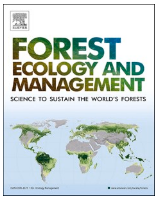
Forest Ecology and Management 580 (2025) 122523

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Consequences of nitrogen deposition and soil acidification in European forest ecosystems and mitigation approaches

Baoguo Du [a,b,*], Ralf Kiese [c], Klaus Butterbach-Bahl [c,d], Thomas Dirnböck [e], Heinz Rennnenberg [b,f]

[a] College of Life Science and Biotechnology, Ecological Security and Protection Key laboratory of Sichuan Province, Mianyang Normal University, Mianxing Road West 166, Mianyang 621000, PR China
[b] Chair of Tree Physiology, Institute of Forest Sciences, University of Freiburg, Georges-Köhler-Allee 53, Freiburg D-79110, Germany
[c] Karlsruhe Institute of Technology, Institute of Meteorology and Climate Research-Atmospheric Environmental Research (IMK-IFU), Kreuzeckbahnstr. 19, Garmisch-Partenkirchen 82467, Germany
[d] Aarhus University, Department of Agroecology - Center for Landscape Research in Sustainable Agricultural Futures - Land-CRAFT, C.F. Møllers Allé 4, Aarhus 8000, Denmark
[e] Department for Ecosystem Research and Environmental Information Management, Environment Agency Austria, Spittelauer Lände 5, Vienna 1090, Austria
[f] Center of Molecular Ecophysiology (CMEP), College of Resources and Environment, Southwest University No. 2, Tiansheng Road, Beibei District, Chongqing 400715, PR China

ARTICLE INFO

Keywords:
Nitrogen deposition
Legacy effects
Forest composition
Cutting regimes
Soil nitrogen fluxes
Forest management

ABSTRACT

European forests have experienced high nitrogen (N) deposition and soil acidification together with sulfur (S) deposition in the recent decades and are still facing challenges in some areas. In the context of elevated CO_2 and air temperature under climate change, the N deposition will initially promote the growth but in the long term it will accelerate nutrient imbalance and reduce tree health. Therefore, forest management must take these aspects into account. Many studies have been carried out on the effects of forest management approaches, i.e., liming, harvesting, and intercropping with other tree species on traits of trees, soil and ecosystem properties and fluxes, however, a comprehensive review summarizing the current consequences of nitrogen saturation and soil acidification in European forest, particularly if current forest management approaches are able to mitigate these consequences in the context of climate change, is still lacking. In our review, we summarize the consequences of N deposition and acidification on trees and soils of forest ecosystems, discuss the importance of the most commonly used management practices in mitigating these consequences, and provide information for future management practices in Europe.

1. Introduction

Atmospheric deposition resulting from drastically increased nitrogen (N) emissions from human activities has contributed to the eutrophication and acidification of terrestrial ecosystems in many regions of the world (Etzold et al., 2020; Janssens et al., 2010), affecting not only the tree health, such as nutrient status, primary production, growth, vitality and mortality, but also affecting plant diversity, microbial activity and nutrient availability as well as gaseous and leaching losses (Cheng et al., 2019; Clark et al., 2019; Du and de Vries, 2018; Du et al., 2024a; He et al., 2024; Tian et al., 2018). A recent summary of those effects are presented by Du and de Vries (2023). Soil acidification caused by N deposition together with sulphur (S) deposition can lead to direct tree damage, reduced tree nutrient health and regeneration rates of trees and increased soil-mediated processes like nutrient imbalances, base cation and nitrate losses (Clark et al., 2019; Du and de Vries, 2018; Etzold et al., 2020).

The global average atmospheric N deposition has declined to about 19 Tg N yr^{-1}, but is still high in some hotspots (Du and de Vries, 2023; Schwede et al., 2018). In Europe, although N and S deposition has declined since 1990s after peaking during the mid-1980s as a result of emission reductions, primarily of SO_4^{2-} and NOx (EMEP, 2023; Johnson et al., 2018). N deposition, particularly reactive N (oxidized N + reduced N) deposition is still high in some areas (Schmitz et al., 2019; Schwede

---

* Corresponding author at: College of Life Science and Biotechnology, Ecological Security and Protection Key laboratory of Sichuan Province, Mianyang Normal University, Mianxing Road West 166, Mianyang 621000, PR China.
E-mail address: baoguo.du@ctp.uni-freiburg.de (B. Du).

https://doi.org/10.1016/j.foreco.2025.122523
Received 31 October 2024; Received in revised form 17 January 2025; Accepted 18 January 2025
Available online 29 January 2025
0378-1127/© 2025 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

et al., 2018) and many other parts of the globe such as Asia (He et al., 2024; Vet et al., 2014; Q. Zhang et al., 2021). The actual deposition of inorganic N in central Europe still amounts to ca. 20 kg ha^{-1} yr^{-1} (Wellbrock et al., 2019), which is 10 times higher than the N deposition in northern Sweden (Ferm et al., 2019), and is about 3.3 times of the global average rate of total N deposition to forests (6 kg N ha^{-1} yr^{-1}) (Schwede et al., 2018). Thus, N deposition remains a matter of concern in the context of forest management globally (Clark et al., 2019; Dirnböck et al., 2018; Du and de Vries, 2023; Flechard, Ibrom, et al., 2020), including urban forests due to increasing urbanization (Du et al., 2022). Decreased N deposition alone may be not sufficient for forests to recover within a reasonable timeframe from the decades-long effects of elevated N deposition (Schmitz et al., 2019). Therefore, management interventions are necessary to promote forest recovery, particularly in Europe where forests cover about one-third of its surface (Etzold et al., 2020; Pretzsch et al., 2023).

Liming together with carbon, wood ash and deficient nutrients addition has been proposed and widely used to mitigate the effects of soil acidification and N eutrophication (Du et al., 2024a; Jansone et al., 2020; Olsson and Kellner, 2002). No other direct, large-scale measures have been taken to mitigate the effects from N and S deposition. However, adaptation measures to improve forest resilience in general, to avoid the consequences of climate change, or to promote greater biodiversity have also had spillover effects on the recovery from acidification and eutrophication. Partial or selective cutting, often referred to as continuous–cover–forestry, is one of these management practices that is commonly applied in Central Europe (Göttlein et al., 2023; Lundmark et al., 2013; Nordén et al., 2019; Wu et al., 2011). Selective cutting is expected to increase N availability (Clark et al., 2019), reduce the sensitivity of forests stands to climatic perturbations and at the same time cause less N losses by gaseous emissions and leaching from forests as compared to clear–cutting, because the N requirements of and the ecosystem N cycling during forest regeneration differ significantly from those in mature forest stands. When only few trees are removed by selective cutting, N uptake of the stand changes only gradually over time since the stand structure is maintained (Gundersen et al., 2006). Another important adaptation of forest management to climate change focusses on either promoting or planting tree species (e.g., replenishing seed banks with liming and replanting tolerant species) that are less susceptible to water limitations (Du et al., 2024a; Kauppi et al., 2018; Pardos et al., 2021). This measure aims at sustained growth and reduced tree mortality, which has shaped European forests at the stand and landscape scale in the recent decades (Forzieri et al., 2021; Senf et al., 2018). In addition to the aspects of plant N supply and the risks of ecosystem N losses, forest policy and forest management need to address biodiversity loss (Gilliam, 2006), tree nutrition and resilience (Schmitz et al., 2019) as well as C sequestration and climate mitigation in a long term and on global scale (Du et al., 2024b; Naudts et al., 2016). Clark et al. (2019) proposed combinations of treatments to promote recovery from N deposition. In the present review, we aim to summarize the consequences of N deposition and soil acidification in European forests at tree, soil and ecosystem levels, and specifically discuss how forest management options such as liming, selective cutting and change of species composition mitigate these effects, in order to shed light on future forest management practices in Europe and worldwide in the context of climate change.

2. Consequences of nitrogen deposition and soil acidification on forest ecosystem

2.1. Tree performance

N supply commonly limits plant production and determines the overall structure and function of many forest ecosystems (Vitousek and Howarth, 1991). During evolution, trees have developed on marginal soils with low nutrient availability, particularly of N (Raven and Andrews, 2010). Consequently, many tree species can take up N in amounts exceeding their actual requirement for growth and development, when high amounts of N become available in the environment (Rennenberg et al., 1998; Rennenberg and Dannenmann, 2015; Sardans et al., 2016). Under these conditions, the excess nitrogen can be used for the production of vegetative bark and wood storage proteins (Rennenberg et al., 2010), the synthesis of rubisco and other enzymes in the leaves in amounts that far exceeds the requirement for photosynthetic carbon fixation and other enzymatic reactions (Mu et al., 2018; Warren et al., 2003), and the expansion of the soluble amino acid pool that cycles in xylem and phloem, particularly by the accumulation of N-rich amino acids such as arginine (Gessler et al., 1998b; Schneider et al., 1996). The N in these storage pools can be mobilized at high N demand, e.g. for new leaf development in deciduous trees in spring (Herschbach et al., 2012; Millard and Grelet, 2010), for mass production of seeds (Rennenberg and Gessler, 1999), or during leaf senescence for bark and wood storage protein synthesis (Feller et al., 2008).

