

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

**Pavla Staňková, Karolina Tahovská & Hana Šantrůčková\***

*University of South Bohemia, Faculty of Science, Branišovská 31, CZ-37005 České Budějovice, Czech Republic*

\* hana.santruckova@prf.jcu.cz

## 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  $\text{Al}^{3+}$  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 ( $\text{NO}_3^-$ ) 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  $\text{N}_2$  in the soil atmosphere). Some forms are in insoluble organic and inorganic material or bound to soil organo-mineral complexes (ammonium  $\text{NH}_4^+$ , polar organics), while the others (nitrates  $\text{NO}_3^-$ , 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  $\text{NH}_4^+$ . 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  $\text{NH}_4^+$  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

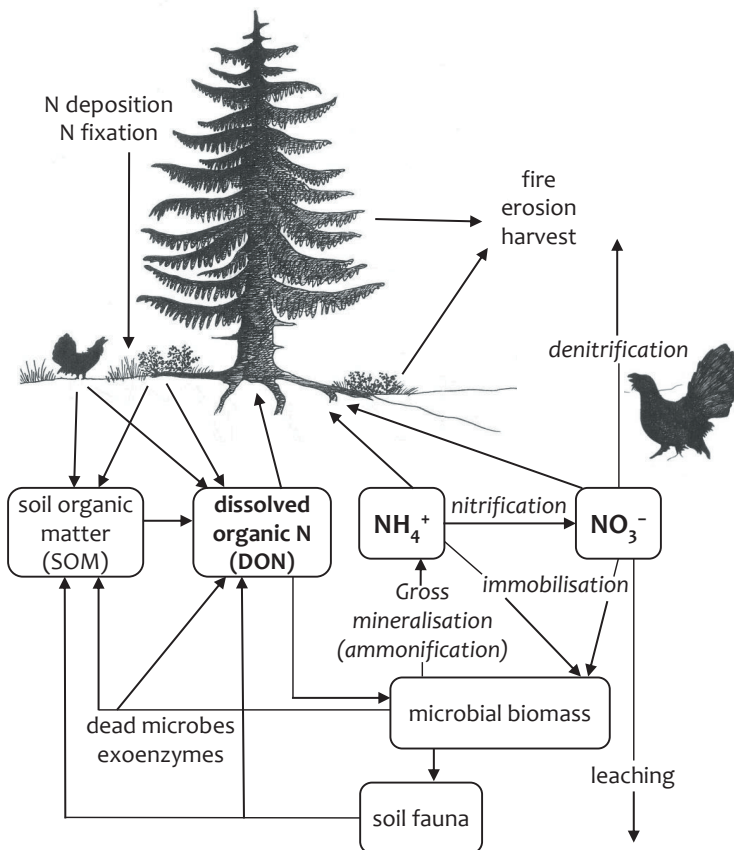


Fig. 1. Scheme of N cycling in the forest soil (adapted from CHAPIN et al. 2002).

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).

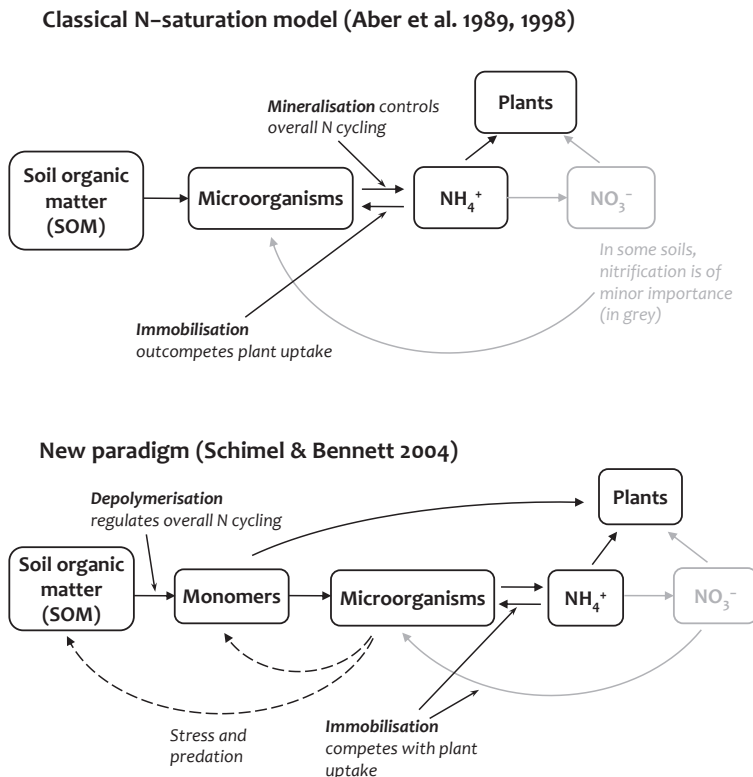
Natural unpolluted spruce forests represent typical N-depleted (N-limited) ecosystems with slow-growing trees and understory vegetation with low nutrient demands (TAMM 1991). A large part of N sources in such forest soils is represented by insoluble complex organic N forms with slow turnover, thus being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

(NÅSHOLM et al. 1998, JONES & KIELLAND 2002, MYRÖLD 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  $\text{NH}_4^+$ . 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  $\text{NH}_4^+$ , starts to dominate over organic N, plants utilise more mineral N, which can promote primary production and increase N concentration in plant biomass.  $\text{NH}_4^+$  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  $\text{NH}_4^+$  remains for nitrifiers and the ecosystem becomes  $\text{NO}_3^-$  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).

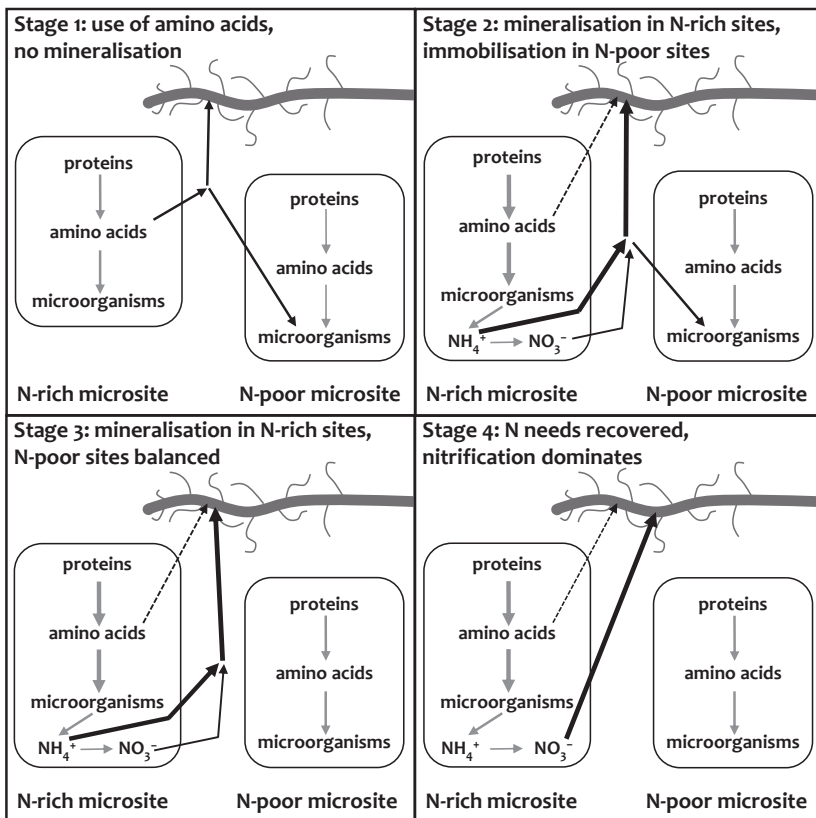
#### The importance of C:N ratio in the N transformation

