

Anthropogenic impact on nitrogen transformation in spruce forests of central European mountains – a review

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Abstract

The review deals with nitrogen transformations in soils of mountain spruce forests of central Europe and how they are affected by anthropogenic acidification and forest management. Special attention is paid to the nitrogen cycle processes in acidified and nitrogen-saturated Norway spruce forests in the Bohemian Forest, Czech Republic. In the first part of the review a general concept of N transformation and N saturation and the importance of the carbon-to-nitrogen (C:N) ratio in N immobilisation and mineralisation are explained and the role of microbial community composition is discussed. Next, the most important anthropogenic impacts – acid deposition and forest management practices – are related to the general concept of N transformation. Finally, the findings of soil N transformation in the spruce forests of the Šumava National Park are shortly summarised and management suggested.

Key words: N transformations, N immobilisation, N mineralisation, N saturation, acid deposition, spruce forest, acidification, forest management, Bohemian Forest

INTRODUCTION

In central Europe, it is almost impossible to find forest ecosystems untouched by people (i.e., natural forests) where their unique plant and animal communities are preserved. People have influenced forest ecosystems since historical times. Firstly, they have done it on a small scale with less severe impacts (local burning for cultivation, logging, etc.), later on a larger scale with bigger and very often long-lasting consequences (intensive forest industry, atmospheric pollution and fertilisation). Since the last century, human activities have more than doubled the input of reactive nitrogen (N) and sulphur (S) into the ecosystems. The depositions of N and S have been continuously increasing in Europe over more than a century and affected mainly mountain forest ecosystems near densely populated areas (HÖGBERG et al. 2014). During the last decades, changing climate is another factor which has shaped the forests' development (PUHE & ULRICH 2001).

Forest management for timber production was of the main concern in the past. Currently, due to the growing knowledge and increasing human impact, this paradigm has shifted more towards near-natural forest management accommodating ecosystem sustainability (DORREN et al. 2004) and biodiversity conservation fundamentals (KRÄUCHI et al. 2000). This approach emphasises the importance of ecological processes and their understanding becomes more and more critical. The application of a near-natural ecosystem management and sustainability approach is of special importance in mountain forests, which are highly suscep-

tible to natural and anthropogenic disturbances, including acid deposition, rapid loss of habitats and genetic diversity, soil (erosion, landslides, and deterioration) and forest degradation (pest attacks, windstorms, and fires) due to the prevailing severe climate and shallow and nutrient-poor soils (BINKLEY & FISHER 2012).

Management of mountain forest ecosystems and their protection is associated with many uncertainties, from which environmental variability is of main importance. This importance is highlighted by the fact that these ecosystems have been exposed to acid deposition with subsequent soil acidification and to ongoing climate change, and their functioning has been significantly affected. Soil pH and soil base cation pool have been lowered, rock weathering rate and aluminium mobility (toxic Al^{3+} form) increased, and soil conditions including abundance and species richness of soil organisms altered from plant to microbial levels (ILLMER et al. 1995, PENNENEN et al. 1998, NORTON & VESELY 2003, EMMET 2007). Last but not least, acid pollution and long-term N loading have changed nutrient stoichiometry, as well as their availability (VERESOGLOU et al. 2014). This is connected with the shift in key processes of soil N transformations, which is not fully understood yet. N loading together with the alteration of N transformation processes increase N availability and trigger N mineralisation connected with the prevalence of mineral N and elevated leaching of nitrate (NO_3^-) and nutrients from soils (ABER et al. 1989, 1998, LOVETT & GOODALE 2011, KOPÁČEK et al. 2013a).

The most extensive forests in central Europe are in the mountain range of the Bohemian Forest (Czech Republic and Germany). Two national parks (the Šumava National Park and the Bavarian Forest National Park) have been established there to protect, observe, and study these unique ecosystems. The spruce (*Picea abies*) forests in the national parks have been shaped by long history of human use and have been strongly acidified by deposition of S and N compounds since the 1950s (KOPÁČEK et al. 2001). In addition, they have been weakened by the effects of unsuitable forest management, which shifted forests to even-aged plantations in several parts of the mountain range, and by climate change (SVOBODA & POUŠKA 2008, HEURICH & ENGLMAIER 2010, BARDGETT et al. 2013).

This review is focused on N transformations in forest soils with respect to anthropogenic impacts. In the first part of the review a general concept of N transformation and N saturation is explained. The most important anthropogenic impacts on mountain spruce forests – acid deposition and forest management practices – are being related to these concepts. The importance of the C:N ratio in N immobilisation and mineralisation and the role of microbial community composition is discussed. Finally, the findings of soil N transformation in the spruce forests of the Šumava NP are shortly summarised.

NITROGEN TRANSFORMATIONS IN FOREST SOILS

Processes involved in N transformations

Most of N in terrestrial ecosystems is found in the soil. Soil, as an interface of the bio-, hydro-, and atmospheres, can contain all forms of N (organic, inorganic, reduced, oxidised, or N_2 in the soil atmosphere). Some forms are in insoluble organic and inorganic material or bound to soil organo-mineral complexes (ammonium NH_4^+ , polar organics), while the others (nitrates NO_3^- , soluble organics) remain mainly in the soil solution and are subject to leaching (SPRENT 1987, BRADY & WEIL 2002). N cycle in soil is very complex (Fig. 1) and it is closely connected to C and the cycles of other nutrients through organic matter decomposition (CHAPIN et al. 2002). It is intimately connected with the activity of soil biota that are responsible for all steps of N transformations. N cycling can be divided into decomposition (ammonification), immobilisation (microbial immobilisation and assimilation, abiotic immobilisation), and oxidation-reduction processes connected with energy metabolism of soil

microorganisms (denitrification, nitrification, dissimilative nitrate reduction to ammonia (DNRA), and anaerobic ammonium oxidation, Anammox; (BOTHE et al. 2007). The vast majority of the reactions is mediated by prokaryotic organisms in soil (such as bacteria or archaea) and can occur simultaneously (SCHIMMEL 2001).

Ammonification (in some cases also called N mineralisation; in this review N mineralisation always denotes sum of ammonification and nitrification) is biochemical decay of organic compounds to NH_4^+ . Ammonium originates either from the activity of extracellular N-acquisition enzymes produced by microbes and after that it can be assimilated into microbial cells (mineralisation-immobilisation route – MIT; GEISSELER et al. 2010) or it is released directly from microbial cells (direct route; GEISSELER et al. 2010) which consume simple organic N-rich compounds (e.g., amino acids) and surplus N release as NH_4^+ to the soil (BARRACLOUGH & PURI 1995). The relative importance of each ammonification route is not static but changes as a result of forms of organic N and C and of the organic matter C:N ratio. These factors are, in turn, affected by the environmental conditions of the site (temperature, soil aeration and moisture). Owing to soil heterogeneity (microsites with different availability of substrates and energy, as further described in the chapter “General concept of the N

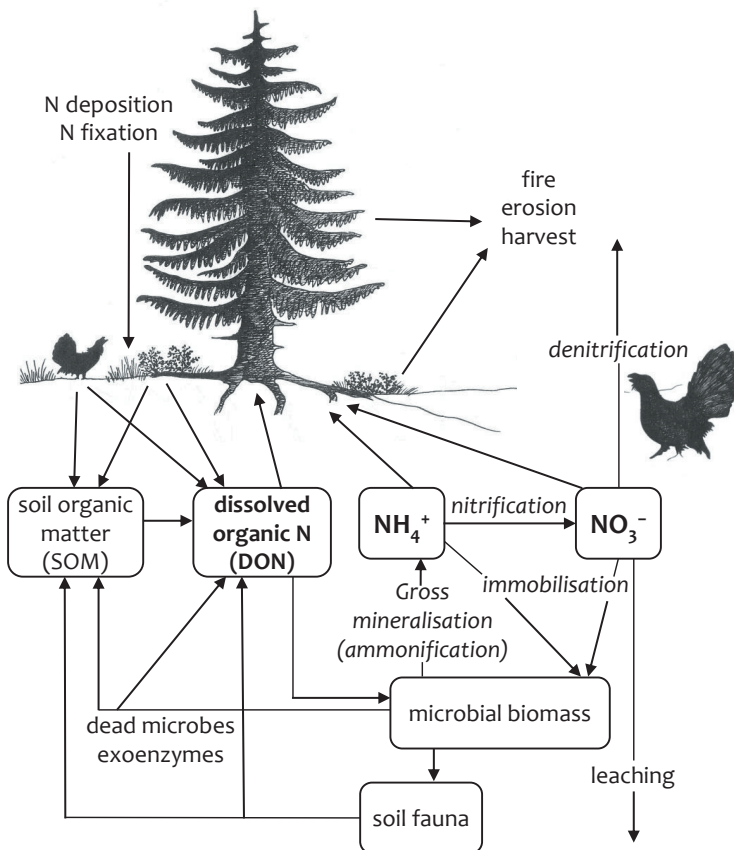


Fig. 1. Scheme of N cycling in the forest soil (adapted from CHAPIN et al. 2002).

cycle in soil”) both routes can occur at the same time and relatively at the same place (GEISELER et al. 2010).

Processes connected with N immobilisation and assimilation are N_2 fixation and assimilatory N reduction (microbial immobilisation). Nitrogen fixation is the only natural process to convert atmospheric N_2 to NH_4^+ as well as into organic compounds. It is carried out solely by prokaryota (heterotrophic bacteria – diazotrophs and cyanobacteria). Diazotrophs are restricted to areas with high C availability or often develop in close symbiosis with vascular plants as N_2 fixation is an energy-demanding process (BOTHE et al. 2007). Microbial N immobilisation to biomass is the most important process of N retention in the soil. Microbes have short generation time and they build consumed N into relatively available compounds of their biomass. After microbial death, N is gradually released back to the soil within a few months providing a supply of N for developing plants. Microbial N pool is generally one to two orders of magnitude higher than mineral N pool.