Apart from storage and reallocation, plants can also mediate N acquiring by the means of stomata regulation and root uptake (Fig. 1) (Rennenberg and Gessler, 1999). Since nitrogen dioxide (NO_2) influx into the leaves can only be reduced by stomatal closure and, hence, at the expense of photosynthetic carbon fixation, root uptake of N can be downregulated at the end (Muller et al., 1996). In addition, root uptake of nitrate can be inhibited completely at excess N availability, when storage pools of N are filled up (Gessler et al., 2004). Under these conditions, ammonium uptake by the roots is maintained and can result in excessive N nutrition (Gessler et al., 1998a). If amino acid uptake by the roots from the soil solution is also maintained under these conditions, has so far not been elucidated. The inhibition of nitrate uptake by the roots contributes to the nitrate losses via soil seepage to ground- and surface waters in ecosystems exposed to high atmospheric N deposition (Rennenberg et al., 1998). The inhibition can be released during enhanced demand for N, e.g., for mass production of seeds (Rennenberg and Gessler, 1999). Thus, N nutrition of trees can be regulated to some extent at excess availability of this essential macro nutrient, but N over-nutrition cannot be prevented in the presence of excessive amounts of reduced N in the soil solution.

Initially, over-nutrition of trees with N can stimulate gross primary productivity and, hence, growth (Etzold et al., 2020; Luo et al., 2020; Pretzsch et al., 2023; Sardans et al., 2016; Tian et al., 2018) as observed for European forests and US forests in the last 40–50 years (Quinn Thomas et al., 2010; de Vries et al., 2006, 2014), but may also result in early senescence thereby counteracting enhanced growth at stimulated primary productivity of photosynthesis (Luo et al., 2020). Non-linear response in forest productivity to N deposition has been observed in several studies (de Vries et al., 2014; Etzold et al., 2014; Xing et al., 2022). At prolonged exposure, the positive effect of excess N acquisition on growth ceases because of nutrient imbalances (Jonard et al., 2015; Netzer et al., 2019; Rothstein, 2018; Sardans et al., 2016), reduced fine root biomass, and a change in the composition and abundance of mycorrhizal fungi (van der Linde et al., 2018). These nutrient imbalances include N and phosphorus (Netzer et al., 2019; Sardans et al., 2016), potassium (Jönsson et al., 2004; Rothstein, 2018; Sardans et al., 2016), calcium (Elvir et al., 2006), and magnesium (Elvir et al., 2006; Jönsson et al., 2004) deficiency as well as general cation deficiency (Duquesnay et al., 2000). There may also be a reason for the enhanced mortality of trees observed under these conditions (Rothstein, 2018) and for an increased attack by parasites (Flückiger and Braun, 1999). The later effect requires further experiments under controlled conditions to test conclusions drawn from field studies (Fig. 1).

Acid precipitation will affect both, directly the shoot and indirectly the root of trees mediated by changes in the soil (Fig. 1) (Zhang et al., 2023). The direct impact of acid precipitation on leaf function is evidenced by the erosion of surface waxes and cuticles, as well as the leaching of base cations from mesophyll cells, despite the simultaneous uptake of nitrates in rainwater, which may confer benefits to leaf

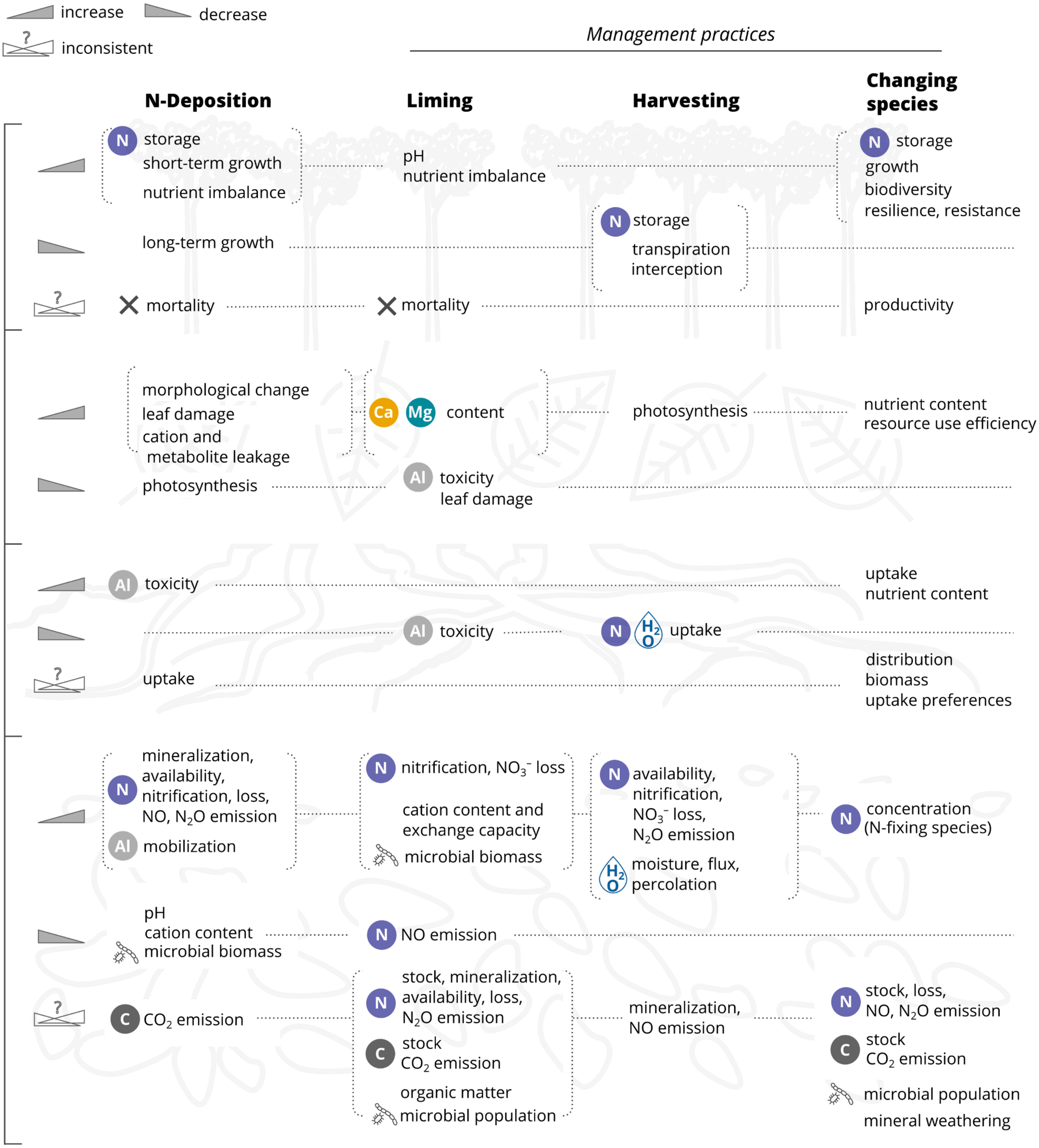


Fig. 1. Schematic diagram showing effects of nitrogen deposition on forest ecosystem and the effects of common management practices. The arrows indicate the general effects of nitrogen deposition and management practices. Red arrows, increasing; blue arrows, decreasing; grey crosses, no consistent results or lack of data.

photosynthesis and plant growth (Dong et al., 2017). In leaves exposure to acid precipitation can be recognized by the development of necrotic spots (Sant'Anna-Santos et al., 2006; Whitney and Ip, 1991). But, before these visible symptoms of damage develop, micro-morphological changes of the leaves are observed, in particular increased roughness and reduced wettability of the cuticle as well as wilting of epidermal cells and reduced turgor of guard cells of the stomata (Andrade et al., 2020; Sant'Anna-Santos et al., 2006; Z. Zhang et al., 2021) indicating uncontrolled water loss. Additional anatomical changes are observed in living buds (Soukupová et al., 2002). Impaired foliar structures are accompanied by a severe leakage of cations such as Ca, Mg, Mn, Zn, Fe (Diatta et al., 2021; McLaughlin et al., 1993; Türk et al., 1993; Tveite et al., 1990) and organic compounds such as sugars from the cell walls (Shigihara et al., 2008) and the cytoplasm, whereas K contents of the leaves are less affected (Tveite et al., 1990) and the contents of phenolic compounds may even increase (Soukupová et al., 2002). Still detailed analyses of the leakage of the cellular metabolites by acid precipitation requires further studies. It may not necessarily result in reduced cellular contents due to stimulated metabolic activity (Shumejko et al., 1996) indicated by increased respiration (McLaughlin et al., 1993). As a consequence of impaired chloroplast structure, also chlorophyll contents and photosynthesis per chlorophyll are reduced by acid precipitation (Shan et al., 1996). These effects are often accompanied by oxidative stress that is not compensated by enhanced anti-oxidative activity (Chen et al., 2013; Z. Zhang et al., 2021). Also, phenological changes such as early onset of bud break and, hence, increased late-frost sensitivity are observed in trees exposed to acid precipitation (Soukupová et al., 2002). In addition, biotic interactions in the above-ground parts of plants are modified by acid precipitation, indicated by impaired development and performance of herbivores (Ruuhola et al., 2009), enhanced susceptibility of insects feeding on acid precipitation exposed foliage to predators (Palokangas et al., 1995), and reduced foliar abundance of endophytic fungi (Asai et al., 1998; Ranta et al., 1995). Studies addressing the indirect effects of acid precipitation on roots are still limited. The effects seem to be largely mediated by soil microorganisms, the abiotic environment and dynamics of substances in the soil rhizosphere (Dong et al., 2017; Zhang et al., 2023).

