competition for N increases, and the availability of mobile forms (NO_3^-) decreases [67,194]. As evidenced by weed control and trials that excluded the roots of competing plants, which increased the nutrition of conifer seedlings, N-limitation can also be linked to competition with ericaceous species and soil microbes [81,82]. The predominance of poor-quality litter, low pH, specific microbial populations, and low temperatures on the forest floors when the canopy closes and organic matter insulation increases could all contribute to the decreased decomposition at high latitudes [19,28,52]. The availability of mineral N in mature stands may be impacted by the buildup of organic matter, higher percentages of resistant chemicals, and increased soil acidity.

6. CONCLUDING REMARKS AND RESEARCH DIRECTIONS

Boreal soils are powerful N sinks, as evidenced by fertilization studies that show the soil retains most of the N rather than vegetation. The history of previous depositions and disturbances (such as fire frequency and intensity), soil chemistry (such as the C:N ratio), and physical characteristics (such as texture) all affect a soil's ability to retain nitrogen [4]. NH_4^+ retention may be increased by the buildup of organic matter, which has a high exchange capacity at low pH. NO_3-leaching has been noted after N-depositions, particularly in systems that are getting close to saturation (which is uncommon in boreal forests at the moment) or in the winter, when N uptake is lower [31,190,191]. The low frequency of applications is one of the issues with many N-addition experiments, in addition to the excessive amount added. The structure and competitiveness of the microbial community can be changed by these artificially high and punctual additions because gradual alterations and lower

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COMPETING INTEREST

No competing interests exist.

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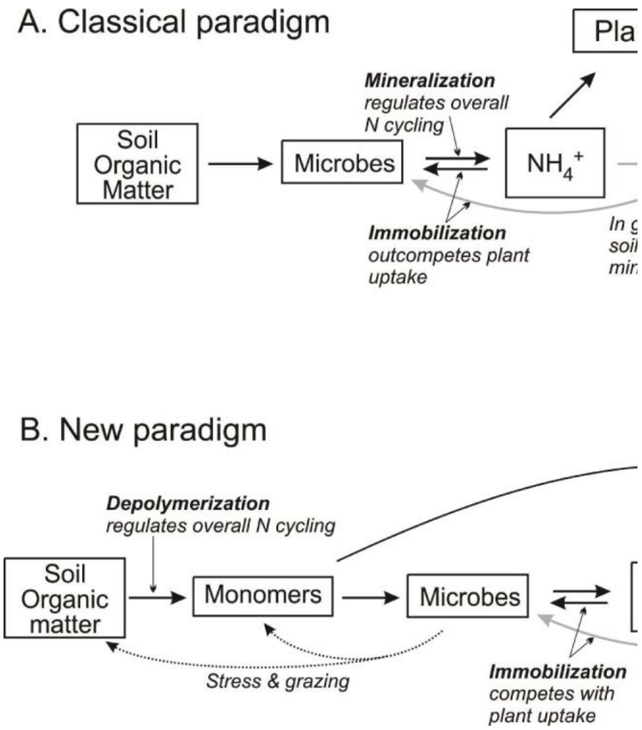

Fig. 1. The changing paradigm of the soil N cycle. (A) The dominant paradigm of N cycling up through the middle 1990s. (B) The paradigm as it developed in the late 1990s (from [57])

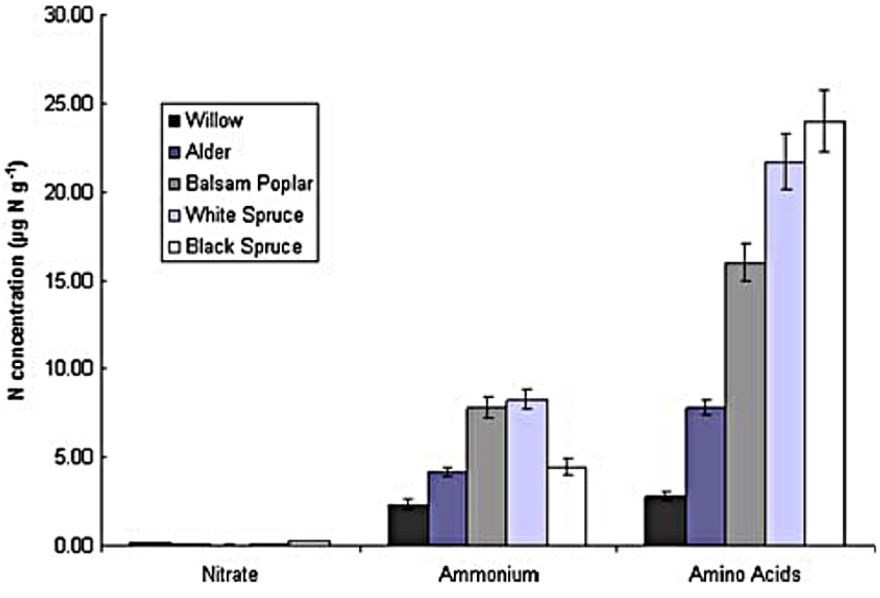

Fig. 2. Concentrations of soil nitrate, ammonium and free amino acids across a primary successional sequence on the Tanana River, interior Alaska. Values are seasonal average concentrations from monthly measurements in June-October. Mean **±SE, n=3 (from [2])**