Nitrification is mainly an autotrophic process of ammonia oxidation in two consecutive steps (ammonia oxidation to nitrite and nitrite oxidation to nitrate) taking place in aerobic conditions. It brings soil acidification as 4 H^+ are released into the soil solution. Produced nitrates are easily consumable but they might be subject to fast leaching in humid areas, especially after heavy rain, as they remain free in the soil solution. In the last decades, it has been shown that besides autotrophic nitrification, heterotrophic nitrification can be important in conditions of high C availability (LEVY-BOOTH et al. 2014). The relative contribution of heterotrophic activity to total nitrification generally ranges widely in forest soils from very low to almost 100% (BARRACLOUGH & PURI 1995, PEDERSEN et al. 1999, ZHANG et al. 2014). Nitrification can be linked to denitrification, which is, together with DNRA, an anaerobic process of nitrate reduction. During these processes nitrates serve as electron acceptors in conditions of oxygen deficiency. Final products of denitrification are N_2O and N_2 , while DNRA releases NH_4^+ to the soil. Nitrogen can be returned to the atmosphere also by Anammox, in which ammonium and nitrite are converted to N_2 in anaerobic conditions. Both inorganic forms of N (NO_3^- , NH_4^+) derived from N-mineralisation processes (ammonification and nitrification) may once again be incorporated into soil organic matter by microbial and plant immobilisation. Microorganisms immobilise NH_4^+ by two primary pathways depending on the NH_4^+ concentration (dehydrogenase pathway and glutamine synthetase–glutamate synthase pathway) and incorporate it into glutamate. Once glutamate is formed, it can be transferred to other carbon (C) skeletons by transaminase reactions to form other amino acids (SYLVIA et al. 2005). Prior to nitrate is incorporated to glutamate, it must be reduced to NH_4^+ .

All of the processes and agents involved in N transformations are complex and interconnected. Low concentrations or even absence of one form of N may be a result of (i) the low rate of its production, (ii) the high rate of its immobilisation, and/or (iii) the high rate of its transformation from one form to another. For example, part of the NH_4^+ produced in the soil is immobilised into microbial biomass, part is oxidised to NO_3^- via nitrification, and, at the same time, new NH_4^+ originates via ammonification. Surplus NH_4^+ in soil can thus be either a result of the high N ammonification rate, low immobilisation rate (microbial N immobilisation or abiotic N immobilisation to soil solid phase), absence of nitrification and/or high DNRA rate. Surplus NO_3^- in soil can be either a result of the high nitrification rate and/or absence of NO_3^- reductions (microbial immobilisation, denitrification or DNRA).

Natural unpolluted spruce forests represent typical N-depleted (N-limited) ecosystems with slow-growing trees and understory vegetation with low nutrient demands (TAMM 1991). A large part of N sources in such forest soils is represented by insoluble complex organic N forms with slow turnover, thus being a large potential N pool for plants and other organisms

(NÅSHOLM et al. 1998, JONES & KIELLAND 2002, MYROLD 2005). Only a small percent of the soil N pool is bound in the soluble organic or inorganic forms with fast turnover and most of the N is difficult to utilise due to its complex composition. Microbial N pools become the most important source of N in the N-limited spruce forest soils. Unfortunately, many central European forests have been exposed to the long-term N deposition, thus, N is no more a limiting nutrient and available N pools have significantly increased there (AGREN & BOSATTA 1988, KOPÁČEK & POSCH 2011). The consequences of N loading are discussed in the chapter "The effects of acid deposition".

General concept of the N cycle in soil

Change in the traditional N-mineralisation paradigm

A new general concept of N cycling in soil was introduced by SCHIMEL & BENNETT (2004) and it is, nowadays, widely accepted. It highlights the process of depolymerisation, not solely ammonification, being the main reaction driving the soil N cycle (Fig. 2). N-containing organic matter in soil includes mostly plant and microbial residues that consist of peptides and proteins and of other structurally complex N compounds (e.g., chitin). These N-containing polymers are cleaved to monomers that can be directly used by microbes and plants and/or mineralised. A primary source of N for microorganisms and plants are low molecular

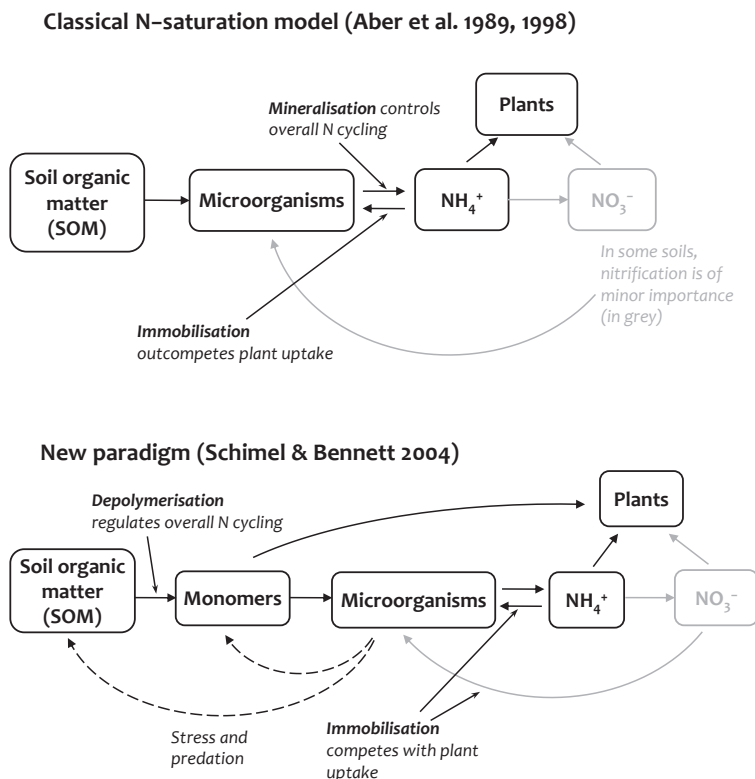


Fig. 2. Comparison of the classical and new paradigm of the soil N cycling (adapted according to SCHIMEL & BENNETT 2004).

weight organic and mineral N forms depending on their relative distribution in the soil, which is very heterogeneous, patchy and with a gradient of microsites with different availability of substrates and energy. In these microsites, different processes of the N cycle may dominate and may run simultaneously, which may explain much of the observed variation in the N cycling of various terrestrial ecosystems.

The main differences between the classical model (ABER et al. 1989) and the new paradigm of the N cycle are described in Fig. 2. They are reflected in the processes considered to be crucial in the cycle – ammonification in the case of the classical model and organic matter depolymerisation in the case of the new paradigm. The concepts also diverge in the forms of N that plants are capable of utilising. Traditionally, plants were considered to take up only mineral N (ABER et al. 1989, 1998), while the new paradigm expects plants to have the capacity to take up also organic forms of N (SCHIMEL & BENNETT 2004). In the last decades, papers have been published giving evidence that various plants including conifers are able to utilise not only mineral but also organic N (amino acids, peptides, and proteins) through the roots, even without any help from symbiotic (mycorrhizal) fungi. Moreover, they are able to compete for it with microorganisms (LIPSON & NÅSHOLM 2001, PERSSON & NÅSHOLM 2001, ÖHLUND & NÅSHOLM 2001, KIELLAND et al. 2006). Plants take up organic N simultaneously with other N forms and they can have different preferences for the N source as the concentrations of different N forms change along a gradient of succession and plant productivity (NORDIN et al. 2001).

N-availability gradients in the soil

According to the new general concept of N cycling, ecosystems exist along N-availability gradients (Fig. 3, SCHIMEL & BENNETT 2004). N availability affects the ongoing processes and leads to shifts in the N forms plants are dependent on. In low-N systems, where N cycling and decomposition are slow, production of inorganic forms is negligible and plants compete with microbes for organic N-monomers (Stage 1, Fig. 3). As N availability rises in N-rich microsites, decomposition increases, and microbes start to mineralise the soil organic matter to NH_4^+ . Ammonium diffuses to N-limited microsites where it is almost fully assimilated by plants and microbes. Only a negligible amount remains available for nitrifiers (Stage 2, Fig. 3). Further on, N availability increases and the competition between plants and microbes decreases. Mineral N, namely NH_4^+ , starts to dominate over organic N, plants utilise more mineral N, which can promote primary production and increase N concentration in plant biomass. NH_4^+ supply to nitrifiers is still low (Stage 3, Fig. 3). Finally, N availability is so high that plant and microbial N demands are covered, more NH_4^+ remains for nitrifiers and the ecosystem becomes NO_3^- dominated. The excess of N is leached from the soil (Stage 4, Fig. 3) and the system is N-saturated (AGREN & BOSATTA 1988, ABER et al. 1989, 1998, LOVETT & GOODALE 2011, KOPÁČEK et al. 2013a). Even in N-saturated soils, however, plants and microbes still take up organic N (SCHIMEL & BENNETT 2004, TAHOVSKÁ et al. 2013).

The importance of C:N ratio in the N transformation

The C:N ratio of the organic material (substrate) is an important factor affecting whether N mineralisation or immobilisation prevails in the soil (BRADY & WEIL 2002, BOOTH et al. 2005). Organic material is a source of C and N for microorganisms and the critical C:N ratio is, thus, related to stoichiometry of the microbial biomass (C:N). When N content of the consumed material is low, N is limiting relative to C (high C:N ratio), microorganisms must use an alternative N source and mineral N forms, and net immobilisation occurs (Fig. 4). In this case, there is a gradual depletion of the mineral soil N pool and more organic N is consumed (shift from mineralisation–immobilisation route to direct immobilisation route; GEIS-

SELER et al. 2010). In reverse, if N content of the consumed material is high, C is limiting relative to N (low C:N ratio). Microorganisms use N-containing organic compounds not only as a C and N source but also solely as a C source, and release the excess N in the form of NH_4^+ (shift from direct route to mineralisation–immobilisation route; GEISELER et al. 2010, TAHOVSKÁ et al. 2013) and the processes of N mineralisation prevail (Fig. 4). The critical C:N ratio value determining whether N is mineralised or immobilised is estimated at around 20 to 40 (PAUL & CLARK 1996, HODGE et al. 2000, MYROLD 2005, GEISELER et al. 2010). According to studies undertaken in European forest ecosystems, soils with C:N ratio lower than 32 (ŠANTRŮČKOVÁ et al. 2006) or even lower than 25 (GUNDERSEN et al. 1998, DISE et al. 1998, KOPÁČEK et al. 2002a, b) are at higher risk of nitrate leaching due to a decrease in N immobilisation.