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-



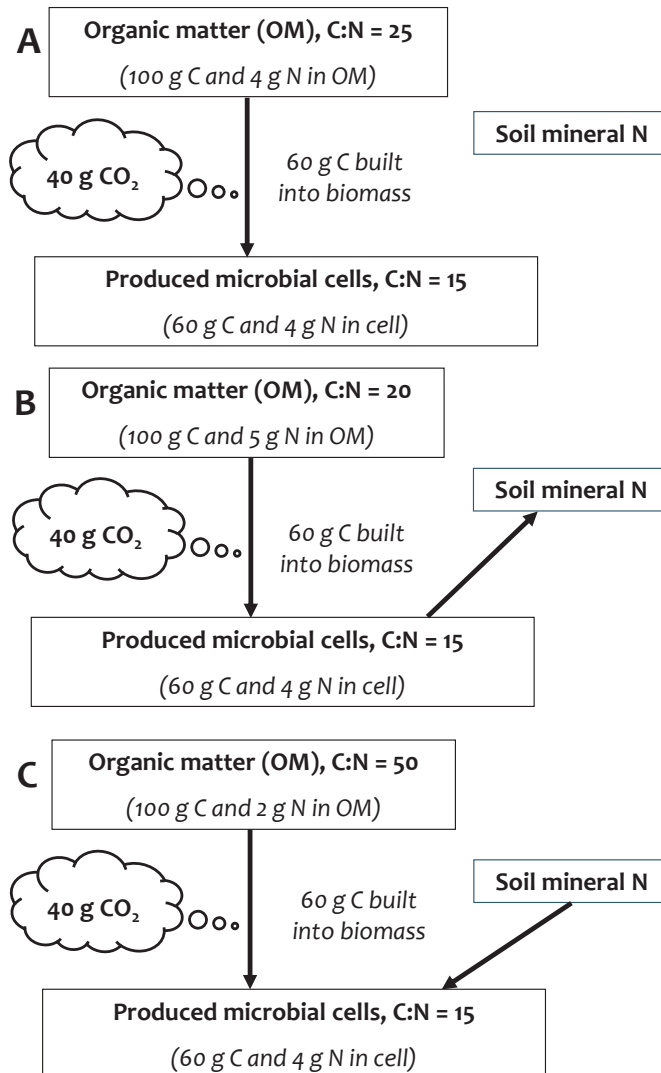
SELER et al. 2010). In reverse, if N content of the consumed material is high, C is limiting relative to N (low C:N ratio). Microorganisms use N-containing organic compounds not only as a C and N source but also solely as a C source, and release the excess N in the form of  $\text{NH}_4^+$  (shift from 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  $\text{NH}_4^+$  and  $\text{NO}_3^-$  and plants and microbes use them as N source. Stages 3-4: Along the N gradient,  $\text{NH}_4^+$  and  $\text{NO}_3^-$  availability increase bringing about excess of  $\text{NO}_3^-$ , 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  $\text{CO}_2$  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  $\text{NO}_3^-$  immobilisation in N-saturated forests was positively related to C availability, which prevents  $\text{NO}_3^-$  leaching. They found a negative correlation between  $\text{NO}_3^-$  microbial immobilisation and C availability, which indicates that C limitation is a controlling factor of susceptibility of N-saturated soils to  $\text{NO}_3^-$  leaching. When the soil C:N ratio decreases, C limitation of microbial metabolism can appear, resulting in decreased N immobilisation. This leads to enhanced  $\text{NH}_4^+$  availability for nitrification and produced  $\text{NO}_3^-$  cannot be, similarly to  $\text{NH}_4^+$ , 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 CO<sub>2</sub> 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 NH<sub>4</sub><sup>+</sup> in soil is high (BENGTSON & BENGTSSON 2005). A unique group of heterotrophic bacteria is N<sub>2</sub>-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<sup>-1</sup>.yr<sup>-1</sup> (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, NH<sub>4</sub><sup>+</sup> is favoured over NO<sub>3</sub><sup>-</sup> 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 NO<sub>3</sub><sup>-</sup> immobilisation is suppressed by high soil NH<sub>4</sub><sup>+</sup> concentration (PAUL & CLARK 1996, MYROLD 2005, TAYLOR & TOWNSEND 2011). However, important NO<sub>3</sub><sup>-</sup> immobilisation has been observed even at high NH<sub>4</sub><sup>+</sup> 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 NH<sub>4</sub><sup>+</sup> 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  $\text{NH}_4^+$ , into the soil in the early stage of decomposition and can temporarily increase  $\text{NH}_4^+$  flux into the soil in the autumn and winter period. In this period,  $\text{NH}_4^+$  can be transformed to  $\text{NO}_3^-$  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  $\text{N}_2$  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  $\text{N}_2$ -fixing bacteria can significantly affect N availability in forest ecosystems. A meta-analysis revealed that symbiotic  $\text{N}_2$ -fixing bacteria can account for significantly more N than N fertilisation or atmospheric deposition inputs, when  $\text{N}_2$ -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,  $\text{N}_2$ -fixing leguminous (e.g., lupin, *Lupinus*, and clover, *Trifolium*) or nonleguminous herbs and grasses which can host associative  $\text{N}_2$ -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<sup>-1</sup>.y<sup>-1</sup> (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, BÁRTA 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 20<sup>th</sup> 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 19<sup>th</sup> 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  $\text{NO}_3^-$  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  $\text{NH}_4^+$  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,  $\text{NO}_3^-$  is in excess, which leads to  $\text{NO}_3^-$  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,  $\text{NO}_3^-$  concentration was low in most cases. The isotopic measurements showed that the vast majority of  $\text{NO}_3^-$  produced was immobilised into microbial biomass. The authors proved that soil microorganisms have the capacity to assimilate  $\text{NO}_3^-$  and, thus, prevent their leaching from the soil. They also suggested that a decrease in microbial immobilisation



of  $\text{NO}_3^-$  may result in greater availability of  $\text{NH}_4^+$  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 ( $\text{NO}_3^-$ ,  $\text{SO}_4^{2-}$ ) 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  $\text{NH}_4^+$  in excess and, in parallel, the pool of bioavailable organic matter decreases due to (i) the enhanced mineralisation of available organic matter to  $\text{CO}_2$ , and (ii) the reduced release of organic material from recalcitrant organic C by fungal activity. Consequently, the ecosystem moves from N limitation to C

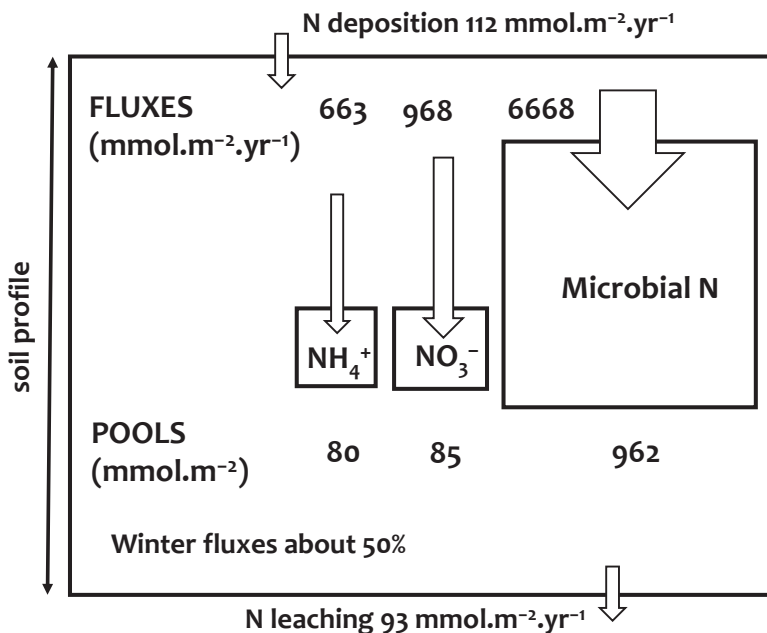


Fig. 5. Microbial and mineral pools of N in N-saturated acidified soil of the Plešné Lake catchment.

limitation and less organic material remains available for microbial growth. Produced  $\text{NH}_4^+$  cannot be immobilised by heterotrophic microbes, the growth of which is C-limited, leaving more  $\text{NH}_4^+$  for nitrifiers. As a result,  $\text{NO}_3^-$  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  $\text{NO}_3^-$  production. Produced  $\text{NO}_3^-$  cannot be removed by denitrification or microbial immobilisation as denitrifiers and heterotrophic microbes are limited by low C availability, and  $\text{NO}_3^-$  thus remain in the soil in excess. Altogether, the ecosystem moves from the 3<sup>rd</sup> to the 4<sup>th</sup> 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,  $\text{NH}_4^+$  remains available for nitrifiers, and the resulting excess of  $\text{NO}_3^-$  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 1<sup>st</sup> or 2<sup>nd</sup> stage of the N-availability gradient, moves towards the 3<sup>rd</sup> or 4<sup>th</sup> 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  $\text{NO}_3^-$  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  $\text{NO}_3^-$  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  $\text{NO}_3^-$  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 3<sup>rd</sup> or 4<sup>th</sup> 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 3<sup>rd</sup> and 4<sup>th</sup> 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<sup>+</sup> are consumed. Even though the pH increase is only short term, it shifts the NH<sub>4</sub><sup>+</sup> equilibrium towards NH<sub>3</sub>, 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 NH<sub>4</sub><sup>+</sup> can also be immobilised by microbes in the forest floor or nitrified to NO<sub>3</sub><sup>-</sup> 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 1<sup>st</sup> or 2<sup>nd</sup> 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, N<sub>2</sub> 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 N<sub>2</sub> fixation can increase N content in soil and soil N mineralisation in forests with high abun-

dance of N<sub>2</sub>-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 N<sub>2</sub>-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 N<sub>2</sub>-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 N<sub>2</sub> 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**