As indicated by atmospheric deposition history, acid precipitation during the last century was predominantly due to S deposition that was gradually replaced by N deposition (EMEP, 2023). Studies have shown N deposition contributed to soil acidification, too (Lu et al., 2014; Chen et al., 2023). Since N deposition enhanced forest growth (Etzold et al., 2020; Luo et al., 2020; Pretzsch et al., 2023; Sardans et al., 2016; Tian et al., 2018), it also enhanced the S requirement of forests at declining availability. A similar situation was observed in agriculture, where reduced atmospheric S deposition resulted in S deficiency and significant yield losses in the 1990s that had to be counteracted by the use of significant amounts of S containing fertilizer (20–60 kg S ha^{-1} y^{-1}) for crops such as wheat and rape until today (Bloem et al., 2015). Yield losses at S deficiency were accompanied by reduced plant fitness and enhanced susceptibility to various diseases, since numerous defence processes of plants against biotic and abiotic stress rely on organic S compounds (Foyer and Rennenberg, 2000; Hell and Rennenberg, 1998; Herschbach et al., 2012). S deficiency was also reported in beech, oak, spruce and pine forests in Central Europe (Wellbrock et al., 2016) that may have contributed to the reduced stress tolerance of these forests to environmental constrains from global climate change such as drought (Fink et al., 2004; Schiermeier, 2018). Thus, S fertilisation of forests may also be required in future to enhance its stress resilience in a changing environment.

2.2. *Soil processes and matter exchange*

Soil characteristics and processes can be affected by N deposition, for instance soil pH, C and N cycling, enzyme activities, as well as soil microbial communities (Fig. 1) (Cheng et al., 2019; Lu et al., 2014; Verma and Sagar, 2020; Zhang et al., 2018). Soil acidification resulting from lower soil pH and declined acid neutralization capacity has been characterised as a major environmental issue in many temperate, boreal regions and tropical forests, which direct impacts on nitrification and mineralization process rates and indirectly regulates soil N turnover through alteration of the soil microbial community (Cheng et al., 2019; Lu et al., 2014). Strong soil acidification causes mobilisation of aluminium and, as a consequence, aluminium toxicity to the roots, including reduced root elongation and biomass production at enhanced phytohormone contents (Hirano et al., 2007; Wang et al., 2020). The reduced contents of cations, particularly of Ca, observed in tree roots under these conditions (Hirano et al., 2007; Li et al., 2014) may be a consequence of both, enhanced leakage and reduced uptake. However, detailed analyses of the consequences of acid precipitation for individual root transport processes have neither been reported for nutrient uptake nor for root exudation of organic compounds. Acid precipitation will also affect biotic interactions in the rhizosphere, indicated by slowed mycorrhiza formation, modified ectomycorrhizal community, and a general decline in microbial biomass (Maehara et al., 1993; Roth and Fahey, 1998; Tian et al., 2008). The latter also includes the reduced abundance of nitrifiers and, hence, shifts the competition for reduced nitrogen in favour of the roots (Papen et al., 1991).

The effects of N deposition on soil N status and transformation in forest ecosystems has been reviewed previously in Cheng et al. (2019). Flechard, van Oijen et al. (2020) estimated that the mean N deposition-induced fertilization effect on C sequestration in European forests was 40–50 g C per g N, while Schulte-Uebbing et al. (2022) found minor contribution of N deposition to global forest C sequestration, and forest C-N response increased from tropical to boreal regions. N deposition has contributed to the net C sequestration in trees and soil in Europe by approximately 11.8 Mton yr^{-1} from 1960 to 2000 (5.1 Mton yr^{-1} in tree wood and 6.7 Mton yr^{-1} in soil) (de Vries et al., 2006). Similar results were also observed in a majority of tree species across the northeastern and north-central USA (Horn et al., 2018; Quinn Thomas et al., 2010). In general, elevated N concentration in the soil may stimulate N mineralization and nitrification. Soil total N and mineral N have been increased by 6.2 % and 114 %, respectively, and the increase of NO_3^- in soil solution was 9 times of NH_4^+ due to elevated N deposition. N deposition also resulted in alteration of organic matter quality as indicated by 6.7 % decreased soil C/N ratio despite an increase of C storage by 4.8 % (Cheng et al., 2019 and the references therein). N is also essential for growth of soil microbes, which are critical drivers for a large number of essential ecosystem processes including N transformation. Global negative effects of elevated N have been observed on soil microbial population, composition, as well as enzymes involved in N transformation (Chen et al., 2018; van der Linde et al., 2018; Zhang et al., 2018; Zhou et al., 2017). In addition to a decreased fungi to bacteria ratio under N deposition (Peguero et al., 2021; Zhou et al., 2017; Zuccarini et al., 2023), Choma et al. (2020) found that bacteria responded to N addition rapidly compared to fungi in spruce and beech forests, hence, bacterial reaction might control the changes in soil enzymatic activity in a long term view of N deposition.

An oversupply of N is thought to gradually diminish N retention in living biomass and the soil so that surplus N is lost from the ecosystem via leaching or gaseous emissions (Fig. 1) (Aber et al., 1998; Emmett, 2007; Kreutzer et al., 2009; Lovett and Goodale, 2011). Apart from the retention of deposited N in plant biomass, substantial amounts end up in the soil (Templer et al., 2012). Fertilization experiments in forests show that N addition generally increases soil organic matter (SOM) storage (Forstner et al., 2019; Janssens et al., 2010), but the amount of retained N depends upon the soil C/N ratio because microbial immobilization of added N may be low in soils with a C/N ratio < 20 (Dannenmann et al., 2007; Lovett and Goodale, 2011). The controlling role of the soil C/N ratio on N immobilization is also reflected in its tight relationship with leaching of dissolved inorganic N (DIN), predominately in the form of nitrate (Dise et al., 2009a; Dise and Wright, 1995; MacDonald et al., 2002; Magill et al., 2004). At the catchment scale, N deposition is a major driver of DIN concentrations and runoff globally (Templer et al., 2022, 2012). Findings from isotope studies confirm the important role of C for the retention of N deposition (Curtis et al., 2011). Furthermore, limitation in available P co-determines N leaching rates, so that high leaching rates occur where forest floor C:N ratios are low and N:P ratios are high (Oulehle et al., 2021). P limitation occurs naturally due to sorption but also due to nutrient imbalances caused by N deposition and because climate warming is increasing plant growth and at the same time leaching losses (Tian et al., 2023). Nevertheless, the retention of DIN in catchments distributed across unmanaged European forest areas with no local N emission sources is high, but decreased with increasing inorganic N deposition owing to elevated gaseous and leaching losses (Vuorenmaa et al., 2018). Declining N availability in ecosystems in recent decades even led to the notion of ecosystem oligotrophication (R. E. Mason et al., 2022). Although little effects (2.8 % from 2000 to 2020) of N addition on soil respiration were observed overall, soil acidification significantly increased the negative effects of N addition on soil respiration, which might in turn impact the roots, microorganisms and their respiration (Chen and Chen, 2023).