Microbial C:N ratio depends on contribution of fungi and bacteria to the total biomass and fungi-to-bacteria ratio is an important factor determining an equilibrium between N mineralisation and N immobilisation in the soil. The cell C:N ratio varies from approximately 5–8

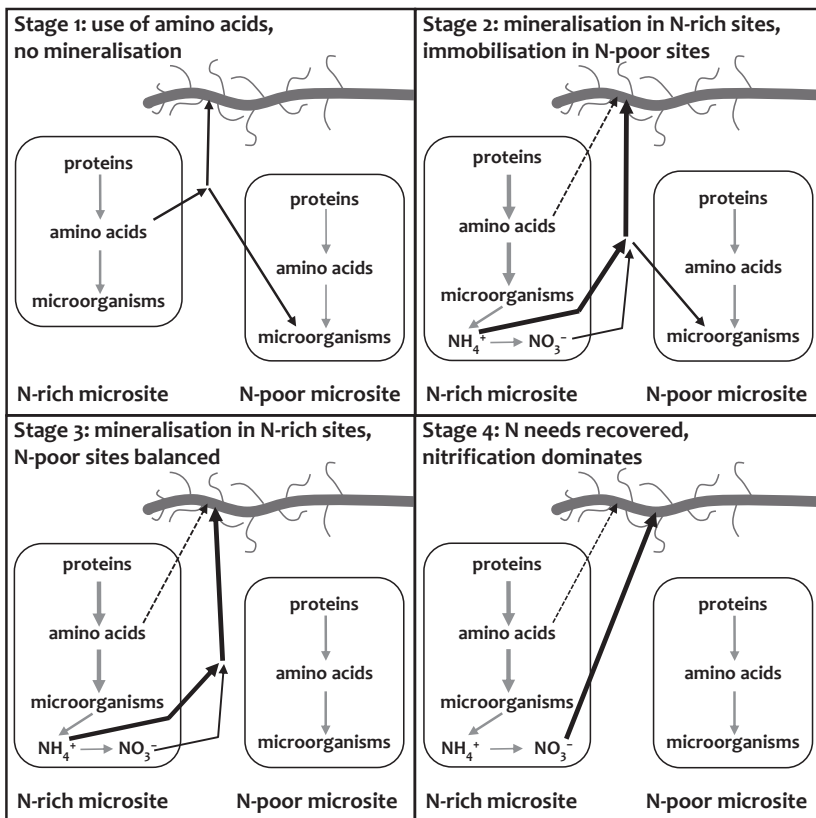


Fig. 3. The diagrams show shifting of key soil processes that regulate N availability to plants and microbes along a gradient of N availability. Stage 1: In N-limited conditions organic N is depolymerised and simple amino acids are immobilised and no N is mineralised. Amino acids are the main source of N for microbes and roots. Stage 2: When N availability increases in N-rich microsites, excess of amino acids is mineralised to NH_4^+ and NO_3^- and plants and microbes use them as N source. Stages 3-4: Along the N gradient, NH_4^+ and NO_3^- availability increase bringing about excess of NO_3^- , which can be leached out from the soil (adapted according to SCHIMEL & BENNETT 2004).

for bacteria to 15–20 for fungi (STRICKLAND & ROUSK 2010). They use about 50% to 80% of consumed organics for energy metabolism (C compounds are mineralised to CO₂ and energy is produced) and the rest (20% to 50%) is built together with N into biomass in the C:N ratio that matches C:N ratio of the cells. Accordingly, the critical C:N ratio of the substrate should vary in dependence on C:N ratio of microbial biomass and its metabolic efficiency. When the

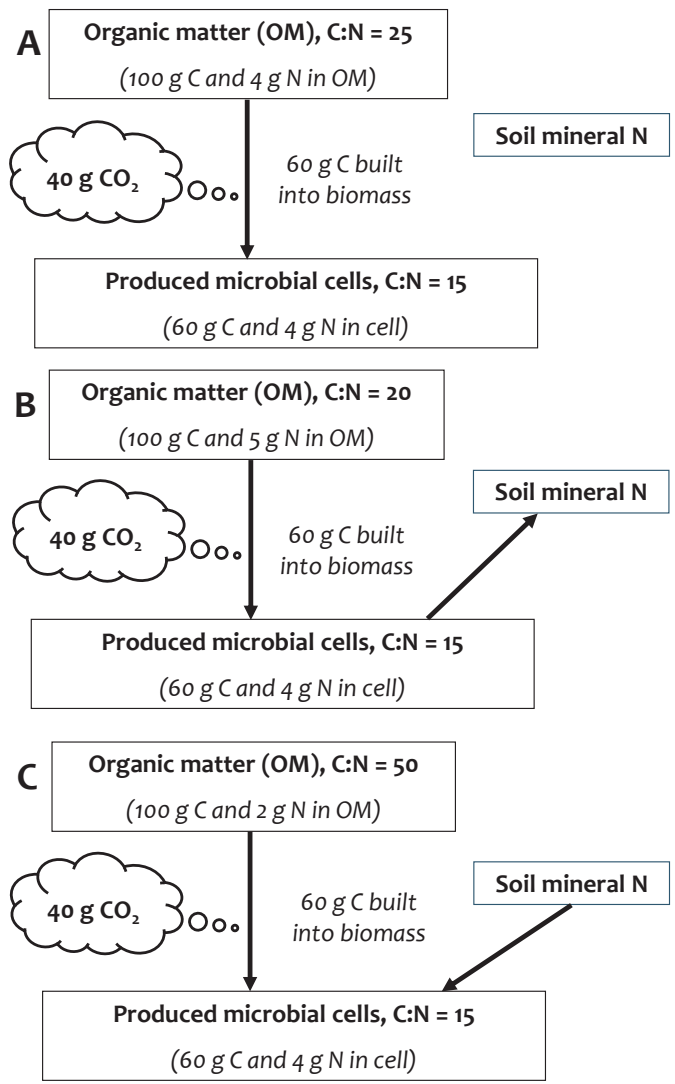


Fig. 4. Simplified relationship between stoichiometry of decomposed organic matter and microbial cell. (A) The C:N ratio of decomposed organic matter matches microbial N demand (reaches the critical value) and all N is immobilised into the microbial cell. (B) The C:N ratio of decomposed organic matter is below the critical value, N is in excess and the remaining N is mineralised. (C) The C:N ratio of decomposed organic matter is above the critical value, N in organic matter does not cover microbial N demand and microbes immobilise mineral N from soil.

C:N ratio of the substrate declines to about 20, fungi having higher C:N ratio of their biomass than bacteria start to release N, whereas bacteria still assimilate. The fungal-to-bacterial biomass ratio usually increases with decreasing pH (BLAGODATSKAYA & ANDERSON 1998, BÄÄTH & ANDERSON 2003) and the shift of microbial community structure towards fungi in acid soils should bring about lowered microbial N demand relatively to C demand. This results in an increase of the critical C:N ratio of consumed organic material.

Microorganisms in the soil rich in available organic C have usually higher metabolic efficiency and the soil has high capacities of N immobilisation and accumulation and less mineral N is released as compared with a system with low organic C pools (EVANS et al. 2006). TAHOVSKÁ et al. (2013) provided evidence that microbial NO_3^- immobilisation in N-saturated forests was positively related to C availability, which prevents NO_3^- leaching. They found a negative correlation between NO_3^- microbial immobilisation and C availability, which indicates that C limitation is a controlling factor of susceptibility of N-saturated soils to NO_3^- leaching. When the soil C:N ratio decreases, C limitation of microbial metabolism can appear, resulting in decreased N immobilisation. This leads to enhanced NH_4^+ availability for nitrification and produced NO_3^- cannot be, similarly to NH_4^+ , immobilised to microbial biomass and can be leached out of the soil profile.

Role of fungi and bacteria on soil N transformation

It is generally accepted that fungi dominate decomposition of organic matter and N liberation from complex compounds in the forest soils. They degrade phenolic and lignin-like compounds more effectively than bacteria because they are equipped with a variety of enzymes allowing them to decompose complex organic substrates (SMITH & READ 2008). Generally, fungi have been shown to be more tolerant to acidic soil conditions than bacteria, having a wide pH-growth optimum (reviewed in STRICKLAND & ROUSK 2010, ROUSK & BÄÄTH 2011). However, LAUBER & STRICKLAND (2008) suggested that the abundance and composition of the fungal community in forest soil is affected by soil nutrient availability (C:N ratio, P) and plant species composition, rather than by soil pH. Fungi are better competitors for N than bacteria in N-poor environments (BOBERG et al. 2010, SCHMIDT et al. 2011), partly because their mycelia can transfer C to nutrient-rich microsites and nutrients to C-rich microsites. In N-rich conditions, however, fungi might be outcompeted by bacteria.

Fungi play an important role not only in plant nutrition (SMITH & READ 2008) but also in forest soil N retention (NILSSON et al. 2012). Fungal necromass has longer residence time than that of bacteria. Dead but still intact mycelia are involved in the translocation of N and nutrients for a relatively long distances (LAUBER & STRICKLAND 2008), connecting rich and poor niches and preventing N mineralisation and leaching. Fungi are mainly involved in N immobilisation and ammonification processes and, to a lesser extent, in denitrification and nitrification (RUTTING et al. 2013, CHEN et al. 2015). They can use different forms of N to build up biomass (MERRICK & EDWARDS 1995, NORDIN et al. 2001), but organic N is believed to be their preferential N source (DUNN et al. 2006, GONOD et al. 2006).