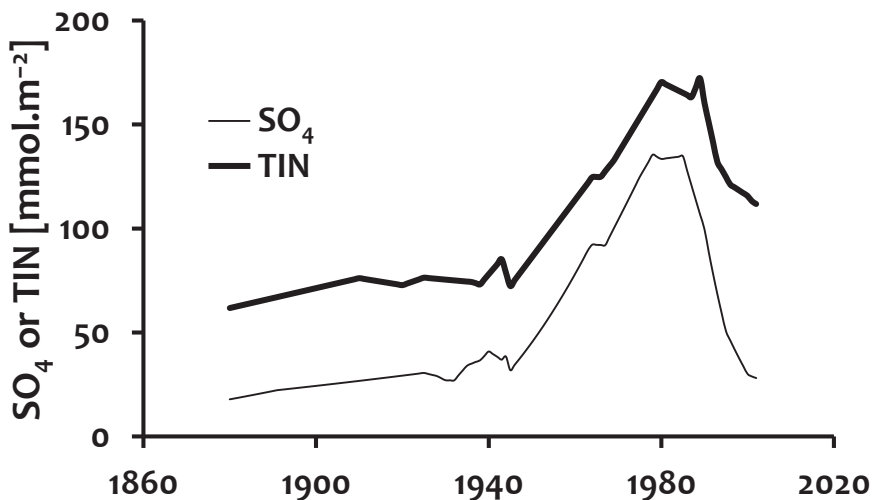
The historical evolution of forests has been traced back by BENEŠ (1995). Briefly, in the region of the Bohemian Forest, origins of the forests can be dated back to the beginning of Holocene. The first tree “invaders” were willow, birch, and pine, followed by hazel (around 7000 BC) and Norway spruce 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 18<sup>th</sup> 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 18<sup>th</sup> 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 20<sup>th</sup> 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 SO<sub>4</sub><sup>2-</sup>, NO<sub>3</sub><sup>-</sup>, and NH<sub>4</sub><sup>+</sup> 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): SO<sub>4</sub><sup>2-</sup> deposition rose from 12–15 (1850s) to 54–66 (1950s), culminated with 111–135 (1980s) and should decline to 13–16 mmol.m<sup>-2</sup>.yr<sup>-1</sup> by the year 2020 (Fig. 6). N deposition (NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>) were dominated first by NH<sub>4</sub><sup>+</sup> (1850–1960), then for four decades by NO<sub>3</sub><sup>-</sup>, and NH<sub>4</sub><sup>+</sup> 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  $\text{NH}_4^+$  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% ( $\text{NO}_x$ ) and by 41% ( $\text{NH}_3$ ) 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  $\text{Al}^{3+}$  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 1<sup>st</sup> to 2<sup>nd</sup> 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  $\text{Al}^{3+}$  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 3<sup>rd</sup> or even 4<sup>th</sup> 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 ( $\text{SO}_4$ ) 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 Al<sup>3+</sup>, 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 3<sup>rd</sup> and 4<sup>th</sup> 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.

**Acknowledgement.** This study was conducted within the framework of the projects CSF 41-504/121/1218 and GAJU 04-146/2013/P. We thank Gabriela Scott Zemanová, Ryan A. Scott, and Keith Edwards for the language corrections.

## REFERENCES

- ABER J.D., NADELHOFFER K.J., STEUDLER P. & MELILLO J.M., 1989: Nitrogen saturation in northern forest ecosystems. *BioScience*, 39: 378–386.
- ABER J.D., MELILLO J.M. & McCLAUGHERTY C.A., 1990: Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Canadian Journal of Botany*, 68: 2201–2208.
- ABER J.D., McDOWELL W., NADELHOFFER K., MAGILL A., BERNTSON G., KAMAKEA M., McNULTY S., CURRIE W., RUSTAD L. & FERNANDEZ I., 1998: Nitrogen saturation in temperate forest ecosystems. *BioScience*, 48: 921–934.
- ABER J.D., OLLINGER S.V., DRISCOLL C.T., LIKENS G.E., HOLMES R.T., FREUDER R.J. & GOODALE C.L., 2002: Inorganic N losses from a forested ecosystem in response to physical, chemical, biotic and climatic perturbations. *Ecosystems*, 5: 648–658.
- ÅGREN, G.I. & BOSATTA, E., 1988: Nitrogen saturation of terrestrial ecosystems. *Environmental Pollution*, 54: 185–197.
- ANDERSSON P. & BERGGREN D., 2005: Amino acids, total organic and inorganic nitrogen in forest floor soil solution at low and high nitrogen input. *Water, Air and Soil Pollution*, 162: 369–384.
- ARNEBRANT K., BÄÄTH E., SODERSTROM B. & NOHRSTEDT H.O., 1996: Soil microbial activity in eleven Swedish coniferous forests in relation to site fertility and nitrogen fertilization. *Scandinavian Journal of Forest Research*, 11: 1–6.
- AUGUSTO L. & RANGER J., 2001: Impact of tree species on soil solutions in acidic conditions. *Annals of Forest Science*, 58: 47–58.
- Bääth E. & Anderson T.H., 2003: Comparison of soil fungal/bacterial ratios in a pH gradient using physiological and PLFA-based techniques. *Soil Biology and Biochemistry*, 35: 955–963.
- BAIER R., MEYER J. & GOTTLIN A., 2005: Regeneration niches of Norway spruce (*Picea abies* [L.] Karst.) saplings in small canopy gaps in mixed mountain forests of the Bavarian Limestone Alps. *European Journal of Forest Research*, 126: 11–22.
- BARDGETT R.D., MANNING P., MORRIÉN E. & DE VRIES F.T., 2013: Hierarchical responses of plant–soil interactions to climate change: consequences for the global carbon cycle. *Journal of Ecology*, 101: 334–343.
- BARRACLOUGH D. & PURI G., 1995: The use of <sup>15</sup>N pool dilution and enrichment to separate the heterotrophic and autotrophic pathways of nitrification. *Soil Biology and Biochemistry*, 27: 17–22.
- BÁRTA J., APPLOVÁ M., VANĚK D., KRÍŠTŮFKOVÁ M. & ŠANTRŮČKOVÁ H., 2010: Effect of available P and phenolics on mineral N release in acidified spruce forest: connection with lignin-degrading enzymes and bacterial and fungal communities. *Biogeochemistry*, 97: 71–87.
- BENES J., 1995: Les a bezlesí. Vývoj synantropizace české části Šumavy – Wald und abgerodete Landschaft. Die Entwicklung der synantropischen Prozesse in böhmischen Teil des Böhmerwaldes [Woodland and secondary grassland in Bohemian forest. History of human influence on primeval Holocene forest from archaeological and historical perspective]. *Zlatá stezka, Sborník Prachatického muzea*, 2: 11–33 (in Czech).
- BENGTSON P. & BENGTSSON G., 2005: Bacterial immobilization and remineralization of N at different growth rates and N concentrations. *FEMS Microbiology Ecology*, 54: 13–19.