Soil is also a major source of greenhouse and N trace gases, i.e., CO_2, CH_4, nitrous oxide (N_2O), nitric oxide (NO) and molecular nitrogen (N_2) (Fig. 1). In general, increased N deposition mostly reduces CO_2 emission by impeding soil autotrophic and/or heterotrophic respiration and organic matter decomposition (Fan et al., 2020; Janssens et al., 2010), with several studies showing either no change or increased soil CO_2 fluxes. For instance no change was found in a Mediterranean dryland dominated by *Quercus coccifera* L. and *Rosmarinus officinalis* L. by N fertilisation (Lafuente et al., 2020), whereas, a meta-analysis showed a 0.3 % increase in China under N enrichment (Deng et al., 2020). Unlike CO_2, N trace gases were apparently impacted by N deposition (Fan et al., 2020, 2020; Lafuente et al., 2020). NO emissions from coniferous forests are highly correlated with N-deposition (Pilegaard et al., 2006; Venterea et al., 2003) with maximum emission rates ranging between 6 and 10 kg N ha^{-1} yr^{-1} reported for a spruce forest with chronic high N deposition of 30 kg N ha^{-1} yr^{-1} (Butterbach-Bahl et al., 2002a). Correlation between N_2O emission and N-deposition are less significant but instead there are significant negative correlation between N_2O emission and the soil C/N ratio (Gundersen et al., 2012; Pilegaard et al., 2006). Overall N_2O emissions (1–3 kg N ha^{-1} yr^{-1}) from temperate forest ecosystems significantly affected by atmospheric nitrogen deposition are likely lower than NO emissions (Butterbach-Bahl et al., 2002a; Luo et al., 2012; Pilegaard et al., 2006). Xia et al. (2020) and Du et al. (2024b) found that effects of N addition on soil N_2O emissions and CH_4 uptake in global forests were biome specific and dose dependent (CH_4 sink). A recent study by Cen et al. (2024) found that current levels of N deposition reduce global forest soil CH_4 uptake by about 3 % and that reductions of atmospheric CH_4 uptake due to atmospheric N deposition was more pronounced in temperate forests than in tropical or boreal forests, probably due to differences in the soil N status.

In recent years, acid precipitation in Europe and North America has greatly decreased due to decreased S deposition (EMEP, 2023). More than 50 % decrease of sulphate (SO_4^{2}) accompanied by significantly decreased concentrations of the nutrient base cations, i.e., calcium, magnesium and potassium and aluminium in the upper mineral soil layer (0–20 cm) was documented in International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) monitoring network plots across Europe (Johnson et al., 2018). With regard to tree growth and C sequestration, Högberg et al. (2006) found that tree growth initially responded positively to N addition, but that the rate of N addition may be more important than the accumulated N dose in a long-term response, and soil pH may recover faster after removal of the N-load than predicted. Therefore, long-term monitoring in forest ecosystem response to both legacy effects of previously increased N deposition and currently decreased deposition deserve more attention and research efforts (Bowman et al., 2008; Dirnböck et al., 2017; Gilliam et al., 2019; Johnson et al., 2018), particularly under climate change conditions (Dirnböck et al., 2017).

3. Significance of management practices in mediating consequences of nitrogen deposition and soil acidification

3.1. Liming

Liming is a long and widely used countermeasure against acidification of forest soils in Europe (Persson et al., 2021; Saarsalmi et al., 2011). In addition to counteract acidification and improvement of the cation exchange capacity, liming also impacts soil C, N and nutrient cycles, macrofaunal and microbial community composition and associated greenhouse gas fluxes, although studies are still limited and results are not consistent. Some studies reported decreased C and N pools (Fig. 1) (Huber et al., 2006; Jansone et al., 2020; Kreutzer, 1995; Marschner and Waldemar Wilczynski, 1991; Persson et al., 1995), while others found increased C and N stocks (Derome, 1990; Long et al., 2022; Melvin et al., 2013; Sridhar et al., 2022; Wang et al., 2021), the effects strongly depended on the liming product and application amount, and the initial status of the soil (Court et al., 2018; Jansone et al., 2020; Saarsalmi et al., 2011). In addition to the effects of liming on the calcium (Ca) and magnesium (Mg) contents of the spruce forest floor (Meiwes et al., 2002), they also had pronounced impacts on the nutrient status of the trees. For example, Ca/$MgCO_3$ liming strongly increased foliar Mg concentrations, whereas they gradually decreased in $CaCO_3$ limed plots (Court et al., 2018). Similar effects were also observed when liming products containing potassium were applied (Court et al., 2018). Ljungström and Nihlgård (1995) found that calcium carbonates improved Ca nutritional status, while dolomite improved both Ca and Mg nutrition. The disparate effects may be ascribed to discrepancies in the release of readily plant-available minerals, the enhancement of organic matter decomposition and soil pH, and decreased aluminum (Al) toxicity across a range of lime products (Court et al., 2018). The pH of the soil organic layer of Scots pine (*Pinus sylvestris* L.) forest exhibited a 0.4-unit increase in plots receiving 4 Mg ha^{-1} of limestone compared to those receiving 2 Mg ha^{-1}, after a 21-year period (Saarsalmi et al., 2011). N mineralization was also found to be stimulated at N-rich sites ($C/N < 30$) but inhibited by liming at N-poor sites (Formánek and Vranova, 2003) or N- poor soil layers (Melvin et al., 2013). Liming can increase nitrification through stimulation of nitrifying bacteria abundance, and hence increase the availability of soil nitrate as well as the loss of NO_3^--N (DeForest and Otuya, 2020; Kreutzer, 1995) and liming is supposed to increase soil organic matter decomposition due to enhanced microbial activities under higher pH (Court et al., 2018). However, results from studies are inconsistent, and the possible reasons have been well discussed by van Straaten (2023), which may be caused by changes of macrofaunal (Baath et al., 1981; Persson et al., 2021), nutrient stoichiometry of soil and plants tissues (Court et al., 2018; Eklund and Eliasson, 1990; Melvin et al., 2013), microbial community structure and abundance (Marschner and Waldemar Wilczynski, 1991; Sridhar et al., 2022; Wan et al., 2019), and increased aboveground and belowground litter inputs (Huettl and Zoettl, 1993; Lin et al., 2015). The latter has been linked to liming-induced improvements of the availability and mobility of plant nutrients (e.g., Ca^{2+} and Mg^{2+}), reductions or removal of Al^{3+} toxicity (Court et al., 2018; Saarsalmi et al., 2011; Sridhar et al., 2022), as well as the quality and quantity of liming materials used and the application time (Wang et al., 2021). Liming can restore the cation contents of the roots and the shoot and, hence, tree growth (Li et al., 2014; Tveite et al., 1990). However, the less acidic pH achieved by liming also supports the abundance of nitrifiers in the rhizosphere thereby competing with the roots for reduced nitrogen. The nitrifiers that develop under these conditions in the soil may at least partially originate from shed foliage that can be occupied by endophytic nitrifiers (Papen et al., 2002). It is expected in the long-run that liming would lead to better exploitation of the potential rooting zone because of more favorable chemical and physical properties for root growth in the mineral soil (Wilpert, 2022). Liming has been found to have a long-lasting positive effect on foliar Ca and Mg concentrations in Scots pine (*Pinus sylvestris* L.) needles (21 years) (Saarsalmi et al., 2011), sugar maple (*Acer saccharum* Marsh.) and black cherry (*Prunus serotina* Ehrh.) foliage (30 years) (Long et al., 2022) due to increased soil Ca and Mg particularly in mineral soil layer (Court et al., 2018). Basal area increment black cherry shew a species specific manner (Long et al., 2022). At stand level, increased stand volume of Scots pines was observed after liming on the unploughed plots (Saarsalmi et al., 2011).

Though only a few studies are available on the effects on N trace gas emissions. Liming of a coniferous stand in a forest in south Germany resulted in a reduction of NO emission rates by 25–30 % as compared to the control, but significantly enhanced (> 60 %) N_2O emission rates (Butterbach-Bahl et al., 2002a, 1997). The latter is in contradiction to Borken and Brumme (1997) who found a reduction in N_2O emissions after liming of up to 60 %. The effect of decreasing NO emissions can be mainly attributed to an increase of oxidative NO consumption processes (Gasche and Papen, 1999) and the strong decline of NO-production by chemodenitrification after increasing the forest floor pH. Since N_2O emission rather originate from the mineral soil, differences in magnitude of pH changes in the mineral soil may explain the contradicting effects. As liming strongly increased net nitrification rates (Gasche et al., 2002; Melvin et al., 2013; Papen and Butterbach-Bahl, 1999), NO_3

concentrations in the organic layer and the mineral soil (Kreutzer, 1995), the inhibition of the N_2O-reductase at enhanced nitrate concentrations (Bremner, 1997; Wild et al., 1995) may have caused an increase of N_2O emissions via denitrification in coniferous forest of south Germany.

Although it is quite modest, the legacy effects of soil liming can persist for several decades in the forest floor (Kellaway et al., 2022; Persson et al., 2021, 1995; Silveira et al., 2021; Sridhar et al., 2022) and leaves (Long et al., 2022), and appeared to increase the risk of frost and drought damage (Huettl and Zoettl, 1993), nutrient imbalances in Mg, K and P (Berger et al., 2016; Court et al., 2018), therefore, long term post liming effects on forest vitality might deserve more attention (De Marco et al., 2022).