Fungal community comprises saprotrophic and mycorrhizal fungi. Saprotrophic fungi dominate dead wood and other decaying organic matter. Mycorrhizal fungi live in symbiotic associations with plants. Mycorrhizal symbionts supply plants with nutrients (mostly P and N) in exchange for assimilates produced in photosynthesis. They, however, can also degrade complex substrates and most likely dig out N and other nutrients not supplied by the host plant (CULLINGS & COURTY 2009). Mycelia of ectomycorrhizal fungi in northern temperate and boreal forests can account for up to one third of the total soil microbial biomass (HÖGBERG & HÖGBERG 2002). In N-rich conditions, fungal abundance generally decreases mainly due to the decrease in mycorrhizal associations (LAUBER & STRICKLAND 2008). Plants

reduce the flux of assimilates to belowground parts when their N demand is met from more available mineral N forms (HAYNES & GOWER 1995) and mycorrhizal fungi are reduced.

Bacteria and archaea form smaller parts of the microbial community in the forest soils, but they are involved in all key processes of N transformation. They are mostly heterotrophs that depend on the organic C supply. However, autotrophs utilising CO₂ also occur there (e.g., nitrifiers).

Heterotrophic bacteria mainly decompose easily available compounds and their growth rate is usually lower under acidic conditions (ROUSK *et al.* 2009). They are less efficient than fungi in decomposing complex organic material, which further decreases their competitiveness in acidic soils. They immobilise, similarly to fungi, various forms of N. In addition, they have been reported to have a high ability to recycle intracellular N not only at low soil N concentrations but also when the concentration of NH₄⁺ in soil is high (BENGTSON & BENGTSSON 2005). A unique group of heterotrophic bacteria is N₂-fixing diazotrophs, among which free-living bacteria as well as bacteria developing close symbiosis with plants are recognised. The abundance of non-symbiotic diazotrophs in temperate forest ecosystems is relatively low. Free-living bacteria usually fix less than 3 kg N.ha⁻¹.yr⁻¹ (VITOUSEK & HOBBI 2000). Symbiotic interactions are rare there, mostly restricted to alder and few understory herbaceous legumes.

Heterotrophic bacteria utilise both the mineral and organic N forms. Generally, it is believed that as a consequence of energy costliness, NH₄⁺ is favoured over NO₃⁻ as a mineral N source for microorganisms (RICE & TIEDJE 1989, SCHIMEL & FIRESTONE 1989, GUNDERSEN *et al.* 1998, BOOTH *et al.* 2005, PERELO *et al.* 2006) and that NO₃⁻ immobilisation is suppressed by high soil NH₄⁺ concentration (PAUL & CLARK 1996, MYROLD 2005, TAYLOR & TOWNSEND 2011). However, important NO₃⁻ immobilisation has been observed even at high NH₄⁺ concentrations (BENGTSON & BENGTSSON 2005). This can be explained by the co-existence of various microsites in the soil matrix, as expected in the general concept of N transformation (SCHIMEL & BENNETT 2004).

Bacteria and archaea also provide nitrification and denitrification. They dominate both steps of autotrophic nitrification (ammonia oxidation and nitrite oxidation). In acid conditions, ammonia oxidation is mostly run by ammonia-oxidising archaea (AOA, phylum Thaumarchaeota) that can use NH₄⁺ more effectively than ammonia oxidising bacteria (AOB). Denitrification bacteria are both heterotrophic and autotrophic. Denitrification occurs in AOA, AOB and fungi (LEVY-BOTH *et al.* 2014).

The effect of plant species on N transformation

Plants affect N-transformation processes by their life history strategy and litter quality. CHAPMAN *et al.* (2006) suggest that plants are able to control N cycling. They distinguish between conservative (conifers, ericaceous plants, etc.) and what they call “extravagant” plant species (grasses, most herbs, etc.) in connection to their environment and ability to control N cycling. Conservative plants usually live in nutrient-poor habitats and are more dependent on symbiosis with microorganisms than “extravagant” species that usually use N mineralised by free-living microorganisms. Conservative species are considered to regulate N cycling more strongly than “extravagant” species (CHAPMAN *et al.* 2006).

The composition of the litter determines its degradability, which further determines the microbial community involved in decomposition and N cycling. The difference in decomposability is usually ascribed to the contents of lignin and soluble carbohydrates in the litter and to the relative content of N expressed as the lignin:N ratio (MELILLO *et al.* 1982, ABER *et al.* 1990, SCOTT & BINKLEY 1997). The lignin:N ratio is a good predictor of decomposition rate for high lignin and recalcitrant litter (MELILLO *et al.* 1982, TAYLOR *et al.* 1989). For litter

low in lignin (TAYLOR et al. 1989) and/or litter high in cutin (sclerophyllous vegetation; GALLARDO & MERINO 1993), and for global scale studies, where a wide range of lignin and N contents has to be considered, the general C:N ratio is a better predictor of the litter decomposition rate (ZHANG et al. 2008).

During litter decay, different rate-regulating factors control the decomposition rate (for a summary see BERG & LASKOWSKI 2006). In the first stage, when easily decomposable carbohydrates, organic N compounds and celluloses are being decomposed, high levels of N and other nutrients such as P, Ca and S enhance litter decay. Conversely, in the later stage when lignin is being decomposed, lignin degradation rules the decomposition rate. Lignin degradation is hampered by a high level of N, whereas it is stimulated by a high level of Mn, which is oxidised by manganese peroxidase during lignin degradation (BERG et al. 2007). High N availability retards the decomposition rate through creating more recalcitrant aromatic compounds of N with lignin. Nitrogen may also restrict the synthesis of lignin-degrading enzymes (BERG 2000, WALDROP et al. 2004, WALDROP & ZAK 2006).

The decomposition rate of needle litter is lower compared to leaf litter type and understory herbaceous litter of other dominant plant species common in mountain spruce forests (e.g., BERG & EKBOHM 1991, ŠANTRŮČKOVÁ et al. 2006, TEJNECKÝ et al. 2014). This is a result of the high content of lignin and phenolics and the low content of soluble carbohydrates, N and P in the former group (BERG & EKBOHM 1991, OSONO & TAKEDA 2005, ŠANTRŮČKOVÁ et al. 2006, SHOROHVA et al. 2008). Grasses tend to produce easily degradable litter with a low C:N ratio. FIALA et al. (2005) observed that *Calamagrostis villosa* efficiently accumulates N in the biomass and can in this way reduce N losses from ecosystems during the growth season. The results by ŠANTRŮČKOVÁ et al. (2006), however, suggest that dead grass leaves release the accumulated N in the form of dissolved inorganic N, mainly NH_4^+ , into the soil in the early stage of decomposition and can temporarily increase NH_4^+ flux into the soil in the autumn and winter period. In this period, NH_4^+ can be transformed to NO_3^- in nitrification processes that can run even at zero temperature (SKOPCOVÁ & ŠANTRŮČKOVÁ 2006, ŠANTRŮČKOVÁ et al. 2009). Bryophytes, on the other hand, are both poor in N and recalcitrant and, thus, decompose more slowly than some herbs and grasses (HOBBIE 1996, SMOLANDER & KITUNEN 2002). Bryophytes and lichens influence their environment through decreasing soil temperatures or increasing soil moisture, changing the density of soil organic matter and reducing the loss of organic N from the ecosystem by decreasing decomposition (TURETSKY 2003). Even though they can contribute to biological N_2 fixation, their contribution is low (ROSÉN & LINDBERG 1980). Dwarf shrubs (such as *Vaccinium* spp.) indicate a thick layer of humus and low pH, which is a favourable microsite for spruce seedling growth (BAIER et al. 2005). The coverage of dwarf shrubs and mosses seems to be beneficial to the N cycling in soils and to regeneration of spruce forests (JONÁŠOVÁ & PRACH 2004).

Plant species which form symbiosis with N_2 -fixing bacteria can significantly affect N availability in forest ecosystems. A meta-analysis revealed that symbiotic N_2 -fixing bacteria can account for significantly more N than N fertilisation or atmospheric deposition inputs, when N_2 -fixing tree species are abundant (JOHNSON & CURTIS 2001). In temperate forests, however, only a few tree species – alder (*Alnus*), poplar (*Populus*), and willow (*Salix*) – can be abundant. In the understory, N_2 -fixing leguminous (e.g., lupin, *Lupinus*, and clover, *Trifolium*) or nonleguminous herbs and grasses which can host associative N_2 -fixing bacteria on roots might significantly enrich soil with N but only when the canopy is not closed (TURVEY & SMETHURST 1983). ROSÉN & LINDBERG (1980) estimated biological nitrogen fixation in coniferous forest in central Sweden to be in the order of $0.5 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$. However, this figure might be underestimated as feather moss (*Pleurozium schreiberi*) alone, which is common in mid- to late successional forests of northern Scandinavia but also in the moun-

tain forests in central Europe, can fix between 1.5 and 2.0 kg N.ha⁻¹.y⁻¹ (DeLUCA et al. 2002).

In mountain conifer forests of central Europe, Norway spruce (*Picea abies*) is the dominant tree species. Spruce needle litter is rich in lignin and other phenolic compounds and poor in nutrients (high lignin:N ratio, high phenolics:available P ratio). Consequently, spruce needles are resistant to biological degradation and decompose slowly, producing more organic acids during decomposition than leaf litter type (HOBBIE et al. 2006, ŠANTRŮČKOVÁ et al. 2006, VESTERDAL et al. 2008, BARTA et al. 2010). Compared to deciduous tree species (birch, beech, rowan, etc.), soils under spruces are characterised by a higher C:N ratio of litter layer, lower pH and base saturation, and by lower content of C and N bound to microbial biomass. Spruce stands are reported to store more C and N in the soil than deciduous stands due to slow decomposition (MERILÄ et al. 2010, HANSSON et al. 2011, SMOLANDER & KITUNEN 2011, KIIKKILÄ et al. 2012). Slow decomposition accompanied by N immobilisation and release of soluble organics, which exacerbate soil acidification and further decelerate organic matter decay, negatively affects N cycling in the spruce forest soils and can deepen the acidification process. The effect of litter quality is much stronger in the forest floor than that in mineral layer so the effect of tree species on mineral soil might not be observed (ERIKSSON & ROSEN 1994).