- BERG B., 2000: Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology and Management*, 133: 13–22.
- BERG B. & EKBÖHM G., 1991: Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long term decomposition in a Scots pine forest. VII. *Canadian Journal of Botany*, 69: 1449–1456.
- BERG B. & LASKOWSKI R., 2006: *Litter decomposition: A guide to carbon and nutrient turnover. Advances in Ecological research. Vol 38.* Elsevier, San Diego, 428 pp.
- BERG B., STEFFEN K.T. & McCLAUGHERTY C., 2007: Litter decomposition rate is dependent on litter Mn concentrations. *Biogeochemistry*, 82: 29–39.
- BINKLEY D. & HÖGGER P., 1997: Does atmospheric deposition of nitrogen threaten Swedish forests? *Forest Ecology and Management*, 92: 119–152.
- BINKLEY D. & GIARDINA CH., 1998: Why do tree species affect soils? The Warp and Woof of tree–soil interactions. *Biogeochemistry*, 42: 89–106.
- BINKLEY D. & FISHER R.F., 2012: *Ecology and Management of Forest Soils. 4<sup>th</sup> edition.* Wiley, New York, 347 pp.
- BLAGODATSKAYA E.V. & ANDERSON T.H., 1998: Interactive effects of pH and substrate quality on the fungal-to-bacterial ratio and qCO<sub>2</sub> of microbial communities in forest soils. *Soil Biology and Biochemistry*, 30: 1269–1274.
- BOBERG J.B., FINLAY R.D., STENLID J. & LINDAHL B.D., 2010: Fungal C translocation restricts N-mineralization in heterogeneous environments. *Functional Ecology*, 24: 454–459.
- BOBERG J.B., FINLAY R.D., STENLID J., EKBLAD A. & LINDAHL B.D., 2014: Nitrogen and carbon reallocation in fungal mycelia during decomposition of boreal forest litter. *Plos One*, 9: e92897.
- BOHRMANN F.H., LIKENS G.E., FISHER D.W. & PIERCE R.S., 1968: Nutrient loss accelerated by clear-cutting of a forest ecosystem. *Science*, 159: 882–884.
- BOOTH M.S., STARK J.M. & RASTETTER E., 2005: Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. *Ecological Monographs*, 75: 139–157.
- BOTHE H., FERGUSON S.J. & NEWTON W.E. (eds), 2007: *Biology of the Nitrogen Cycle.* Elsevier, Amsterdam, 427 pp.
- BRADY N.C. & WEIL R.R. (eds), 2002: *The nature and properties of soils. 13<sup>th</sup> edition.* Upper Saddle River, New Jersey, 960 pp.
- BYRD K.B., PARKER V.T., VOGLER D.R. & CULLINGS K.W., 2000: The influence of clear-cutting on ectomycorrhizal fungus diversity in a lodgepole pine (*Pinus contorta*) stand, Yellowstone National Park, Wyoming, and Gallatin National Forest, Montana. *Canadian Journal of Botany*, 78: 149–156.
- ČÁDA V., SVOBODA M. & JANDA P., 2013: Dendrochronological reconstruction of the disturbance history and past development of the mountain Norway spruce in the Bohemian Forest, central Europe. *Forest Ecology and Management*, 295: 59–68.
- CAMPBELL J.L., SOCCI A.M. & TEMPLER P.H., 2014: Increase nitrogen leaching following soil freezing in due to decreased root uptake in a northern hardwood forest. *Global Change Biology*, 20: 2663–2673.
- CHEN H., MOTHAPPO N.V. & SHI W., 2015. Soil Moisture and pH Control Relative Contributions of Fungi and Bacteria to N<sub>2</sub>O Production. *Microbial Ecology*, 69: 180–191.
- CHAPIN F.S. III, MATSON P.A. & MOONEY H.A. (eds), 2002: *Principles of terrestrial ecosystem ecology. 1<sup>st</sup> edition.* Springer, New York, 450 pp.
- CHAPMAN S.K., LANGLEY J.A., HART S.C. & KOCH G.W., 2006: Plants actively control nitrogen cycling: uncorking the microbial bottleneck. *New Phytologist*, 169: 27–34.
- ČÍŽKOVÁ P., SVOBODA M. & KRÉNOVÁ Z., 2011: Natural regeneration of acidophilous spruce mountain forests in non-intervention management areas of the Šumava National Park – the first results of the Biomonitoring project. *Silva Gabreta*, 17: 19–35.
- CULLINGS K. & COURTY P.E., 2009: Saprotrophic capabilities as functional traits to study functional diversity and resilience of ectomycorrhizal community. *Oecologia*, 161: 661–664.
- CUMMINS T. & FARRELL E.P., 2003: Biogeochemical impacts of clearfelling and reforestation on blanket-peatland streams – II. major ions and dissolved organic carbon. *Forest Ecology and Management*, 180: 557–570.
- DELUCA T.H. & ZOUHAR K.L., 2000: Effects of selection harvest and prescribed fire on the soil nitrogen status of ponderosa pine forests. *Forest Ecology and Management*, 138: 263–271.
- DELUCA T.H., ZACKRISSON O., NILSSON M.C. & SELLSTEDT A., 2002: Quantifying nitrogen-fixation in feather moss carpets of boreal forests. *Nature*, 419: 917–920.
- DEMOLING F., NILSSON L.O. & BÅÅTH E., 2008: Bacterial and fungal response to nitrogen fertilization in three coniferous forest soils. *Soil Biology and Biochemistry*, 40: 370–379.
- DEVINE W.D., FOOTEN P.W., STRAHM B.D., HARRISON R.B., TERRY T.A. & HARRINGTON T.B., 2012: Nitrogen leaching following whole-tree and bole-only harvests on two contrasting Pacific Northwest sites. *Forest Ecology and Management*, 267: 7–17.
- DISE N.B., MATZNER E. & FORSIUS M., 1998: Evaluation of organic horizon C:N ratio as an indicator of nitrate

- leaching in conifer forests across Europe. *Environmental Pollution*, 102(S1): 453–456.
- DORREN L.K.A., BERGER F., IMESON A.C., MAIER B. & REY F., 2004: Integrity, stability and management of protection forests in the European Alps. *Forest Ecology and Management*, 195: 165–176.
- DRISCOLL C.T., LAWRENCE G.B., BULGER A.J., BUTLER T.J., CRONAN, C.S., EAGAR C., LAMBERT K.F., LIKENS G.E., STODDARD J.L. & WEATHERS K.C., 2001: Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies. *BioScience*, 51: 180–198.
- DUNN R.M., MIKOLA J., BOL R. & BARDGETT R.D., 2006: Influence of microbial activity on plant–microbial competition for organic and inorganic nitrogen. *Plant Soil*, 289: 321–334.
- EDMAN M., MÖLLER R. & ERICSON L., 2006: Effects of enhanced tree growth rate on the decay capacities of three saprotrophic wood-fungi. *Forest Ecology and Management*, 232: 12–18.
- EMMER I.M., WESSEL W.W., KOOIJMAN A., SEVINK J. & FANTA J., 2000: Restoration of degraded Central-European mountain forest soils under changing environmental circumstances. In: *Spruce Monocultures in Central Europe: Problems and Prospects. EFI Proceedings No 33*, KLIMO E., HAGER, H. & KULHAVÝ J. (eds) European Forest Institute, Finland: 81–92.
- EMMETT B.A., 1999: The impact of nitrogen on forest soils and feedbacks on tree growth. *Water, Air and Soil Pollution*, 116: 65–74.
- EMMETT, B.A., 2007: Nitrogen Saturation of Terrestrial Ecosystems: Some recent findings and their implications for our conceptual framework. *Water, Air, & Soil Pollution*, 7: 99–109.
- ENTRY J.A., STARK N.M. & LOEWENSTEIN H., 1986: Effect of timber harvesting on microbial biomass fluxes in a northern rocky-mountain forest soil. *Canadian Journal of Forest Research*, 16: 1076–1081.
- ERIKSSON H.M. & ROSEN K., 1994: Nutrient distribution in a Swedish tree species experiment. *Plant and Soil*, 164: 51–59.
- EVANS C.D., REYNOLDS B., JENKINS A., HELLIWELL R.C., CURTIS C.J., GOODALE C.L., FERRIER R.C., EMMETT B.A., PILKINGTON M.G., CAPORN S.J.M., CARROLL J.A., DAVIES J. & COULL M.C., 2006: Evidence that soil carbon pool determines susceptibility of semi-natural ecosystems to elevated nitrogen leaching. *Ecosystems*, 9: 453–462.
- EVANS C.D., NORRIS D., OSTLE N., GRANT H., ROWE E.C., CURTIS C.J. & REYNOLDS B., 2008: Rapid immobilisation and leaching of wet-deposited nitrate in upland organic soils. *Environmental Pollution*, 156: 636–643.
- FARSKÁ J., PREJZKOVÁ K. & RUSEK J., 2014: Management intensity affects traits of soil microarthropod community in montane spruce forest. *Applied Soil Ecology*, 75: 71–79.
- FENTON N.J., FREGO K.A. & SIMS M.R., 2003: Changes in forest floor bryophyte (moss and liverwort) communities 4 years after forest harvest. *Canadian Journal of Botany*, 81: 714–731.
- FIALA K., TŮMA I., HOLUB P. & JANDAČ J., 2005: The role of *Calamagrostis* communities in preventing soil acidification and base cation losses in a deforested mountain area affected by acid deposition. *Plant and Soil*, 268: 35–49.
- FORGE T.A. & SIMARD S.W., 2000: Trophic structure of nematode communities, microbial biomass, and nitrogen mineralization in soils of forests and clearcuts in the southern interior of British Columbia. *Canadian Journal of Soil Science*, 80: 401–410.
- GALLARDO A. & MERINO J., 1993: Leaf decomposition in two mediterranean ecosystems of southwest Spain: Influence of substrate quality. *Ecology*, 74: 152–161.
- GALLOWAY J.N., 1998: The global nitrogen cycle: Changes and consequences. *Environmental Pollution*, 102(S1): 15–24.
- GEISELLER D., HORWATH W.R., JOERGENSEN R.G. & LUDWIG B., 2010: Pathways of nitrogen utilization by soil microorganisms – a review. *Soil Biology and Biochemistry*, 42: 2058–2067.
- GONOD V.L., JONES D.L. & CHENU C., 2006: Sorption regulates the fate of amino acids lysine and leucine in soil aggregates. *European Journal of Soil Science*, 57: 320–329.
- GRAYSTON S.J. & RENNENBERG H., 2006: Assessing effects of forest management on microbial community structure in a central European beech forest. *Canadian Journal of Soil Science*, 36: 2595–2604.
- GUNDERSEN P., CALLESEN I. & DE VRIES W., 1998: Nitrate leaching in forest ecosystems is related to forest floor C/N ratios. *Environmental Pollution*, 102(S1): 403–407.
- GUNDERSEN P., EMMETT B.A., KJØNAAS O.J., KOOPMANS C.J. & TIETEMA A., 1998: Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data. *Ecological Management*, 101: 37–55.
- GUNDERSEN P., SCHMIDT I.K. & RAULUND-RASMUSSEN K., 2006: Leaching of nitrate from temperate forests – effects of air pollution and forest management. *Environmental Reviews*, 14: 1–57.
- HAIS M. & KUČERA T., 2008: Surface temperature change of spruce forest as a result of bark beetle attack: remote sensing and GIS approach. *European Journal of Forest Research*, 127: 327–336.
- HANSSON K., OLSSON B.A., OLSSON M., JOHANSSON U. & KLEJJA D.B., 2011: Differences in soil properties in adjacent stands of Scots pine, Norway spruce and silver birch in SW Sweden. *Forest Ecology and Management*, 262: 522–530.
- HARTMANN H., DAoust G., BIGUÉ B. & MESSIER C., 2010: Negative or positive effects of plantation and intensive forestry on biodiversity: A matter of scale and perspective. *Forestry Chronicle*, 86: 354–364.