3.2. *Harvesting (selective cutting and clear cutting)*

Partial or complete removal of trees from intact stands, either through management or through wind, drought, or insect outbreaks, has a dramatic impact on ecosystem N cycling and N losses due to the temporal partial or full removal of the plant N sink (Dirnböck et al., 2016; James et al., 2021; Valipour et al., 2021). Forest stand replacement has drastic effects on N cycle resulting in N loss to the ground and surface water and elevated gaseous N emission from the soil (Fig. 1). In Europe clear-cut felling is still the dominant practice and only approximately 30 % of the managed forest area belongs to continuous cover forestry (W. L. Mason et al., 2022). Similar effects from stand replacement on N cycling are also apparent after disturbances events such as elevated DIN in catchment runoff as reported for bark beetle and storm disturbances, e.g., in the Bavarian National Park (Beudert and Gietl, 2015; Jung et al., 2021) and the Kalkalpen National Park in Austria (Dirnböck et al., 2020; Hartmann et al., 2016). Thus, studies on the interactive effects of long-term chronic N deposition with stand-replacing disturbances are still timely (Schleppi et al., 2017). Even more, since in Europe's forests, disturbances from wind, insects (mostly spruce bark beetle) and fires are expected to further increase with ongoing climate change (Patacca et al., 2023; Senf et al., 2018). These disturbances, further interact with forest management. While the plant N sink is removed, mineralization of organic matter in the forest floor or mineral soil continues or may even be accelerated due to more favorable micro-climatic conditions, which results in a strong increase in the availability of mineral N (but as well of dissolved organic N, DON) for microbial processes and environmental N loss pathways (James et al., 2021; Kreutzweiser et al., 2008; Prescott, 1997; Valipour et al., 2022).

Clearing or thinning as well as disturbances causing tree mortality will significantly reduce root N uptake due to the lower fine root biomass of tree saplings and accompanying vegetation compared to mature trees. As the shade effect of the canopy is lacking, higher soil temperatures may be observed at least during the growing season. Also, higher peak and average soil moisture values have been observed following clear- or selective cutting due to reduced plant root water uptake, plant transpiration and interception (Hashimoto and Suzuki, 2004; Kovács et al., 2020; Tanaka and Hashimoto, 2006). In consequence, also soil water fluxes increase sharply. E.g. Piirainen et al. (2002) reported that annual percolation rates following clear-cutting of a boreal forest with a dense undergrowth of dwarf shrubs and *Vaccinium myrtillus* increased by about 6–9 % below the main rooting zone. In a study reporting on a comparison of soil water and nutrient fluxes at clear-cutted and control sites of spruce forest stands without significant undergrowth in South Germany, Huber et al. (2004) found an increase of the percolation rate in 40 cm soil depth, i.e. below the main rooting zone, of about 20–40 % in the first three years after cutting. Similar increases in percolation of 20–50 % following clear-cutting have been observed in other studies as well, e.g., for a Douglas-fir plantation in France (Ranger et al., 2007), an oak forest in Greece (Ganatsios et al., 2010) or a Norway spruce stand in Ireland (Huber et al., 2010).

The changes in micro-climate as well as the availability of harvest residues and decaying tree roots, significantly affects soil microbial C and N turnover processes by increased rates of organic matter mineralization (e.g. Kreutzweiser et al., 2008; Mayer et al., 2020; Piirainen et al., 2007). While clear-cutting may slow down the decomposition of leaf litter, specifically of coniferous needles, likely due to the accelerated drying out of the organic layers (Jerabkova et al., 2011), soil mineral N as well as DON (and DOC) concentrations have often been found to increase, specifically nitrate concentrations in the organic and upper mineral soil layers (Bergholm et al., 2015; Huber et al., 2010, 2004). This points towards the stimulation of organic matter mineralization and nitrification. However, the meta-data analysis by Jerabkova et al. (2011) on published studies investigating clear-cutting effects on soil N-dynamics didn't reveal significant effects on N mineralization. On the other hand, Jerabkova et al. (2011) as well as most other studies found a significant stimulation of nitrification rates (e.g. Smolander et al., 2019; Törmänen et al., 2018) and significant increases in soil water NH_4^+ and NO_3^--concentrations (e.g. Huber et al., 2010; Matejek et al., 2010; Valipour et al., 2022). Given that soils generally have a much greater cation than anion exchange capacity and in view of increased percolation rates following clear-cutting, NO_3^- rather than NH_4^+ is dynamically relocated along the soil profile and finally leached. Increased rates of nitrate leaching were observed specifically in the first- or second-year following clear-cutting (Bergholm et al., 2015; Huber et al., 2010), with NO_3^- leaching rates gradually decreasing with increasing plant biomass and returning to values before clear-cutting within about five years (e.g. Huber et al., 2010). Observed annual peak fluxes of NO_3^- leaching were reported to be as high as 170 kg NO_3-N ha^{-1} yr^{-1} following clearing of a N saturated spruce forest stand in South Germany (or 10-fold higher as compared to an undisturbed control stand) (Huber et al., 2010), though in most other studies much lower peak leaching rates in a range of 2–10 kg NO_3^--N ha^{-1} yr^{-1} were reported (8 kg NO_3^--N ha^{-1} yr^{-1}, Norway spruce stand in Sweden (Bergholm et al., 2015); 2–10 kg NO_3^--N ha^{-1} yr^{-1}, meta-analysis by Jerabkova et al. 2011, considering boreal and temperate forests). Observed differences in N leaching losses following clear-cutting may be attributed not only to differences in climate, soil edaphic conditions or history and magnitude of atmospheric N deposition (MacDonald et al., 2002), but also depend on ground vegetation biomass and forest re-growth dynamics and the presence, distribution and abundance of logging residues (Bergholm et al., 2015; Smolander et al., 2019).

Estimates of N uptake by intact forests can be derived from measurements of N in litter-fall and forest growth rates. Based on observations by the pan-European forest monitoring network of the "International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests" (short: ICP-Forest), the annual litter-fall at 1604 forest monitoring sites across Europe was about 4 tons ha^{-1} yr^{-1} (Neumann et al., 2018). Litter-fall values are approximately 3 tons ha^{-1} yr^{-1} for North-European coniferous and broadleaved forest stands, while for South- and Central European broadleaved forest stands values of litter-fall range mostly between 4.5 and 5 tons ha^{-1} yr^{-1}. Across all climate zones the average N content of the total litter-fall is about 1.04 % (Neumann et al., 2018). This means, that on average 40 kg N, mainly organically bound, returns to the soil by aboveground litter-fall mostly in autumn. In addition, also annual fine root litter production should be considered. Annual fine root production by forests has been estimated at about 4 tons ha^{-1} yr^{-1} (Addo-Danso et al., 2016). Though significant differences between different forest types in various climates do exist, total nitrogen contents in fine root litter are likely to amount to 30–50 kg N ha^{-1} yr^{-1} in addition to aboveground litter (e.g. Kreutzer et al., 2009; Yuan and Chen, 2010). Fixation of N in the growing forest biomass is in the range of 5–10 kg N ha^{-1} yr^{-1}, i.e. about 5–10 % of annual litter-fall, while the remaining N, about 30–100 kg N ha^{-1} yr^{-1} dependent on forest type, age and site properties, is returned to the soil as litter, predominantly in form of organic N. The N requirements of a mature forest stand is predominantly met by root N uptake, though foliar N uptake in the canopy may be substantial (Ferraretto et al., 2022). E.g., Kreutzer et al. (2009) estimated root N uptake by a mature spruce forest in Southern Bavaria at 129 ± 26 kg N ha^{-1} yr^{-1} and foliar N uptake at about 8 kg N ha^{-1} yr^{-1}, indicating that the N demand of the forest stand is mostly covered by root N uptake, with soil N being provided by the mineralization of above- and belowground litter. Therefore, effects of harvesting on forest N are impact both soil and plant N turnover.