HUMAN IMPACTS ON N TRANSFORMATIONS IN FOREST SOILS

Forest soil quality and soil N-transformation processes in central Europe have been affected by management practices and disturbances for centuries and by acid deposition for decades. The effect of the human activities on forest ecosystem functioning and susceptibility of soil to physical, chemical and biological changes or even to soil degradation is higher for ecosystems with soils of comparatively low quality, on which most of the forests in central Europe have been historically located, than for rich fertile soils.

The effect of acid deposition

Ecosystems (not only) in central Europe experienced huge loads of N and S from anthropogenic activities through acid deposition in the second half of the 20th century (KOPÁČEK et al. 2001, 2010). Though these depositions decreased by the end of the last century, forest soils still show an acidification effect and N saturation (PUHE & ULRICH 2001). The soil acidification effect is stimulated by (i) acidification due to spruce plantations that have been selected in central Europe since the 19th century (OULEHLE et al. 2006), (ii) low base saturation of soils in areas with crystalline rocks (e.g., KENNEDY 1992), (iii) global warming (KETTLE et al. 2003), and (iv) plantation of coniferous species (AUGUSTO & RANGER 2001, SCHWARZ et al. 2009). Coniferous tree species intercept atmospheric deposition more efficiently than the hardwood species do (AUGUSTO & RANGER 2001, ROTHE & BINKLEY 2001). Apart from acidification, long-term N deposition increases N input into the soils. Such N loads over the long term have slowly, but significantly, increased N content in soil and affected N-transformation processes and finally, caused N saturation of mountain spruce forest soils in central Europe.

Due to human activities leading to increased atmospheric N deposition, many nutrient-limited ecosystems (forests, as well) have developed towards the N-saturation state (TAMM 1991, GALLOWAY 1998). N inputs increased the productivity in the previously N-limited ecosystems (BINKLEY & HÖGBERG 1997). However, in the long term, N loading and N surplus lead to changes in ecosystems, their diversity and ongoing processes, cause soil acidification or even deterioration (GALLOWAY 1998), which can be followed by a decline of tree growth

(EMMETT 1999). The concepts of N saturation have become increasingly important when interpreting N cycling and its changes above all in the mountain forest as they have been developing on poor soils and exposed to N and S deposition more than lowland forests.

N saturation of forest soils

The definition of N saturation is not uniform in literature. However, ecosystems are generally considered to be N-saturated when NO_3^- appears in soil leachate (STODDARD 1994, VENTEREA et al. 2004). In its widest meaning, N saturation can be viewed as a permanent alteration of the soil N cycle from closed internal cycling to an open cycle where the excess N flows out of the ecosystem (KÄMÄRI et al. 1992).

The traditional conceptual model of N saturation characterises this process as a sequence of environmental changes that occur as an N-limited ecosystem accumulates deposited N (ABER et al. 1989, 1998). It is based on the classical paradigm of N transformation, assuming that ammonification and release of NH_4^+ is a crucial point of the N cycle (Fig. 2). The enhanced N deposition increases N availability to plants. Plants incorporate N into their biomass and, thus, decrease the C:N ratio of their litter. N ammonification and nitrification accelerate due to litter-N enrichment of the upper parts of the soil profile. When the demands of vegetation for N are met, NO_3^- is in excess, which leads to NO_3^- leaching in the last stage of N saturation of the ecosystem. It is recognised that vegetation and soil accumulate N until they are N-saturated (ABER et al. 1998). Then, N accumulation is zero (or even negative in some cases) and the ecosystem loses N. Ammonification and nitrification are assumed to be key processes of soil N transformations, whereas microbial immobilisation of N is expected to be of minor importance (ABER et al. 1998), which contradicts the findings that microbial N immobilisation is important in preventing N loss (STARK & HART 1997, TAHOVSKÁ et al. 2013).

Based on a long-term N manipulation experiment in an oak forest, LOVETT & GOODALE (2011) modified the conceptual model of N saturation. Similarly to the model by ABER et al. (1989, 1998), it focuses on the mass balance, which is characterised by N inputs (deposition or fertilisation), internal sinks (vegetation and soil) and outputs (nitrate leaching and volatilisation of N-containing gases). The key point of the model, however, is that added N can flow simultaneously to all sinks in the system and that these sinks do not have to reach their saturation capacity, which matches a general concept of N cycling introduced by SCHIMEL & BENNETT (2004). The flow of N through these sinks and its final fate depends on the size of the sinks and the factors that control them. The losses from the system may be the results of either the filled capacity of the sinks or kinetics of N saturation, which occurs when a sink accumulates N at a lower rate than the rate of N input (LOVETT & GOODALE 2011). The weakness of the model, similarly to ABER's N saturation model, is that immobilisation of mineral N into microbial biomass is neglected (ABER et al. 1998, LOVETT & GOODALE 2011). However, the pathway of N immobilisation was shown to be common in the forest ecosystems (BOOTH et al. 2005). Based on the results from mountain spruce forest soil in the Bohemian Forest, ŠANTRŮČKOVÁ et al. (2009) further documented, that microbial N pool is by far the most important available N pool in the forest soils (Fig. 5).

STARK & HART (1997) already drew attention to the importance of the microbial immobilisation of mineral N. They focused on 11 undisturbed forest ecosystems and found out that, despite the low soil pH, low N availability and deposition, the rates of nitrification were high. Surprisingly, NO_3^- concentration was low in most cases. The isotopic measurements showed that the vast majority of NO_3^- produced was immobilised into microbial biomass. The authors proved that soil microorganisms have the capacity to assimilate NO_3^- and, thus, prevent their leaching from the soil. They also suggested that a decrease in microbial immobilisation

of NO_3^- may result in greater availability of NH_4^+ and reduced inputs of plant C after some disturbances (STARK & HART 1997). Similarly, TAHOVSKÁ et al. (2013) studying N transformation in both Bohemian Forest and Ukraine soils showed the important role of microbial N immobilisation in preventing N loss from N-saturated ecosystems.

The N cycle is closely connected with other element cycles (SANDERSON et al. 2008). Recently, KOPÁČEK et al. (2013a) reviewed the above mentioned N-saturation concepts. They reflected the changes in nutrient cycling and organic C availability in soils after being affected by long-term massive N and S deposition, and linked N saturation to C limitation coming up with a new conceptual hypothesis. In short, elevated availability of mineral N diminishes plant dependence on the mycorrhizal supply of N (WALLEND & KOTTKE 1998), which reduces the fine root biomass and flux of photosynthates to roots and, therefore, decreases the abundance of mycorrhizal fungi and fungal activity in soil. At the same time, N content in plant litter increases resulting in a decreased C:N ratio, increase in litter decomposition and N fluxes back to the soil. The reduced supply of available C and elevated availability of N affect microbial community composition and functioning. Fungi-to-bacteria ratio decreases and bacterial mineralisation, unlike fungal mineralisation, is enhanced by the elevated availability of N (HÖGBERG et al. 2007) and electron acceptors (NO_3^- , SO_4^{2-}) for anaerobic respiration. Fungal-to-bacterial activity ratio decreases resulting in enhanced N mineralisation (SCHMIDT et al. 2004). It also leads to decrease in the critical C:N ratio of decomposed organic matter when N mineralisation outbalances N immobilisation in the soil, as bacterial biomass has low C:N ratio (see chapter “General concepts of the N cycle in soil”). Elevated N mineralisation produces NH_4^+ in excess and, in parallel, the pool of bioavailable organic matter decreases due to (i) the enhanced mineralisation of available organic matter to CO_2 , and (ii) the reduced release of organic material from recalcitrant organic C by fungal activity. Consequently, the ecosystem moves from N limitation to C

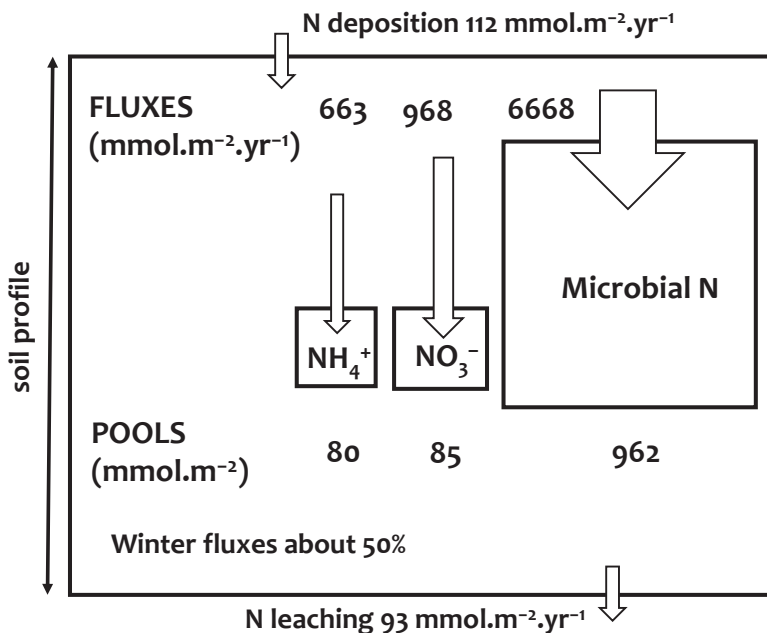


Fig. 5. Microbial and mineral pools of N in N-saturated acidified soil of the Plešné Lake catchment.

limitation and less organic material remains available for microbial growth. Produced NH_4^+ cannot be immobilised by heterotrophic microbes, the growth of which is C-limited, leaving more NH_4^+ for nitrifiers. As a result, NO_3^- production in soil increases. The negative influence of C limitation on the growth of heterotrophic microorganisms is exacerbated by increasing the chemical suppression of DOC solubility in acidified soils (EVANS et al. 2008), which further promotes autotrophic nitrifiers and NO_3^- production. Produced NO_3^- cannot be removed by denitrification or microbial immobilisation as denitrifiers and heterotrophic microbes are limited by low C availability, and NO_3^- thus remain in the soil in excess. Altogether, the ecosystem moves from the 3rd to the 4th stage of the conceptual N-availability model by SCHIMMEL & BENNET (2004).