- HAYNES B.E. & GOWER S.T., 1995: Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. *Tree Physiology*, 15: 317–325.
- HAZLETT P.W., GORDON A.M., VORONEY R.P. & SIBLEY P.K., 2007: Impact of harvesting and logging slash on nitrogen and carbon dynamics in soils from upland spruce forests in northeastern Ontario. *Soil Biology and Biochemistry*, 39: 43–57.
- HEURICH M., 2009: Progress of forest regeneration after a large-scale *Ips typographus* outbreak in the subalpine *Picea abies* forest of the Bavarian Forest National Park. *Silva Gabreta*, 15: 49–66.
- HEURICH M. & ENGLMAIER K.H., 2010: The development of tree species composition in the Rachel–Lusen region of the Bavarian Forest National Park. *Silva Gabreta*, 16: 165–186.
- HOBBIE S.E., 1992: Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution*, 7: 336–339.
- HOBBIE S.E., 1996: Temperature and plant species control over litter decomposition in Alaska tundra. *Ecological Monographs*, 66: 503–522.
- HOBBIE S.E., REICH P.B., OLEKSYN J., OGDahl M., ZYTKOWIAK R., HALE C. & KAROLEWSKI P., 2006: Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology*, 87: 2288–2897.
- HODGE A., ROBINSON D. & FITTER A., 2000: Are microorganisms more effective than plants at competing for nitrogen? *Trends in Plant Science*, 5: 304–308.
- HÖGBERG M.N. & HÖGBERG P., 2002: Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. *New Phytologist*, 154: 791–795.
- HÖGBERG P., FAN H., QUIST M., BINKLEY D. & TAMM C.O., 2006: Tree growth and soil acidification in response to 30 years of experimental nitrogen loading on boreal forest. *Global Change Biology*, 12: 489–499.
- HÖGBERG M.N., CHEN Y. & HÖGBERG P., 2007: Gross nitrogen mineralisation and fungi-to-bacteria ratios are negatively correlated in boreal forests. *Biology and Fertility of Soils*, 44: 363–366.
- HÖGBERG M.N., BRIONES M.J.I., KEEL S.G., METCALFE D.B., CAMPBELL C., MIDWOOD A.J., THORNTON B., HURRY V., LINDER S., NASHOLM T. & HÖGBERG P., 2010: Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. *New Phytologist*, 187: 485–493.
- HÖGBERG M.N., BLAŠKO R., BACH L.H., HASSELQUIST N.J., EGNELL G., NASHOLM T. & HÖGBERG P., 2014: The return of an experimentally N-saturated boreal forest to an N-limited state: observations on the soil microbial community structure, biotic N retention capacity and gross N mineralisation. *Plant and Soil*, 381: 45–60.
- HOMYAK P.M., YANAI R.D., BURNS D.A., BRIGGS R.D. & GERMAIN R.H., 2008: Nitrogen immobilization by wood-chip application: Protecting water quality in a northern hardwood forest. *Forest Ecology and Management*, 255: 2589–2601.
- HOULTON B.Z., DRISCOLL C.T., FAHEY T.J., LIKENS G.E., GROFFMAN P.M., BERNHARDT E.S. & BUSO D.C., 2003: Nitrogen dynamics in Ice storm-damaged forest ecosystems: Implication for nitrogen limitation theory. *Ecosystems*, 6: 431–443.
- HŘUŠKA J., MOLDAN F. & KRÁM P., 2002: Recovery from acidification in central Europe – observed and predicted changes of soil and streamwater chemistry in the Lysina catchment, Czech Republic. *Environmental Pollution*, 120: 261–274.
- HŘUŠKA J. & CIENCIALA E., 2005: *Dlouhodobá acidifikace a nutriční degradace lesních půd – limitující faktor současného lesnictví* [Long-term acidification and nutrition degradation of forest soils – limiting factors of current forestry. 2<sup>nd</sup> edition]. Česká geologická služba, Praha, 159 pp. (in Czech).
- HUBER C., 2005: Long lasting nitrate leaching after bark beetle attack in the highlands of the Bavarian Forest National Park. *Journal of Environmental Quality*, 34: 1772–1779.
- HUBER C., BAUMGARTEN M., GÖTTLEIN A. & ROTTER V., 2004a: Nitrogen turnover and nitrate leaching after bark beetle attack in mountainous spruce stands of the Bavarian Forest National Park. *Water, Air and Soil Pollution: Focus*, 4: 391–414.
- HUBER C., WEIS W., BAUMGARTEN M. & GÖTTLEIN A., 2004b: Spatial and temporal variation of seepage water chemistry after felling and small scale clear-cutting in a N-saturated Norway spruce stand. *Plant and Soil*, 267: 23–40.
- ILLMER P., MARSCHALL K. & SCHINNER F., 1995: Influence of available aluminium on soil microorganisms. *Letters in Applied Microbiology*, 21: 393–397.
- IWALD J., LÖFGREN S., STENDAHL J. & KARLTUN E., 2013: Acidifying effect of removal of tree stumps and logging residues as compared to atmospheric deposition. *Forest Ecology and Management*, 290: 49–58.
- JOHNSON D.W. & CURTIS P.S., 2001: Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology and Management*, 140: 227–238.
- JONÁŠOVÁ M., 2001: Regenerace horských smrčů po kůrovcové kalamitě [Regeneration of mountain spruce forests after a destructive bark beetle outbreaks]. *Silva Gabreta*, 6: 241–248 (in Czech).
- JONÁŠOVÁ M. & MATĚJKOVÁ I., 2007: Natural regeneration and vegetation changes in wet spruce forests after natural and artificial disturbances. *Canadian Journal of Forest Research*, 37: 1907–1914.