So far minor attention has been given to the alteration of N-GHGs (N_2O) exchange induced by specific forest management practices such as selective cutting and clear cutting. Forest clear cutting is a commonly used management practice for timber harvesting worldwide (Ma et al., 2013; Rosenvald and Lõhmus, 2008) and particularly in temperate and boreal forests (Keenan et al., 2015), but other methods like selective cutting are increasingly discussed and implemented (Pukkala et al., 2009). So far, most of the still few investigations of the alteration of soil N-GHGs exchange after clear cutting and selective cutting events are short-term studies covering about 1–3 years. At the Höglwald spruce forest N_2O emission changes were followed for 12 years after clear-cutting and selective logging (30 % biomass harvest) events and compared to the control. The effects of clear cutting on soil N_2O emissions were significant for at least 10 years after logging, with emissions being increased on average by 147.6 % as compared to the control site. Short-term increase of N_2O emissions after full forest harvesting is a general phenomenon and was also observed by others (e.g. Korkiakoski et al., 2019; Zerva and Mencuccini, 2005), but could not be confirmed by Tate et al. (2006), who explained the rather small increase of N_2O emissions by the highly porous and free draining volcanic soil. However, it is difficult to compare different thinning studies as the method of thinning varies, which affects the measured greenhouse gas fluxes (Mazza et al., 2019). Compared to clear cuts, selective cutting shows much lower or even no increases of soil N_2O emissions, with effects diminishing 2–3 years after removal of part of the trees (Korkiakoski et al., 2019; Mazza et al., 2019). Increased soil water content, enhanced soil C and N cycling and shifts in microbial populations involved in N cycling (nitrification and denitrification) were found to be responsible for the observed changes in soil N_2O emissions (e.g. Zerva and Mencuccini, 2005). At the Höglwald forest site, clear cutting and associated multi-year increases in soil N_2O emissions and reductions of the soil CH_4 oxidation activity (Wu et al., 2011) reduced the overall GHG sink strength of the forest over the entire rotation period by 3 %, which agrees with numbers of Peichl et al. (2010) reported for a forest chronosequence study. Even though this seems to be a tiny number, it is significant and can be strongly reduced if forest renewal is done by selective cutting.

With climate change even becoming more important in future, interactions with the N cycle will obvious tighten and will also affect N leaching and gaseous N losses under the different forest management systems (Dirnböck et al., 2017, 2016; Porter et al., 2013). Knowledge on these issues is still scarce and therefore further studies are required.

3.3. Changes of tree species composition

Mixed-species forests are intensively discussed as management option for large portions of monocultures in Europe and worldwide under projected climate change (Pretzsch et al., 2021). Monocultures are often associated with low ecological values, and high vulnerability to disturbances caused by anthropogenic climate change (Forzieri et al., 2021). For instance, the preference to plant Norway Spruce in Europe has resulted in even-aged single-species forests, which are much more vulnerable to disturbances such as wind throw, parasite infections (e.g. bark beetle) and fire than natural tree species mixtures would be (Krejza et al., 2021; Thom et al., 2018). Therefore, replacing or transforming monocultures particularly the coniferous monocultures to mixed-species forests has long been recommended (Felton et al., 2010; Hlásny et al., 2021; Pretzsch et al., 2021). Apart from advantages in biodiversity, resistance and resilience over monocultures (Liu et al., 2018), mixing tree species favour diameter growth increment (Piotto, 2008), increases of the mean productivity compared to monoculture stands up to 50 % depending on tree species, climate and soil fertility (Ammer, 2019; Bielak et al., 2014; Blaško et al., 2020; Forrester et al., 2006; Pretzsch and Schütze, 2016).

Mixing had strong effects on above-ground nutrients status of individual trees (Fig. 1) (Du et al., 2019; Richards et al., 2010; Thelin et al., 2002). For instance, Richards et al. (2010) found more than half of the mixed-species studies he surveyed reported a shift to greater above-ground nutrient content of species grown in mixtures, particularly when monocultures were mixed with nitrogen-fixing species. These findings indicated increased resource-use efficiency (including nutrients, water and light) in mixed forests compared to monocultures (Richards et al., 2010). Mixing also had effects on below-ground part of trees, for example root distribution and biomass, nutrient and uptake preferences (Fig. 1). Spruce rooted more shallowly, whereas beech rooted more deeply when they were mixed with each other (Rothe and Binkley, 2001). Wambsganss et al. (2021) recently found mixing induced less fine-root biomass than pure stands, but higher root length density in the most nutrient-rich upper soil layer, which may support higher resource uptake capacity in mixed compared to monospecific stands. Knowledge on the effects of mixing on root nutrition is till scare, but studies have shown calcium and N concentrations in beech and lime (*Tilia cordata*, *Tilia platyphyllos*) roots were significantly positively correlated with belowground root diversity (Lang and Polle, 2011). Similarly, increased root C, N and inorganic phosphorus contents were also observed in roots of *Juglans regia*, when it was mixed with N_2-fixing *Robinia pseudoacacia* (Du et al., 2019). Moreover, the presence of *R. pseudoacacia* enhanced the uptake capacity of *Juglans* roots for NO_3^- (Du et al., 2019).

Tree species can influence the soil nutrient status, microbiome and gene abundance related to N and C cycling (Fig. 1) (Du et al., 2019; Kelly et al., 2021; Kjønaas et al., 2021; Vesterdal et al., 2008). Recently, Gillespie et al. (2021) and Hedĕnec et al. (2023) found that tree species identity, traits and their mycorrhizal association can either directly - via litter chemistry - and/or indirectly - through litter- and root-mediated soil properties - influence soil microbial functioning, which plays a crucial role in key ecosystem processes. Instead of species diversity, species identity was the most significant factor influencing soil C stock, C/N ratio and pH in topsoil layers (Dawud et al., 2017). In addition, the resilience of coniferous forest litter to biological degradation was shown to be greater compared to litter from hardwood trees (Augusto et al., 1998 and the references therein). Kjønaas et al. (2021) found tree species had significant effects on soil C and N concentrations, C/N, base saturation, exchangeable acidity and cation pool in the upper mineral soil layer. Norway spruce (*Picea abies* Karsten) and Scots pine favoured the formation of Al-hydroxylated intergrades and, consequently, enhanced the acidification of soils and weathering of Al in comparison with the other tree species tested under the same condition (Augusto et al., 1998). Studies have shown changing the dominant tree species from conifers to deciduous trees results in lower N deposition because conifers exert higher rates of canopy exchange (Draaijers et al., 1997; Gundersen et al., 2012). Furthermore, as mentioned above DIN leaching is relatively tightly linked to the soil C:N ratio (Dise et al., 2009b; MacDonald et al., 2002), and tree species are next to atmospheric N deposition the main determinant of the soil C:N ratio (Cools et al., 2014). As an example, Templer et al. (2005) found, that N retention in the different ecosystem pools varies between tree species in the Catskill Mountains, USA. Braun et al. (2020) compared neighbouring stands of Norway spruce and European beech and found significantly higher N leaching rates under spruce compared to beech trees. Similarly, the evergreen Sitka spruce (*Picea sitchensis*) was able to intercept atmospheric SO_2, thereby leading to accumulations of excess sulphate in tree foliage (Miller et al., 1991). This would point towards co-benefits of forest adaptation with higher shares of broadleaf trees to climate change and N management. However, Gundersen et al. (2009) reported that the lower soil C/N ratios offset the effect of throughfall N deposition and thus N leaching did not differ between spruce and beech forests across Denmark, indicating the importance of the N deposition history together with tree species effects on soil N availability and leaching.

Regarding different tree species, NO emissions of coniferous stands by far exceeded N_2O emissions, while this is opposite for deciduous stands with higher N_2O than NO emissions (Butterbach-Bahl et al., 1997) (Fig. 1). However, also considering N_2 emissions Butterbach-Bahl et al. (2002a) found that total N trace gas emissions with 14.0 and 15.5 kg N ha^{-1} yr^{-1} for spruce and beech, respectively, did not differ between the two forest stands. Overall, these results indicate a strong differentiating impact of tree species on environmental conditions controlling the ratio of NO to N_2O to N_2 emitted from soil. In general, the litter layer of coniferous forests is thick (MacDonald et al., 2002) and well aerated and, thus, favouring nitrification induced NO emissions. Conversely, due to compact and more moist litter layers, deciduous forests rather support N_2O production and NO consumption by denitrification (Gundersen et al., 2012; Pilegaard et al., 2006). However, the high importance of N_2 emissions representing 50–80 % of gaseous N losses at the low number of measurements of this compound still hampers our understanding of nitrogen cycling and budgets of forest ecosystems, particularly when exposed to high loads of atmospheric N. Considering increased soil moisture and N availability through stemflow, Butterbach-Bahl et al. (2002b) demonstrated higher N_2O emissions in the stem area of deciduous and to a lower degree in coniferous forests, which could lead to an underestimation of up to 25 % if this effect is disregarded. Further uncertainty in N trace gas emission estimates may result from the periodicity of emissions. While NO emissions mainly follow the seasonality of soil and air temperature (Medinets et al., 2019), N_2O emission budgets are mainly controlled by peak events such as frost-thaw and re-wetting events in summer periods (e.g. Luo et al., 2012). In addition, the effects of different microbial communities in coniferous and broadleaved forests involved in gaseous N production are likely also contributing to the observed differences between NO and N_2O emissions (Chen et al., 2019). Nevertheless, denitrification may not constitute the main source of N_2O under various climatic and biological conditions (Berendt and Wrage-Mönnig, 2023). Therefore, more research is still needed in order to fully understand patterns of microbial N-cycling and N-gas production/emission in forest ecosystems with different tree species (Butterbach-Bahl et al., 2002a; Chen et al., 2024; Hedĕnec et al., 2023; Gillespie et al., 2021).