The effect of forest development and management practices

Forest development affects soil over time and its effect is highly dependent on the tree species, their growth, forest disturbances and forest management practices during the forest life cycle. A disturbance always affects soil properties, but the extent of the soil changes depends on its type and intensity and also on the management used after disturbances. Forest management varies from no intervention to highly intensive silvicultural intervention. Replacement of secondary or semi-natural forests to mono-species plantation and clear-cutting with whole-tree harvesting is undoubtedly more invasive than sustainable forestry practices, which consider regeneration and the long-term well-being of the forest (HARTMANN et al. 2010, WALL 2012). As forest management affects soil properties, it inevitably influences also N-transformation processes, namely by tree species composition, canopy density, fertilisation, and, finally, by organic matter and nutrient removal, soil disturbance and exposure connected with harvesting.

Anthropogenic and natural disturbances

After either an anthropogenic (i.e., harvesting) or natural disturbance, N leaching usually occurs within a few years and remains for several years (HUBER 2005). After the disturbance (natural and clear-cutting), trees and associated mycorrhizas, which are an important sink for soil N, die off and more N remains available for decomposers. A massive input of plant secondary compounds, dead roots and aboveground plant debris to soil accelerates activity of heterotrophic microflora and organic matter mineralisation. Although N immobilisation to microbial biomass increases, its turnover time is shortened and more organics of microbial origin with low C:N ratio enter the soil. A shift in the microbial community from dominance of fungi to bacteria due to the root and mycorrhiza death, soil disturbance, supposable compaction by heavy machinery, and change in quality of organic matter input can decrease C:N ratio of microbial biomass. However, N immobilisation does not increase as the microbial biomass mostly decreases (e.g., ENTRY et al. 1986, OHTONEN et al. 1992, GRAYSTON & RENNENBERG 2006). Tree decline and clear-cutting diminishes priming of decomposition by root exudation and leads to the loss of species richness of ectomycorrhizal fungi, which negatively alters the fungal community and their functioning in the soil (BYRD et al. 2000). Changes in component processes disequilibrate N-transformation cascade, which becomes leakier. N immobilisation is outbalanced by N mineralisation, NH_4^+ remains available for nitrifiers, and the resulting excess of NO_3^- leads to significant losses of N and other nutrients within 2–3 years after the disturbance (PAUL & CLARK 1996, ABER et al. 2002, HAZLETT et al. 2007). The ecosystem, being previously in the 1st or 2nd stage of the N-availability gradient, moves towards the 3rd or 4th stage of the N-availability gradient (SCHIMMEL & BENNETT 2004; Fig. 4). The stage to which the ecosystem is shifted, possible N-leaching rate and its duration depend on the productivity of the site, soil quality (GUNDERSEN et al.

2006, DEVINE et al. 2012), on the original stage of the N-availability gradient, the ability of microorganisms to immobilise N, and intensity of soil disturbance and development of new vegetation. The amplitude of NO_3^- losses from soils is lower but has a longer duration (7–8 years) after natural forest diebacks than after clear-cuts, when quick and higher NO_3^- losses usually occur for a shorter period (3–5 years) (CUMMINS & FARRELL 2003, HUBER 2004a,b, McHALE et al. 2007). In general, the tempo of N losses is higher when there is greater soil disturbance. Also, N losses are enhanced by increased outflow of seepage and run-off water due to lower evapotranspiration. Post-harvest or disturbance N leaching is obviously greater than any other pulses connected with seasonal changes. However, they remain small, up to 2–3% relative to the total N pool in the soil (GUNDERSEN et al. 2006, DEVINE et al. 2012). Thus, it is not surprising that a meta-analysis on forest management effect on C and N storage has revealed no or only small decrease of N storage (JOHNSON & CURTIS 2001).

Clear-cutting with the whole-tree harvesting and wood extraction can further threaten the soil by mechanical disturbance and possible soil compaction and erosion. The deterioration of the uppermost organic horizons, in which the majority of soil biota develops, removes substrate and destroys the niche occupied by soil organisms. In this way, it affects mainly fungal and faunal communities, decreases decomposition and the input of N and other nutrients needed for a new forest development (MARSHALL 2000). Coarse particles and woody debris on the forest floor are at the stand scale a major determinant of fungal populations (EDMAN et al. 2006). The loss of woody debris has drastically declined the number of species of wood-decaying fungi in Scandinavia, which can slow down N release from decaying wood as bacteria cannot efficiently decompose wood (EDMAN et al. 2006). In addition, N content within fungal tissue is considerably higher than in plant tissue, and might constitute an important pool of relatively accessible N within the soil or might be a sink for inorganic N (LINDAHL et al. 2002). Finally, plant uprooting and soil disturbance disrupts the network of mycorrhizal hyphae in soil resulting in reduced colonisation of small saplings (SMITH & READ 2008).

Changes in N transformations and soil nutrient pools are smaller if thinning is used instead of clear-cutting or if whole-tree harvesting is changed to stem-only harvesting (ROLFF & ÅGREN 1999, PARÉ et al. 2002). Harvesting without removal of residues might result in an increase of microbial activity (DELUCA & ZOUHAR 2000). HOMYAK et al. (2008) propose the application of wood chips as a tool for decreasing the negative effects of harvesting, such as NO_3^- and nutrient leaching to waters. This is based on their observation that C:N ratio of wood chips decreased significantly (from 125:1 to 70:1) one year after their application at the clear-cut plots, suggesting that the microorganisms decomposing the wood chips have a potential for N immobilisation.

Besides these changes in soil chemistry and biochemistry, there is also the negative effect of changes in microclimatic conditions. The absence of tree vegetation has several consequences. There is a decrease in nutrient uptake and respiration by plants, which leads to an increase in water passing through the system (BOHRMANN et al. 1968). Moreover, the upper layers of soils of the clear-cut plots tend to be more overheated due to the vegetation removal. HAIS & KUČERA (2008) observed an increase in soil surface temperature by 3.5°C and 5.2°C in the non-intervention and clear-cut plots, respectively. The increase in temperature was accompanied by a large temperature fluctuation. Both temperature increase and fluctuation alter N-transformation processes and it is likely that this can stress the above-mentioned effects of clear-cutting.

All the above-mentioned changes in soil after clear-cut promote the expansion of pioneer species, such as competitive grasses (FIALA et al. 2005). Bryophytes, on the other hand, seem to be susceptible to changes in microclimate at the clear-cut plots and they decline not only

in % coverage but primarily in diversity (FENTON et al. 2003, PALVIAINEN et al. 2005, JONÁŠOVÁ & PRACH 2008). Dwarf shrubs (such as *Vaccinium* spp.) decreased after clear-cutting but still remained a significant nutrient sink, and were able to recover after a few years (PALVIAINEN et al. 2005). Compared to the clear-cut plots, at those left without intervention, both mosses and herbs survived relatively well (JONÁŠOVÁ & PRACH 2008) and the regeneration of tree cover was faster (JONÁŠOVÁ & PRACH 2004).

N fertilisation

Nitrogen fertilisation is a routine silvicultural practice, which increases net primary production. However, it is not widely used in the mountain forests of central Europe, where high N deposition has supplied ecosystems with N in excess for a long time. Nevertheless, we briefly discuss the possible N-fertilisation effect to give a comprehensive overview.

The effect of N fertilisation depends on the stand conditions, the pattern of N immobilisation/mineralisation, and availability of water and other nutrients that can be co-limiting factors. On the other hand, it changes soil conditions and the plant C and nutrient allocation pattern supporting the growth of aboveground biomass and decreasing C allocation to roots (HAYNES & GOWER 1995). As N fertilisation increases the N availability in soil, trees do not have to invest C and energy to support mycorrhizal association and the role of mycorrhiza is reduced (NILSSON & WALLANDER 2003). It results in a decrease in the proportion of soil fungi in the microbial community (DEMOLING et al. 2008), which is indicated by the decrease in microbial C:N ratio (OHTONEN et al. 1992), and may bring on the reduction of microbial biomass (SÖDERSTRÖM et al. 1983, ARNEBRANT et al. 1996, DEMOLING et al. 2008). A reduction in the tree belowground allocation is, therefore, expected, but has not been quantified directly in the field (HÖGBERG et al. 2010). However, it was strongly supported by OLSSON et al. (2005) who measured twice as high autotrophic soil respiratory component in non-fertilised as compared with high N-fertilised spruce forest. Soils in an intensively fertilised forest plantation on acid soils or N-fertilised soils, which have been exposed to acid deposition, can move towards the 3rd or 4th stage of the N-availability gradient, similarly to the situation in the acidified, N-saturated soils or in the soils after disturbance. If soils cross the border between the 3rd and 4th stage, nitrification and N leaching are enhanced. Nitrate leaching itself is negative. Furthermore, it deepens nutrient losses and soil deterioration as nitrates are not leached alone but together with base cations. Thus, N losses are accompanied with losses of other nutrients, decline in base cations:Al ratios, acidification, and decrease in tree growth (MCNULTY et al. 1996, EMMETT 1999, HÖGBERG et al. 2006, IWALD et al. 2013).

The effect of N fertilisation alters with fertiliser chemistry. Urea, when applied, must be transferred to ammonia, which is accompanied by a short-term pH increase as H⁺ are consumed. Even though the pH increase is only short term, it shifts the NH₄⁺ equilibrium towards NH₃, which cause ammonia volatilisation. The losses are usually less than 10% of the added N (BINKLEY & FISHER 2012). Ammonium from fertiliser can be bound on exchangeable sites of organo-mineral complexes and is not simply leached out. Added NH₄⁺ can also be immobilised by microbes in the forest floor or nitrified to NO₃⁻ without reaching the roots (OHTONEN et al. 1992).