- JONÁŠOVÁ M. & PRACH K., 2004: Central-European mountain spruce (*Picea abies* (L.) Karst.) forests: regeneration of tree species after a bark beetle outbreak. *Ecological Engineering*, 23: 15–27.
- JONÁŠOVÁ M. & PRACH K., 2008: The influence of bark beetles outbreak vs. salvage logging on ground layer vegetation in Central European mountain spruce forests. *Biological Conservation*, 141: 1525–1535.
- JONES D.L. & KIELLAND K., 2002: Soil amino acid turnover dominates the nitrogen flux in permafrost-dominated taiga forest soils. *Soil Biology and Biochemistry*, 34: 209–219.
- KÁMÁRI J., JEFFRIES D.S., HESSEN D.O., HENRIKSEN A., POSCH M. & FORSIUS M., 1992. In: GRENNFELT P., THÖRNELO F.E. (eds), *Nitrogen critical loads and their exceedance for surface waters*. Report from a workshop held at Lökeborg, Sweden, 6–10 April 1992, Nord 1992:41. Copenhagen: Nordic Council of Ministers: 161–200.
- KAŇA J., TAHOVSKÁ K. & KOPÁČEK J., 2013: Response of soil chemistry to forest dieback after bark beetle infestation. *Biogeochemistry*, 113: 369–383.
- KAŇA J., ŠANTRŮČKOVÁ H., KOPÁČEK J., PEROUTKOVÁ M. & MATĚJČÍKOVÁ I., 2014: Chemical and biochemical characteristics of soils in the catchments of Čertovo and Plešné lakes (Bohemian Forest) in 2010. *Silva Gabreta*, 20: 97–129.
- KAŇA J., TAHOVSKÁ K., KOPÁČEK J., ŠANTRŮČKOVÁ H., 2015: Excess of organic carbon in mountain spruce forest soils after bark beetle outbreak altered microbial N transformations and mitigated N-saturation. *PLOS ONE*, 10:0134165
- KENNEDY I.R., 1992: *Acid soil and acid rain*. John Wiley and Sons Inc, New York, 254 pp.
- KIKILÄ O., KITUNEN V., SPETZ P. & SMOLANDER A., 2012: Characterization of dissolved organic matter in decomposing Norway spruce and silver birch litter. *European Journal of Soil Science*, 63: 476–486.
- KETTLE H., KOPÁČEK J. & HEJZLAR J., 2003: Modelling air temperature at Čertovo Lake back to 1781. *Silva Gabreta*, 9: 15–32.
- KIELLAND K., MCFARLAND J. & OLSON K., 2006: Amino acid uptake in deciduous and coniferous taiga ecosystems. *Plant and Soil*, 288: 297–307.
- KOPÁČEK J. & HRUŠKA J., 2010: Reconstruction of acidic deposition in the catchments of Plešné and Čertovo lakes (the Bohemian Forest). *Silva Gabreta*, 16: 149–163.
- KOPÁČEK J. & POSCH M., 2011: Anthropogenic nitrogen emissions during the Holocene and their possible effects on remote ecosystems. *Global Biogeochemical Cycles*, 25: 1–16.
- KOPÁČEK J. & VESELÝ J., 2005: Sulfur and nitrogen emissions in the Czech Republic and Slovakia from 1850 till 2000. *Atmospheric Environment*, 39: 2179–2188.
- KOPÁČEK J., VESELÝ J. & STUHLÍK E., 2001: Sulphur and nitrogen fluxes and budgets in the Bohemian Forest and Tatra Mountains during the Industrial Revolution (1850–2000). *Hydrology and Earth System Sciences*, 5: 391–405.
- KOPÁČEK J., KAŇA J., ŠANTRŮČKOVÁ H., PORCAL P., HEJZLAR J., PICEK T. & VESELÝ J., 2002a: Physical, chemical, and biochemical characteristics of soils in watersheds of the Bohemian Forest lakes: I. Plešné Lake. *Silva Gabreta*, 8: 43–66.
- KOPÁČEK J., KAŇA J., ŠANTRŮČKOVÁ H., PORCAL P., HEJZLAR J., PICEK T., ŠIMEK M. & VESELÝ J., 2002b: Physical, chemical, and biochemical characteristics of soils in watersheds of the Bohemian Forest lakes: II. Čertovo and Černé Lake. *Silva Gabreta*, 8: 67–94.
- KOPÁČEK J., COSBY B.J., EVANS C.D., HRUŠKA J., MOLDAN F., OULEHLE F., ŠANTRŮČKOVÁ H., TAHOVSKÁ K. & WRIGHT R., 2013a: Nitrogen, organic carbon and sulphur cycling in terrestrial ecosystems: Linking nitrogen saturation to carbon limitation of soil microbial processes. *Biogeochemistry*, 115: 33–51.
- KOPÁČEK J., FLUKSOVÁ H., KAŇA J., PORCAL P., TUREK J. & ŽALOUDÍK J., 2013b: Chemical composition of atmospheric deposition in the catchments of Plešné and Čertovo lakes in 1998–2012. *Silva Gabreta*, 19: 1–23.
- KRANKINA O.N., HARMON M.E. & GRIAZKIN A.V., 1999: Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. *Canadian Journal of Forest Research*, 29: 20–32.
- KRÄUCHI N., BRANG P. & SCHÖNENBERGER W., 2000: Forests of mountainous regions: gaps in knowledge and research needs. *Forest Ecology and Management*, 132: 73–82.
- KRAUSOVÁ M., 2011: Odhad dostupnosti živin v půdě asanovaných a přirozených se vyvíjejících porostů po kůrovcové kalamitě na území NP Šumava [Estimate of available nutrients in forest soil after bark beetle outbreak of stands after salvage logging and of stands left without intervention in the Šumava National park]. Ms., bachelor thesis, Faculty of Science, University of South Bohemia, České Budějovice, 41 pp. (in Czech).
- KREUTZER K., 1995: Effects of forest liming on soil processes. *Plant and Soil*, 168–169: 447–470.
- LAUBER C.L., STRICKLAND M.S., BRADFORD M.A. & FIERER N., 2008: The influence of soil properties on the structure of bacterial and fungal communities across land-use types. *Soil Biology and Biochemistry*, 40: 2407–2415.
- LEVY-BOOTH D.J., PRESCOTT C.E. & GRAYSTON S.J., 2014: Microbial functional genes involved in nitrogen fixation, nitrification and denitrification in forest ecosystems. *Soil Biology and Biochemistry*, 75: 11–25.
- LINDAHL B.O., TAYLOR A.F.S. & FINLAY R.D., 2002: Defining nutritional constraints on carbon cycling in boreal



- forests – towards a less ‘phytcentric’ perspective. *Plant and Soil*, 242: 123–135.
- LIPSON D. & NÄSHOLM T., 2001: The unexpected versatility of plants: organic nitrogen use and availability in terrestrial ecosystems. *Oecologia*, 128: 305–316.
- LOVETT G.M. & GOODALE C.L., 2011: A new conceptual model of nitrogen saturation based on experimental nitrogen addition to an oak forest. *Ecosystems*, 14: 615–631.
- MAJER V., COSBY B.J., KOPÁČEK J. & VESELÝ J., 2003: Modelling reversibility of Central European mountain lakes from acidification: Part 1 – the Bohemian Forest. *Hydrology and Earth System Sciences*, 7: 494–509.
- MARSHALL V.G., 2000: Impacts of forest harvesting on biological processes in northern forest soils. *Forest Ecology and Management*, 133: 43–60.
- MATZNER E., & MEIWES K.J., 1991: Effects of liming and fertilization on soil solution chemistry in North German forest ecosystems. *Water, Air and Soil Pollution*, 54: 377–389.
- McHALE M.R., BURNS D.A., LAWRENCE G.B. & MURDOCH P.S. 2007: Factors controlling soil water and stream water aluminum concentrations after a clearcut in a forested watershed with calcium-poor soils. *Biogeochemistry*, 84: 311–331.
- MCNULTY S.G., ABER J.D. & NEWMAN S.D., 1996: Nitrogen saturation in a high elevation New England spruce-fir stand. *Forest Ecology and Management*, 84: 109–121.
- MEIWES K.J., 1995: Application of lime and wood ash to decrease acidification of forest soils. *Water, Air and Soil Pollution*, 85: 143–152.
- MELILLO J.M., ABER J.D. & MURATORE J.F., 1982: Nitrogen and lignin control of hard wood leaf litter decomposition dynamics. *Ecology*, 63: 621–626.
- MERILÄ P., MALMIVAARA-LÄMSÄ M., SPETZ P., STARK S., VIERIKKO K., DEROME J. & FRITZE H., 2010: Soil organic matter quality as a link between microbial community structure and vegetation composition along a successional gradient in a boreal forest. *Applied Soil Ecology*, 46: 259–267.
- MERRICK M.J. & EDWARDS R.A., 1995: Nitrogen control in bacteria. *Microbiological Reviews*, 59, 604–622.
- MYROLD D.D., 2005: Transformations of nitrogen. In: *Principles and Applications of Soil Microbiology*. 2<sup>nd</sup> edition, SYLVIA D.M., FUHRMANN J.J., HARTEL P.G. & ZUBERER D.A. (eds) Pearson Prentice Hall, New Jersey: 333–372.
- NÄSHOLM T., EKLBAD A., NORDIN A., GEISLER R., HÖGBERG M. & HÖGBERG P., 1998: Boreal forest plants take up organic nitrogen. *Nature*, 392: 914–916.
- NILSSON L.O. & WALLANDER H., 2003: Production of external mycelium by ectomycorrhizal fungi in a Norway spruce forest was reduced in response to nitrogen fertilization. *New Phytologist*, 158: 409–416.
- NILSSON M.C. & WARDLE D.A., 2005: Understorey vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment*, 3: 421–428.
- NILSSON L.O., WALLANDER H. & GUNDERSEN P., 2012: Changes in microbial activities and biomasses over a forest floor gradient in C-to-N ratio. *Plant and Soil*, 355: 75–86.
- NORDIN A., HÖGBERG P. & NÄSHOLM T., 2001: Soil nitrogen form and plant nitrogen uptake along a boreal forest productivity gradient. *Oecologia*, 129: 125–132.
- NOVÁK F., 2000: Vliv vápnění na transformace dusíku v půdě horského smrkového lesa na Boubíně (Šumava) [Nitrogen transformation in limed and unlimed Norway spruce forest soils in Boubín stand (Bohemian Forest)]. *Silva Gabreta*, 5: 41–50.
- NOVÁKOVÁ M.H. & EDWARDS-JONÁŠOVÁ M., 2015: Restoration of Central-European mountain Norway spruce forest 15 years after natural and anthropogenic disturbance. *Forest Ecology and Management*, 344: 120–130.
- NORTON S.A. & VESELÝ J., 2003: Acidification and acid rain. In: *Environmental Geochemistry, Treatise on Geochemistry*, 9, LOLLARD B.S. (ed.) Elsevier–Pergamon, Oxford: 367–406.
- ÖHLUND J. & NÄSHOLM T., 2001: Growth of conifer seedlings on organic and inorganic nitrogen sources. *Tree Physiology*, 21: 1319–1326.
- OHTONEN R., MUNSON A. & BRAND D., 1992: Soil microbial community response to silvicultural intervention in coniferous plantation ecosystems. *Ecological Applications*, 2: 363–375.
- OLSSON P., LINDER S., GIESLER R. & HÖGBERG P., 2005: Fertilization of boreal forest reduces both autotrophic and heterotrophic soil respiration. *Global Change Biology*, 11: 1745–1753.
- OSONO T. & TAKEDA H., 2005: Decomposition of organic chemical components in relation to nitrogen dynamics in leaf litter of 14 tree species in a cool temperate forest. *Ecological Research*, 20: 41–49.
- OULEHLE F., HOFMEISTER J., CUDLÍN P. & HRUŠKA J., 2006: The effect of reduced atmospheric deposition on soil and soil solution chemistry at a site subjected to long-term acidification, Načetín, Czech Republic. *Science of the Total Environment*, 370: 532–544.
- OULEHLE F., HOFMEISTER J. & HRUŠKA J., 2007: Modeling of the long-term effect of tree species (Norway spruce and European beech) on soil acidification in the Ore Mountains. *Ecological Modelling*, 204: 359–371.
- OULEHLE F., CHUMAN T., MAJER V. & HRUŠKA J., 2013: Chemical recovery of acidified Bohemian lakes between 1984 and 2012: the role of acid deposition and bark beetle induced forest disturbance. *Biogeochemistry*, 116: 83–101.