Mixed forests provide more ecological and environmental advantages over monocultures from stand to global levels, mixing does not mean simply increase of tree species diversity. Depending on local environmental conditions, complementary functional traits, and the ecosystem goods and services of interest, mixtures should be carefully designed with proper management (Blaško et al., 2020; Liu et al., 2018; Schuler et al., 2017).

4. Summary and future perspectives

Forests globally, but specifically in China, SE Asia, Europe and parts of North America have experienced high rates of N deposition (Bebber, 2021; Cen et al., 2024). Apart from the benefit of stimulating regional growth (Etzold et al., 2020; Pretzsch et al., 2023), there are negative effects of N deposition, that can affect tree and soil health and the exchange of C and N compounds between the biosphere, atmosphere and hydrosphere. While current discussions of management practices are often focusing on improving climate change resilience of forest stands, recreational values and biodiversity, there is little recognition that each forest management activity also directly affects ecosystem N cycling. Limiting stand replacing disturbances is likely to reduce N losses, and changes in tree species may also have direct effects on N retention (Ji et al., 2023; Reverchon et al., 2015; Templer et al., 2005). Adaptation of the forest sector towards tree species that are better to cope with future climate is already underway and will continue in the future (Keskitalo et al., 2015; Kolström et al., 2011; Sousa-Silva et al., 2018; Verkerk et al., 2020) and also has a higher potential to reduce N leaching and gaseous losses. However, even species that today seem to be a way out of the climate crisis also face performance uncertainties related to future climate change as reported by Gessler et al. (2006) for European beech and other dominant trees in Europe (Chakraborty et al., 2024). The identified regional growth trends suggest adaptive management at the regional level to achieve climate-smart forests (Pretzsch et al., 2023). It is therefore important that any policy aimed at improving forest health and greenhouse gas mitigation considers not only potential forest management actions but also the feedback mechanisms of a future, more variable climate. This is likely to increase the demand and complexity of continental forest monitoring, such as the ICP Forests in Europe, which has recently been discussed with regard to lack of complete and harmonized measuring programs (EFI, 2021; EMEP, 2023; Ferretti et al., 2024). It is problematic to make future projections of the impact of lower levels of N deposition based on short-term studies using high addition rates (Högberg et al., 2006). Long-term ecosystem research infrastructures, which are now being formally developed and implemented in Europe (Dirnböck et al., 2019; Futter et al., 2023) are complementary tools to deepen our understanding of this complexity (Templer et al., 2022). It appears that no single treatment is effective in lowering negative impacts of N deposition, and combinations of treatments should be explored (Clark et al., 2019).

CRediT authorship contribution statement

Rennnenberg Heinz: Writing – review & editing, Validation, Supervision, Resources, Methodology, Conceptualization. **Dirnböck Thomas:** Writing – review & editing, Writing – original draft, Funding acquisition. **Butterbach-Bahl Klaus:** Writing – review & editing, Writing – original draft, Funding acquisition. **Kiese Ralf:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Du Baoguo:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (32271863). We are grateful to the EU Horizon 2020 funded eLTER PLUS project (Grand Agreement No. 871128) for financial support to Th. Dirnböck. Klaus Butterbach-Bahl was funded by the Pioneer Centre Land-CRAFT. Ralf Kiese was partly funded by the Helmholtz Research Program Changing Earth – Sustaining our Future, The Atmosphere in Global Change. This article is dedicated to Prof. Dr. Hans Papen in acknowledgement of his outstanding research in the Höglwald Forest, Germany.

Data availability

No data was used for the research described in the article.

References

Aber, J., 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: hypotheses revisited. BioScience 48, 921–934. https://doi.org/10.2307/1313296.

Addo-Danso, S.D., Prescott, C.E., Smith, A.R., 2016. Methods for estimating root biomass and production in forest and woodland ecosystem carbon studies: a review. For. Ecol. Manag. 359, 332–351.

Ammer, C., 2019. Diversity and forest productivity in a changing climate. N. Phytol. 221, 50–66. https://doi.org/10.1111/nph.15263.

Andrade, G.C., Castro, L.N., da, Silva, L.C., 2020. Micromorphological alterations induced by simulated acid rain on the leaf surface of *Joannesia princeps* Vell. (Euphorbiaceae). Ecol. Indic. 116, 106526.

Asai, E.-I., Hata, K., Futai, K., 1998. Effect of simulated acid rain on the occurrence of Lophodermium on Japanese black pine needles. Mycol. Res. 102, 1316–1318.

Augusto, L., Bonnaud, P., Ranger, J., 1998. Impact of tree species on forest soil acidification. For. Ecol. Manag. 105, 67–78. https://doi.org/10.1016/S0378-1127(97)00270-3.

Baath, E., Berg, B., Lohm, U., Lundgren, B., Lundkvist, H., Rosswall, T., Soderstrom, B., Wire, A., 1981. Effects of experimental acidification and liming on soil organisms and decomposition in a Scots pine forest. Pedobiologia 20, 85–100.

Bebber, D.P., 2021. The gap between atmospheric nitrogen deposition experiments and reality. Sci. Total Environ. 801, 149774. https://doi.org/10.1016/j.scitotenv.2021.149774.

Berendt, J., Wrage-Mönnig, N., 2023. Denitrification is not necessarily the main source of N2O from rewetted fens. J. Soil Sci. Plant Nutr. 23, 3705–3713.

Berger, T.W., Türtscher, S., Berger, P., Lindebner, L., 2016. A slight recovery of soils from Acid Rain over the last three decades is not reflected in the macro nutrition of beech (*Fagus sylvatica*) at 97 forest stands of the Vienna Woods. Environ. Pollut. 216, 624–635. https://doi.org/10.1016/j.envpol.2016.06.024.

Bergholm, J., Olsson, B.A., Vegerfors, B., Persson, T., 2015. Nitrogen fluxes after clear-cutting. Ground vegetation uptake and stump/root immobilisation reduce N leaching after experimental liming, acidification and N fertilisation. For. Ecol. Manag. 342, 64–75.

Beudert, B., Gietl, G., 2015. Long-term monitoring in the Große Ohe catchment. Bavar. For. Natl. Park. Silva Gabreta 21, 5–27.

Bielak, K., Dudzińska, M., Pretzsch, H., 2014. Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) Karst] can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments. For. Syst. 23, 573–589. https://doi.org/10.5424/fs/2014233-06195.

Blaško, R., Forsmark, B., Gundale, M.J., Lundmark, T., Nordin, A., 2020. Impacts of tree species identity and species mixing on ecosystem carbon and nitrogen stocks in a boreal forest. For. Ecol. Manag. 458, 117783. https://doi.org/10.1016/j.foreco.2019.117783.

Bloem, E., Haneklaus, S., Schnug, E., 2015. Milestones in plant sulfur research on sulfur-induced-resistance (SIR) in Europe. Front. Plant Sci. 5, 779.

Borken, W., Brumme, R., 1997. Liming practice in temperate forest ecosystems and the effects on CO_2, N_2O and CH_4 fluxes. Soil Use Manag. 13, 251–257. https://doi.org/10.1111/j.1475-2743.1997.tb00596.x.

Bowman, W.D., Cleveland, C.C., Halada, Ĺ., Hreško, J., Baron, J.S., 2008. Negative impact of nitrogen deposition on soil buffering capacity. Nat. Geosci. 1, 767–770. https://doi.org/10.1038/ngeo339.

Braun, S., Tresch, S., Augustin, S., 2020. Soil solution in Swiss forest stands: a 20 year's time series. PLoS One 15, e0227530.

Bremner, J.M., 1997. Sources of nitrous oxide in soils. Nutr. Cycl. Agroecosyst. 49, 7–16. https://doi.org/10.1023/A:1009798022569.

Butterbach-Bahl, K., Gasche, R., Breuer, L., Papen, H., 1997. Fluxes of NO and N2O from temperate forest soils: impact of forest type, N deposition and of liming on the NO and N_2O emissions. Nutr. Cycl. Agroecosyst. 48, 79–90. https://doi.org/10.1023/A:1009785521107.

Butterbach-Bahl, K., Gasche, R., Willibald, G., Papen, H., 2002a. Exchange of N-gases at the Höglwald Forest – a summary. Plant Soil 240, 117–123. https://doi.org/10.1023/A:1015825615309.

Butterbach-Bahl, K., Rothe, A., Papen, H., 2002b. Effect of tree distance on N_2O and CH_4-fluxes from soils in temperate forest ecosystems. Plant Soil 240, 91–103.