Dead wood and plant debris

Forest fertilisation can partly but not fully compensate the continual supply of nutrients from decaying organic matter. Analyses of wood and bark of major tree species of north western Russia forests suggested that post-disturbance release of N and other nutrients from woody detritus can potentially supply a large proportion of net N accumulation in the live forest biomass (KRANKINA et al. 1999).

Many studies confirm that dead wood plays a very important role in mountain spruce forest regeneration as a microsite with favourable conditions for many species of animals, plants and fungi, which play an important role in N and C cycling (WU et al. 2005, ZIELONKA 2006, SVOBODA & POUŠKA 2008, SVOBODA & ZENÁHLÍKOVÁ 2009, ČÍŽKOVÁ et al. 2011). Animals fragment and transport plant debris and prepare organic material for further mineralisation. Fungi, as mentioned above, are important in decaying complex compounds and releasing N and other nutrients for developing vegetation, which prevents N leaching. DEVINE et al. (2012) suggested that more N is leached from soil than from plant debris. Plant debris and woody material is, in general, an important source of C for microorganisms, whose development and activity increase N immobilisation; first into microbial biomass and then into more resistant soil organic matter. Hence, dead plant material can protect N against leaching via microbial immobilisation on one hand and improve soil organic matter quantity and quality on the other.

Decay of woody material with a high C:N ratio needs some additional N to cover microbial N demand (Fig. 4). Furthermore, decomposers compete for soil N with young trees under such conditions; the system is in the 1st or 2nd stage of the N-availability continuum (Fig. 3). The decomposer community is dominated by fungi that are very efficient in extracting N from decaying material and transporting it from relatively long distances through their widespread mycelia web (BOBERG et al. 2010, 2014). This ability makes fungi highly competitive under these conditions of low N availability.

Effect of the canopy

Natural (and semi-natural) forest stands and plantations differ in species composition and density of canopy and understory as well, which in turn affects the biochemical processes, N transformations and N mobility in soil via nutrient uptake, N₂ fixation, litter quantity and quality. N leaching is accelerated by forest disturbance because of root damage, mortality and abrupt decrease of plant N uptake (HOULTON et al. 2003, CAMPBELL et al. 2014). Natural and semi-natural forests are more diverse, with lower tree density and more dense and diverse understory than forest plantations, which can drive forest belowground properties and regeneration (NILSSON & WARDLE 2005). The effect of plant species has been already discussed in the chapter “The effect of plant species on N transformation”. Here we mainly focus on the whole ecosystem effect.

There is a mutual relationship between soil and vegetation, but it is difficult to separate the effect of various species on soil development, mostly due to the lack of long-term data. The effect of species might be most pronounced on the relatively small, rapidly cycling pools of N (e.g., mineral N forms), with little influence on the larger, more stable N pool (BINKLEY & FISHER 2012). The tree effect on N cycling is definitely species-specific and is connected with between-species differences in N acquisition, N-use efficiency, litter production, and litter quality, and interaction with microbes (BINKLEY & GIARDINA 1998, KOPÁČEK et al. 2015). Coniferous trees acidify soil more than broadleaved trees, which is associated with a shift in C and N cycling and in organic matter quality, availability, and decomposition. Studies of different tree species have suggested that the uptake of nutrients and their allocation to tree biomass can variously influence N and nutrient content in the soil (ERIKSSON & ROSEN 1994). In temperate coniferous forests, the annual circulation of N is much lower than in deciduous forests as a result of lower leaf turnover (foliage persists for 8–10 years), lower N content, and the lower decomposition rate of the litter. These together with higher photosynthesis per unit of leaf nitrogen result in greater N-use efficiency in coniferous as compared with deciduous forests (SCHLESINGER & BERNHARDT 2013). Nitrogen input by biological symbiotic N₂ fixation can increase N content in soil and soil N mineralisation in forests with high abun-

dance of N₂-fixing trees several fold compared to the canopy with non-fixing species (BINKLEY & GIARDINA 1998). Soil N accretion appears to increase with the proportion of N₂-fixing species in the forest (ROTHER & BINKLEY 2001).

All plant species, trees as well as herbs and grasses in the understory, substantially affect forest floor and soil N content and availability by differences in litter properties. BINKLEY & GIARDINA (1998) compiled evidence how these differences result in the characteristic of forest floor. They found out that forest floor masses commonly differ by 20% among the species on the same site. The rates of litter mass and N content showed a similar difference of 20%. The differences were even larger, as much as 50%, when comparison included also N₂-fixing species. Net N mineralisation differed by 50% or more among species indicating strong feedback between N mineralisation and N content in the litterfall. This generalisation is supported by evidence that lignin:N ratio of aboveground litter negatively correlates with N mineralisation (SCOTT & BINKLEY 1997). There is increasing evidence that plants actively control N cycling through (i) species-specific litter quality as an immediate source of plant available N, through (ii) effect of N₂ fixation and mycorrhizal facilitation of N uptake on litter quality, and, finally, by (iii) direct plant and mycorrhiza N uptake (HOBBIE 1992, READ & PEREZ-MORENO 2003, CHAPMAN et al. 2006).

MOUNTAIN SPRUCE FORESTS OF THE BOHEMIAN FOREST

The historical evolution of forests has been traced back by BENEŠ (1995). Briefly, in the region of the Bohemian Forest, origins of the forests can be dated back to the beginning of Holocene. The first tree “invaders” were willow, birch, and pine, followed by hazel (around 7000 BC) and Norway spruce and later by beech (6000 BC) and fir. Other species such as oak, lime or elm are relatively scarce. The first significant human impacts on the appearance of this region occurred during the Middle Ages through expansion of arable land in lower elevations, through gold mining and pasture in forests, which discriminated against beech and fir and in favour of spruce. Later, in the 18th century, the largest areas of the Bohemian Forest were deforested due to the development of glass production, trade, and mining. These activities affected not only the forest area but also tree diversity. Both fir and beech declined. After massive deforestation during the 18th century, planting of spruce monocultures was adopted in the following century in order to provide constant timber production. The monocultures were seriously damaged by a series of windstorms in the years 1868 to 1870 (ČADA et al. 2013). The impact was amplified by previous high forest density and pasture. However, even semi-natural stands that were able to resist the effects of windstorm succumbed to the bark beetle outbreak in that time (ZATLOUKAL 1998). The impacted areas were reforested again by dense spruce monoculture even in the area of naturally occurring mixed forests.

Furthermore, during the second half of the 20th century, the Bohemian Forest experienced the impacts of the Industrial Revolution in similar amounts and rates as the whole of central Europe, which further impaired the forest stands. Until the 1950s, the depositions of SO₄²⁻, NO₃⁻, and NH₄⁺ were relatively stable but increased rapidly in the following thirty years and culminated in the early 1980s (KOPÁČEK et al. 2001, 2010). For the Plešné and Čertovo lakes catchments, the acid deposition was reconstructed and modelled for periods 1850s, 1950s, 1980s and 2020s by KOPÁČEK et al. (2010) as follows (lower values refer to the Plešné catchment probably due to a greater distance downwind from the N and S emission sources): SO₄²⁻ deposition rose from 12–15 (1850s) to 54–66 (1950s), culminated with 111–135 (1980s) and should decline to 13–16 mmol.m⁻².yr⁻¹ by the year 2020 (Fig. 6). N deposition (NO₃⁻ and NH₄⁺) were dominated first by NH₄⁺ (1850–1960), then for four decades by NO₃⁻, and NH₄⁺ should be dominant again after 2010. Nitrate deposition increased from 4 (1850s) to 44

(1950s) and $99 \text{ mmol.m}^{-2}\text{.yr}^{-1}$ (1980s) and should decrease to $35 \text{ mmol.m}^{-2}\text{.yr}^{-1}$ by the year 2020. The values were only by 1–2% higher in the Čertovo catchment. The average value of NH_4^+ deposition for the Bohemian Forest was 37 (1850s), 56 (1950s), and $85 \text{ mmol.m}^{-2}\text{.yr}^{-1}$ (1980s). The modelled deposition by the year 2020 should be $61 \text{ mmol.m}^{-2}\text{.yr}^{-1}$ (KOPÁČEK & HRUŠKA 2010). Acid deposition and, thus, its direct effect on ecosystems have gradually decreased since 1980s (KOPÁČEK et al. 2001, KOPÁČEK & HRUŠKA 2010). In the Czech Republic, S emissions were dramatically reduced by 87% thanks to desulfurisation of power plants and modernisation of technologies. Emissions of N decreased by 51% (NO_x) and by 41% (NH_3) mainly due to decrease in cattle production and the application of synthetic fertilisers (KOPÁČEK & VESELÝ 2005).

Soils of the Bohemian Forest developed on acid parent material of granites and mica-schist and are, therefore, naturally acidic with low content of N and other nutrients, which together with unfavourable climate conditions determined the vegetation cover and soil processes (VESELÝ 1994). Natural acidity and concomitant nutrient depletion and mobilisation of Al^{3+} were exacerbated by the long-term preference for spruce cultivation, which lead to the accumulation of strongly acidic organic matter. The changes were, however, slow, more pronounced in areas where nutrients in biomass were removed by litter raking, tree burning for potash production, and pasturing. Still, the soils remained N-limited, in the 1st to 2nd stage of the N-availability continuum, and N immobilisation was the most important process of N transformations. Acid deposition lasting for decades accelerated acidification, nutrient depletion, and Al^{3+} mobility. Soil acidification over recent decades has been larger than over centuries (MAJER et al. 2003). Drop in pH and nutrient availability together with large N loads and ecosystems history has brought N saturation, and ecosystems shifted to the 3rd or even 4th stage of N-availability continuum in the historically shortest period.