- PALVIAINEN M., FINÉR L., MANNERKOSKI H., PIIRAINEN S. & STARR M., 2005: Responses of ground vegetation species to clear-cutting in a boreal forest: aboveground biomass and nutrient contents during the first 7 years. *Ecological Research*, 20: 652–660.
- PARÉ P., ROCHON P. & BRAIS S., 2002: Assessing the geochemical balance of managed boreal forests. *Ecological Indicators*, 1: 293–311.
- PAUL E.A. & CLARK F.E. (eds), 1996: *Soil Microbiology and Biochemistry*. 2<sup>nd</sup> edition. Academic Press, San Diego, 340pp.
- PEDERSEN H., DUNKIN K.A. & FIRESTONE M.K., 1999: The relative importance of autotrophic and heterotrophic nitrification in a conifer forest soil as measured by <sup>15</sup>N tracer and pool dilution techniques. *Biochemistry*, 44: 135–150.
- PENNANEN T., FRITZE H., VANHALA P., KIIKKILÄ O., NEUVONEN S. & BÄÄTH E., 1998: Structure of a microbial community in soil after prolonged addition of low levels of simulated acid rain. *Applied and Environmental Microbiology*, 64: 2173–2180.
- PERELO L.W., JIMENEZ M. & MUNCH J.C., 2006: Microbial immobilisation and turnover of <sup>15</sup>N labelled substrates in two arable soils under field and laboratory conditions. *Soil Biology and Biochemistry*, 38: 912–922.
- PERSSON J. & NÅSHOLM T., 2001: Amino acid uptake: a widespread ability among boreal forest plants. *Ecology Letters*, 4: 434–438.
- POUSKA V., SVOBODA M. & LEPŠOVÁ A., 2010: The diversity of wood-decaying fungi in relation to changing site conditions in an old-growth mountain spruce forest, Central Europe. *European Journal of Forest Research*, 129: 219–231.
- PUHE J. & ULRICH B. (eds), 2001: *Global climate change and human impacts on forest ecosystems: postglacial development, present situation, and future trends in Central Europe*. Ecological Studies 143, Springer, Berlin–Heidelberg–New York, 593 pp.
- READ D.J. & PEREZ-MORENO J., 2003: Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist*, 157: 475–492.
- RICE C.W. & TIEDJE J.M., 1989: Regulation of nitrate assimilation by ammonium in soils and in isolated soil microorganisms. *Soil Biology and Biochemistry*, 21: 597–602.
- ROLFF C. & ÅGREN G.I., 1999: Predicting effects of different harvesting intensities with a model of nitrogen limited forest growth. *Ecological Modelling*, 118: 193–211.
- ROSÉN K. & LINDBERG T., 1980: Biological nitrogen fixation in coniferous forest watershed areas in Central Sweden. *Holarctic Ecology*, 3: 137–140.
- ROTTE A. & BINKLEY D., 2001: Nutritional interactions in mixed species forests: a synthesis. *Canadian Journal of Forest Research*, 31: 1855–1870.
- ROUSK J. & BÄÄTH E., 2011: Growth of saprotrophic fungi and bacteria in soil. *FEMS Microbiology Ecology*, 78: 17–30.
- ROUSK J., BROOKES P.C. & BÄÄTH E., 2009: Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. *Applied and Environmental Microbiology*, 75: 1589–1596.
- RUTTING T., HUYGENS D., BOECKX P., STAELENS J., & KLEMEDTSSON L., 2013: Increased fungal dominance in N<sub>2</sub>O emission hotspots along a natural pH gradient in organic forest soil. *Biology and Fertility of Soils*, 49: 715–721.
- SANDERSON M.G., COLLINS W.J., JOHNSON C.E. & DERWENT R.G., 2008: Present and future acid deposition to ecosystems. The effect of climate change. *Atmospheric Environment*, 40: 1275–1283.
- ŠANTRŮČKOVÁ H., GRUND M., PICEK T. & ŠIMEK M., 2001: Estimation of net nitrification in mountain soil. *Silva Gabreta*, 7: 79–86.
- ŠANTRŮČKOVÁ H., KRISTŮFKOVÁ M. & VANĚK D., 2006: Decomposition rate and nutrient release from plant litter of Norway spruce forest in the Bohemian Forest. *Biologia*, 61: S499–S508.
- ŠANTRŮČKOVÁ H., ŠANTRŮČEK J., ŠETLÍK J., SVOBODA M. & KOPÁČEK J., 2007: Carbon isotopes in tree rings of Norway spruce exposed to atmospheric pollution. *Environmental Science & Technology*, 41: 5778–5782.
- ŠANTRŮČKOVÁ H., TAHOVSKÁ K. & KOPÁČEK J., 2009: Nitrogen transformations and pools in N saturated mountain spruce forest soils. *Biology and Fertility of Soils*, 45: 395–404.
- SCHIMEL J., 2001: Biogeochemical models: implicit vs. explicit microbiology. In: *Global Biogeochemical Cycles in the Climate System*, SCHULZE E.D., HEIMANN M., HARRISON S., HOLLAND E., LLOYD J., PRENTICE I.C. & SCHIMEL D. (eds) Academic Press, San Diego: 177–183.
- SCHIMEL J.P. & BENNETT J., 2004: Nitrogen mineralization: challenges of a changing paradigm. *Ecology*, 85: 591–602.
- SCHIMEL J.P. & FIRESTONE M.K., 1989: Nitrogen incorporation and flow through a coniferous forest soil profile. *Soil Science Society of America Journal*, 53: 779–784.
- SCHLESINGER W.H. & BERNHARDT E.S., 2013: *Biogeochemistry: an analysis of global change*. 3rd edition. Waltham: Elsevier, 672 pp.
- SCHMIDT M.W., TORN M.S., ABIVEN S., DITTMAR T., GUGGENBERGER G., JANSSENS I.A., KLEBER M., KÖGEL-KNABNER



- I., LEHMANN J., MANNING D.A.C., NANNIPIERI P., RASSE D.P., WEINER S. & TRUMBORE S.E., 2011: Persistence of soil organic matter as an ecosystem property. *Nature*, 478: 49–56.
- SCHMIDT S.K., LIPSON D.A., LEY R.E., FISK M.C. & WEST A.E., 2004: Impacts of chronic nitrogen additions vary seasonally and by microbial functional group in tundra soils. *Biogeochemistry*, 69: 1–17.
- SCHWARZ O., HOŠEK J., ANDĚL P., HRUŠKA J., HOFMEISTER J., SVOBODA T. & PETRŽILKA L., 2009: *Soubor map atmosférické depozice, překročení kritických zátěží síry a dusíku pro lesní ekosystémy a lišejníkové indikace imisní zátěže v KRMAP a CHKO Jizerské hory* [Set of maps of atmospheric deposition, exceedance of sulphur and nitrogen critical loads for forest ecosystems, and lichen indication of imission loads in the Krkonoše National Park and Jizerské hory Landscape Protected Area]. Kostelec nad Černými lesy, Lesnická práce, s.r.o., 34 pp. (in Czech).
- SCOTT N.A. & BINKLEY D., 1997: Foliage litter quality and annual net N mineralization: comparison across North American forest sites. *Oecologia*, 111: 151–159.
- SHOROHOVA E., KAPITSA E. & VANHA-MAJAMAA I., 2008: Decomposition of stumps 10 year after partial and complete harvesting in southern boreal forest in Finland. *Canadian Journal of Forest Research*, 38: 2414–2421.
- SKOPOVÁ K. & ŠANTRŮČKOVÁ H., 2006: The effect of temperature on N transformations in mountain forest soils of Čertovo, Černé and Plešné watersheds. *Silva Gabreta*, 12: 3–14.
- SMITH S.E. & READ D., 2008: *Mycorrhizal symbiosis*. 3<sup>rd</sup> edition. Academic Press, London, UK, 800 pp.
- SMOLANDER A. & KITUNEN V., 2002: Soil microbial activities and characteristics of dissolved organic C and N in relation to tree species. *Soil Biology and Biochemistry*, 34: 651–660.
- SMOLANDER A. & KITUNEN V., 2011: Comparison of tree species effects on microbial C and N transformations and dissolved organic matter properties in the organic layer of boreal forests. *Applied Soil Ecology*, 49: 224–233.
- SODERSTROM B., BÄÄTH E. & LUNDGREN B., 1983: Decrease in soil microbial activity and biomasses owing to nitrogen amendments. *Canadian Journal of Microbiology*, 29: 1500–1506.
- SPRENT J.I., 1987: *The ecology of the nitrogen cycle*. Cambridge University Press, Cambridge, 160 pp.
- STAŇKOVÁ P., 2013: The effect of forest management and plant dominant on nitrogen transformation in soils of acidified mountain spruce forests in the Bohemian Forest National Park. Ms., diploma thesis, Faculty of Science, University of South Bohemia, České Budějovice, 74 pp.
- STARK J.M. & HART S.C., 1997: High rates of nitrification and nitrate turnover in undisturbed coniferous forests. *Nature*, 385: 61–64.
- STRICKLAND M.S. & ROUSK J., 2010: Considering fungal:bacterial dominance in soils – Methods, controls, and ecosystem implications. *Soil Biology and Biochemistry*, 42: 1385–1395.
- STODDARD J.L., 1994: Long-term changes in watershed retention of nitrogen – its causes and aquatic consequences. In: *Environmental chemistry of lakes and reservoirs*. *Advances in Chemistry Series 237*, BAKER L.A. (ed.) American Chemical Society, Washington: 223–284.
- SVOBODA M. & POUŠKA V., 2008: Structure of a Central-European mountain spruce old-growth forest with respect to historical development. *Forest Ecology and Management*, 255: 2177–2188.
- SVOBODA M. & ZENÁHLÍKOVÁ J., 2009: Historický vývoj a současný stav lesa v NP Šumava kolem „Kalamitní svážnice“ v oblasti Trojmezí [Past development and recent structure of forest stands in the Bohemian Forest National Park in area of Trojmezí]. *Příroda*, 28: 71–122 (in Czech).
- SYLVIA D.M., FUHRMANN J.J., HARTEL P.G. & ZUBERER D.A., 2005: *Principles and applications of soil microbiology*. 2<sup>nd</sup> edition. Pearson Education Inc., New Jersey, 672 pp.
- TAHOVSKÁ K., KOPÁČEK J. & ŠANTRŮČKOVÁ H., 2010: Nitrogen availability in Norway spruce forest floor – the effect of forest defoliation induced by bark beetle infestation. *Boreal Environmental Research*, 15: 553–564.
- TAHOVSKÁ K., KAŇA J., BARTA J., OULEHLE F., RICHTER A. & ŠANTRŮČKOVÁ H., 2013: Microbial N immobilization is of great importance in acidified mountain spruce forest soils. *Soil Biology and Biochemistry*, 59: 58–71.
- TAMM C.O., 1991: *Nitrogen in Terrestrial Ecosystems. Questions of Productivity, Vegetational Changes, and Ecosystem Stability*. Springer-Verlag, Berlin, Heidelberg, 115 pp.
- TAYLOR B.R., PARKINSON D. & PARSONS W.F.J., 1989: Nitrogen and lignin content as predictors of litter decay rates: A microcosm test. *Ecology*, 70: 97–104.
- TAYLOR P. & TOWNSEND A.R., 2011: Stoichiometric control of organic carbon-nitrate relationships from soils to the sea. *Nature*, 464: 1178–1181.
- TEJNECKÝ V., ŘEŘICHOVÁ N., BRADOVÁ M., NĚMEČEK K., ŠANTRŮČKOVÁ H., ASH C. & DRÁBEK O., 2014: Litter decomposition as a source of active phosphates in spruce and beech mountainous forests affected by acidification. *Geochemistry of the Earth's Surface (GES-10)*, 10: 130–132.
- TURETSKY M.R., 2003: The role of bryophytes in carbon and nitrogen cycling. *The Bryologist*, 106: 395–409.
- TURVEY N.D. & SMETHURST P.J., 1983: Nitrogen fixing plants in forest plantation management. In: *Biological Nitrogen Fixation in Forest Ecosystems. Foundations and Applications*, GORDON G.C. & WHEELER C.T. (eds) Martnus Nuhoff, Dr. W. Junk: 233–259.
- VENTEREA R.T., GROFFMAN P.M., VERCHOT L.V., MAGILL A.H. & ABER J.D., 2004: Gross nitrogen process rates in temperate forest soils exhibiting symptoms of nitrogen saturation. *Forest Ecology and Management*, 196:

- VERESOGLOU S.D., PEÑUELAS J., FISCHER R., RAUTIO P., SARDANS J., MERILÄ P., TABAKOVIC-TOSIC M. & RILLIG M.C., 2014: Exploring continental-scale stand health – N:P ratio relationships for European forests. *New Phytologist*, 202: 422–430.
- VESELÝ J., 1994: Investigation of the nature of the Šumava lakes: a review. *Časopis Národního muzea, Řada Přírodovědná*, 163: 103–120.
- VESTERDAL L., SCHMIDT I.K., CALLESEN I., NILSSON L.O. & GUNDERSEN P., 2008: Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *Forest Ecology and Management*, 255: 35–48.
- VITOUSEK P.M. & HOBBIIE S., 2000: Heterotrophic nitrogen fixation in decomposing litter: Patterns and regulation. *Ecology*, 81: 2366–2376.
- WALDROP M.P. & ZAK D.R., 2006: Response of oxidative enzyme activities to nitrogen deposition affects soil concentrations of dissolved organic carbon. *Ecosystems*, 9: 921–933.
- WALDROP M.P., ZAK D.R., SINSABAUGH R.L., GALLO M. & LAUBER C., 2004: Nitrogen deposition modifies soil carbon storage through changes in microbial enzymatic activity. *Ecological Applications*, 14: 1172–1177.
- WALL A., 2012: Risk analysis of effects of whole-tree harvesting on site productivity. *Forest Ecology and Management*, 282: 175–184.
- WALLENDÄ T. & KOTTKE I., 1998: N deposition and ectomycorrhizas. *New Phytologist*, 139: 169–187.
- WARDLE D.A., NILSSON M.C., ZACKRISSON O. & GALLET C., 2003: Determinants of litter mixing effects in a Swedish boreal forest. *Soil Biology and Biochemistry*, 35: 827–835.
- WU J., GUAN D., HAN S. & ZHANG M., 2005: Ecological functions of coarse woody debris in forest ecosystem. *Journal of Forestry Research*, 16: 247–252.
- ZATLOUKAL V., 1998: Historické a současné příčiny kůrovcové kalamity v Národním parku Šumava [Historical and current factors of the bark beetle calamity in the Šumava National Park]. *Silva Gabreta*, 2: 327–357 (in Czech).
- ZATLOUKAL V., KADERA J., ČERNÁ J. & PŘÍLEPKOVÁ S., 2001: Předběžné vyhodnocení stavu a vývoje přirozené obnovy v NP Šumava v prostoru Mokrůvka–Špičnick–Březnická hájenka [Preliminary evaluation of the state and regeneration of the forest stand in area Mokrůvka–Špičnick–Březnická hájenka, the Šumava National Park]. In: *Aktuality Šumavského Výzkumu*, MÁNEK J. (ed.) Správa NP a CHKO Šumava, Vimperk: 110–115 (in Czech).
- ZHANG D., HUI D., LUO Y. & ZHOU G., 2008: Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *Journal of Plant Ecology*, 1: 85–93.
- ZHANG J., SUN W., ZHONG W. & CAI Z., 2014: The substrate is an important factor in controlling the significance of heterotrophic nitrification in acidic forest soils. *Soil Biology and Biochemistry*, 76: 143–148.
- ZIELONKA T., 2006: When does dead wood turn into a substrate for spruce replacement? *Journal of Vegetation Science*, 17: 739–746.

Received: 14 June 2015

Accepted: 14 December 2015