The current status of soils in the upper parts of the Bohemian Forest, natural area of mountain spruce forests, can be illustrated by data from Čertovo and Plešné catchments. At present, soils are strongly acidic with exchangeable $\text{pH}_{\text{CaCl}_2}$ values from 2.5 to 3.3 in the organic horizons (KOPÁČEK et al. 2002a, b, KAŇA et al. 2013, 2014) and base saturation 12–15%

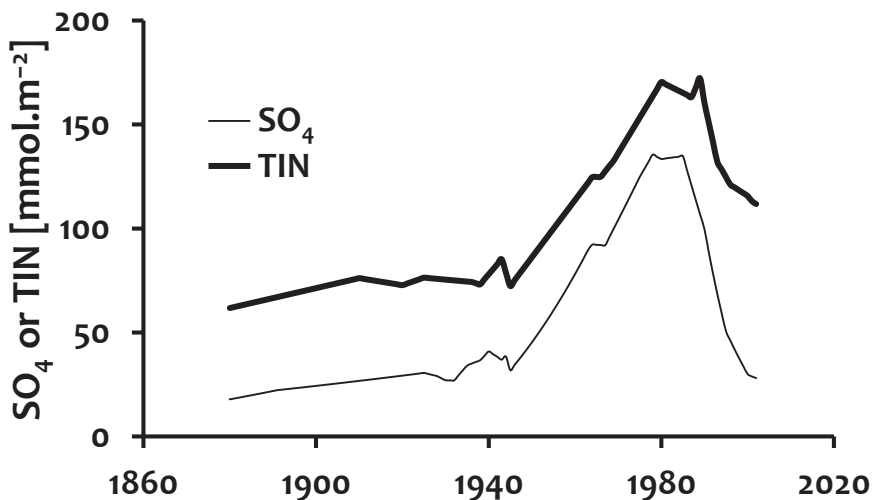


Fig. 6. Long-term trends in atmospheric deposition of N (total inorganic nitrogen; TIN) and S compounds (SO_4) in the Bohemian Forest region.

on average, while the modelled pre-industrial values of base saturation in 1860 were 12–27% (MAJER et al. 2003). High rates of gross N ammonification and nitrification (TAHOVSKÁ et al. 2013) resulted in the excess of mineral N forms in soils (ŠANTRŮČKOVÁ et al. 2001, 2009, SKOPCOVÁ & ŠANTRŮČKOVÁ 2006, KAŇA et al. 2015). It was followed by high N mobility in soils (TAHOVSKÁ et al. 2010) and nutrient leaching to the tributaries (KOPÁČEK et al. 2013b). Soil deterioration negatively affected tree physiology (ŠANTRŮČKOVÁ et al. 2007, unpubl.). Subsequent tree dieback due to bark beetle attack has contemporarily exacerbated N mobility and nutrient depletion (KAŇA et al. 2013). Six to seven years after forest dieback, N mobility in soils started to decrease (TAHOVSKÁ et al. 2010). Furthermore, decrease in N leaching to tributaries has also been measured (KOPÁČEK, pers. comm.).

Linked to the already reviewed information in the previous chapters, changes in the composition of forest stands can also affect soil properties and processes, mainly organic matter decomposition and N transformations. On that account, tree dieback and regeneration of new forests will inevitably affect the recovery of acidified soils. The current practices are removing of the wind-fallen trees. Soil removal into windrows and the harvest of intact wind-fallen trees can have harmful effect on subsequent tree growth because of limited nutrient supply and high Al^{3+} mobility in the acidified soils of this area. The non-intervention regime (i.e. leaving the fallen trees “*in situ*”) that was adopted in the core zones in both national parks (Šumava and Bavarian Forest) is a better option as undamaged forest floor protects soil against erosion and harmful temperature fluctuation (HAIS & KUČERA 2008) and is, together with decaying trees, important source of organic matter and nutrients that are needed for enhancement of soil biological activity and N immobilisation in the soil. Moreover, forest shows natural regeneration, the rate of which was dependent on how severe conditions were at particular sites (HEURICH 2009, HEURICH & ENGLMAIER 2010, NOVÁKOVÁ & EDWARDS-JONÁŠOVÁ 2014). Nitrate concentrations in runoff increased significantly after forest dieback but only temporarily (OULEHLE et al. 2013, BEUDERT et al. 2014). After ten years regeneration has been observed in nearly all (99.9%) inventory plots on the Bavarian side (HEURICH 2009). On the Czech side, regeneration at non-intervention and even at clear-cut and reforested plots was also observed (ZATLOUKAL et al. 2001, JONÁŠOVÁ 2001, JONÁŠOVÁ & PRACH 2004, ČÍŽKOVÁ et al. 2011). The tree species composition of the regenerated forest stands was, however, much closer to the natural forest conditions at non-intervention plots (JONÁŠOVÁ & MATĚJKOVÁ 2007). The regeneration of Norway spruce was positively affected when plots were left without any management. ZATLOUKAL et al. (2001) concludes that the regeneration of spruces under dead trees and at the clear-cut plots is sufficient for re-establishment of a new forest generation and that reforestation is, therefore, inappropriate. The contribution of other tree species (such as rowan, *Sorbus aucuparia*, or sycamore maple, *Acer pseudoplatanus*) to regeneration is, however, quite small and should be fostered (ZATLOUKAL et al. 2001).

In the late 1990s, bark beetle attacked forest stands in the Březník area located in the central part of the Šumava NP. Some parts were then left without any forest management, while in some sites clear-cutting with log removal followed by wood and bark chips application was adopted (ZATLOUKAL, pers. comm.). It has been now more than one decade since this huge natural and in some parts also anthropogenic disturbance and all the sites went through succession. Long-term research in this area further documents that used management changed moisture and temperature regimes (HAIS & KUČERA 2008), which together with mechanical disruption and partial removal of forest floor and soil fermentation layers enhanced the abundance of *Calamagrostis* and slowed down forest regeneration (NOVÁKOVÁ & EDWARDS-JONÁŠOVÁ 2015). Moreover, the soil disruption was accompanied by shifts in the functional groups of soil mesofauna (FARSKÁ et al. 2014). Long-term effect of management

on soil properties was summarised by STAŇKOVÁ (2013). Briefly, most of the soil properties were more variable within the non-intervention sites compared to the clear-cut sites. The C:N ratio of the Březník soils ranged from 20.5 to 41.5 and was, in general, lower at clear-cut plots. Moreover, in the litter layer, the C:N ratio was the highest for soils under moss and dwarf shrubs (around 30), while it was the lowest (and thus at higher risk of N leaching) under grass vegetation (mean values were around 25). Microbial biomass N was significantly higher at the clear-cut plots, which was accompanied with lower C:N ratio of the microbial biomass, as well as with lower soil C:N ratio (STAŇKOVÁ 2013). An explanation can be the general dominance of grass species (*Calamagrostis villosa* and *Avenella flexuosa*) at the clear-cut plot that have been reported to have low C:N ratio of their biomass (WARDLE et al. 2003). The expansion of grass species may be connected with adverse changes in soil chemistry, such as increase in availability of N and Al³⁺, decrease in base cations content, and overall cation-exchange capacity (KRAUSOVÁ 2011), as already mentioned above.

SPRUCE FORESTS OF CENTRAL EUROPE

Most of the spruce forest ecosystems in central Europe are acidified as the result of the cumulative effect of long-lasting atmospheric depositions of S and N and the acidifying effect of spruce monocultures (HRUŠKA & CIENCIALA 2005, EMMER et al. 2006, KOPÁČEK & POSCH 2011, BINKLEY & FISHER 2012). While the N and S loads were already reduced several decades ago, their acidifying effect still persists and is amplified in spruce forest soils under continuous pressure from forestry (HRUŠKA et al. 2002). Recovery of the spruce forest ecosystem is dependent on recovery of soil chemistry and biochemistry, which require decades in most cases (DRISCOLL et al. 2001). The future models suggest that recovery will be delayed by the removal of base cations through harvesting (OULEHLE et al. 2007). The detrimental effect of acidification and long-term N load can be mitigated by appropriate forest management, which should necessarily respect the current state of knowledge.

Besides marked acid deposition enhancement since the 1950s, soils have been exposed to chronic N deposition from anthropogenic sources over the last 10,000 years and its effect could play an important role in N cycling, especially in Europe where cumulative anthropogenic N emissions on a land area basis have been much higher than globally (KOPÁČEK & POSCH 2011). In the acid spruce forest soils that were exposed to high N loads, processes of N mineralisation can exceed N immobilisation and the surplus nitrate produced causes N and base cations losses from the soils. Nowadays spruce forest ecosystems are apparently in the 3rd and 4th stages of the N-availability gradient (N saturation) with the excess mineral N being most likely triggered by C limitation of microbial metabolism and thus lowered N immobilisation into microbial biomass. Liming, which represents one of the most important measures of silviculture to mitigate the effect of acid deposition, cannot itself alleviate the negative effects of acidification. Liming was even followed by increased rates of nitrification and nitrate leaching in central Europe, especially at the sites previously loaded by N (MATZNER & MEIWES 1991, KREUTZER 1995, MEIWES 1995, BINKLEY & HÖGGER 1997, NOVÁK 2000). The effect of acidification can be rather relieved by management practices, which increase the input and quality of organic matter. These include changing the tree species composition towards deciduous trees in lower altitudes, increasing the contribution of pioneer and soil-improving species, supporting natural regeneration, preferring selective logging over clear-cutting and leaving decaying wood standing or fallen in connection with regeneration.

CONCLUSIONS

Mountain spruce forest ecosystems in the high elevations of the Bohemian Forest (core zones of both national parks), which developed in harsh climate conditions and on sparse and thin, nutrient poor, and acid soils, usually exhibit a limited ability to retain N. This, together with, in general, larger quantities of N deposited in mountain than lowland areas, could have decreased the soil C:N ratio long before they were affected by humans, and predisposed their sensitivity to N saturation during the later, industrial period. In such areas, soil protection against mechanical disturbance, increased biodiversity, and input of nutrients from decaying wood are crucial. Priority should be given to natural developmental processes and a non-intervention regime should be applied. Such a conclusion is supported by the results of the long-term research presented in this review and elsewhere.

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