Cen, X., He, N., Li, M., Xu, L., Yu, X., Cai, W., Li, X., Butterbach-Bahl, K., 2024. Suppression of nitrogen deposition on global forest soil CH_4 uptake depends on nitrogen status. Glob. Biogeochem. Cycles 38, e2024GB008098. https://doi.org/10.1029/2024GB008098.

Chakraborty, D., Ciceu, A., Ballian, D., Benito Garzón, M., Bolte, A., Bozic, G., Buchacher, R., Čepl, J., Cremer, E., Ducousso, A., Gaviria, J., George, J.P., Hardtke, A., Ivankovic, M., Klisz, M., Kowalczyk, J., Kremer, A., Lstibůrek, M., Longauer, R., Mihai, G., Nagy, L., Petkova, K., Popov, E., Schirmer, R., Skrøppa, T., Solvin, T.M., Steffenrem, A., Stejskal, J., Stojnic, S., Volmer, K., Schueler, S., 2024. Assisted tree migration can preserve the European forest carbon sink under climate change. Nat. Clim. Chang. 14, 845–852. https://doi.org/10.1038/s41558-024-02080-5.

Chen, C., Chen, H.Y.H., 2023. Mapping global nitrogen deposition impacts on soil respiration. Sci. Total Environ. 871, 161986. https://doi.org/10.1016/j.scitotenv.2023.161986.

Chen, J., Li, J., Shen, W., Xu, H., Li, Y., Luo, T., 2019. The structure and species co-occurrence networks of soil denitrifying bacterial communities differ between a coniferous and a broadleaved forests. Microorganisms 7, 361.

Chen, H., Li, D., Zhao, J., Xiao, K., Wang, K., 2018. Effects of nitrogen addition on activities of soil nitrogen acquisition enzymes:a meta-analysis. Agric., Ecosyst. Environ. 252, 126–131. https://doi.org/10.1016/j.agee.2017.09.032.

Chen, S., Lin, L., Deng, Y., Yuan, S., Zhang, N., 2024. Tree species richness and mycorrhizal types drive soil nitrogen cycling by regulating soil microbial community composition and diversity in tropical forests. For. Ecol. Manag. 569, 122187. https://doi.org/10.1016/j.foreco.2024.122187.

Chen, J., Wang, W.-H., Liu, T.-W., Wu, F.-H., Zheng, H.-L., 2013. Photosynthetic and antioxidant responses of *Liquidambar formosana* and *Schima superba* seedlings to sulfuric-rich and nitric-rich simulated acid rain. Plant Physiol. Biochem. 64, 41–51.

Chen, C., Xiao, W., Chen, H.Y., 2023. Mapping global soil acidification under N deposition. Glob. Change Biol. 29, 4652–4661.

Cheng, Y., Wang, J., Chang, S.X., Cai, Z., Müller, C., Zhang, J., 2019. Nitrogen deposition affects both net and gross soil nitrogen transformations in forest ecosystems: a review. Environ. Pollut. 244, 608–616. https://doi.org/10.1016/j.envpol.2018.10.054.

Choma, M., Tahovská, K., Kaštovská, E., Bárta, J., Růžek, M., Oulehle, F., 2020. Bacteria but not fungi respond to soil acidification rapidly and consistently in both a spruce and beech forest. FEMS Microbiol. Ecol. 96, fiaa174. https://doi.org/10.1093/femsec/fiaa174.

Clark, C.M., Richkus, J., Jones, P.W., Phelan, J., Burns, D.A., de Vries, W., Du, E., Fenn, M.E., Jones, L., Watmough, S.A., 2019. A synthesis of ecosystem management strategies for forests in the face of chronic nitrogen deposition. Environ. Pollut. 248, 1046–1058. https://doi.org/10.1016/j.envpol.2019.02.006.

Cools, N., Vesterdal, L., De Vos, B., Vanguelova, E., Hansen, K., 2014. Tree species is the major factor explaining C: N ratios in European forest soils. For. Ecol. Manag. 311, 3–16.

Court, M., van der Heijden, G., Didier, S., Nys, C., Richter, C., Pousse, N., Saint-André, L., Legout, A., 2018. Long-term effects of forest liming on mineral soil, organic layer and foliage chemistry: Insights from multiple beech experimental sites in Northern France. For. Ecol. Manag. 409, 872–889. https://doi.org/10.1016/j.foreco.2017.12.007.

Curtis, C.J., Evans, C.D., Goodale, C.L., Heaton, T.H.E., 2011. What have stable isotope studies revealed about the nature and mechanisms of N saturation and nitrate leaching from semi-natural catchments? Ecosystems 14, 1021–1037. https://doi.org/10.1007/s10021-011-9461-7.

Dannenmann, M., Gasche, R., Papen, H., 2007. Nitrogen turnover and N_2O production in the forest floor of beech stands as influenced by forest management. J. Plant Nutr. Soil Sci. 170, 134–144. https://doi.org/10.1002/jpln.200620644.

Dawud, S.M., Raulund-Rasmussen, K., Ratcliffe, S., Domisch, T., Finér, L., Joly, F.X., Hättenschwiler, S., Vesterdal, L., 2017. Tree species functional group is a more important driver of soil properties than tree species diversity across major European forest types. Funct. Ecol. 31, 1153–1162.

De Marco, A., Sicard, P., Feng, Z., Agathokleous, E., Alonso, R., Araminiene, V., Augustatis, A., Badea, O., Beasley, J.C., Branquinho, C., 2022. Strategic roadmap to assess forest vulnerability under air pollution and climate change. Glob. Change Biol. 28, 5062–5085.

de Vries, W., Du, E., Butterbach-Bahl, K., 2014. Short and long-term impacts of nitrogen deposition on carbon sequestration by forest ecosystems. Curr. Opin. Environ. Sustain. 9, 90–104.

de Vries, W., Reinds, G.J., Gundersen, P., Sterba, H., 2006. The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. Glob. Change Biol. 12, 1151–1173. https://doi.org/10.1111/j.1365-2486.2006.01151.x.

DeForest, J.L., Otuya, R.K., 2020. Soil nitrification increases with elevated phosphorus or soil pH in an acidic mixed mesophytic deciduous forest. Soil Biol. Biochem. 142, 107716. https://doi.org/10.1016/j.soilbio.2020.107716.

Deng, L., Huang, C., Kim, D.-G., Shangguan, Z., Wang, K., Song, X., Peng, C., 2020. Soil GHG fluxes are altered by N deposition: new data indicate lower N stimulation of the N_2O flux and greater stimulation of the calculated C pools. Glob. Change Biol. 26, 2613–2629. https://doi.org/10.1111/gcb.14970.

Derome, J., 1990. Effects of forest liming on the nutrient status of podzolic soils in Finland. Water Air Soil Pollut. 54, 337–350. https://doi.org/10.1007/BF00298677.

Diatta, J., Youssef, N., Tylman, O., Grzebisz, W., Markert, B., Drobek, L., Wünschmann, S., Bebek, M., Mitko, K., Lejwoda, P., 2021. Acid rain induced leakage of Ca, Mg, Zn, Fe from plant photosynthetic organs – testing for deciduous and dicotyledons. Ecol. Indic. 121, 107210. https://doi.org/10.1016/j.ecolind.2020.107210.

Dirnböck, T., Brielmann, H., Djukic, I., Geiger, S., Hartmann, A., Humer, F., Kobler, J., Kralik, M., Liu, Y., Mirtl, M., 2020. Long-and short-term inorganic nitrogen runoff from a karst catchment in Austria. Forests 11, 1112.

Dirnböck, T., Foldal, C., Djukic, I., Kobler, J., Haas, E., Kiese, R., Kitzler, B., 2017. Historic nitrogen deposition determines future climate change effects on nitrogen retention in temperate forests. Clim. Change 144, 221–235. https://doi.org/10.1007/s10584-017-2024-y.

Dirnböck, T., Haase, P., Mirtl, M., Pauw, J., Templer, P.H., 2019. Contemporary International Long-Term Ecological Research (ILTER)—from biogeosciences to socio-ecology and biodiversity research. Reg. Environ. Change 19, 309–311. https://doi.org/10.1007/s10113-018-1445-0.

Dirnböck, T., Kobler, J., Kraus, D., Grote, R., Kiese, R., 2016. Impacts of management and climate change on nitrate leaching in a forested karst area. J. Environ. Manag. 165, 243–252. https://doi.org/10.1016/j.jenvman.2015.09.039.

Dirnböck, T., Pröll, G., Austnes, K., Beloica, J., Beudert, B., Canullo, R., De Marco, A., Fornasier, M.F., Futter, M., Goergen, K., 2018. Currently legislated decreases in nitrogen deposition will yield only limited plant species recovery in European forests. Environ. Res. Lett. 13, 125010.

Dise, N.B., Rothwell, J.J., Gauci, V., van der Salm, C., de Vries, W., 2009a. Predicting dissolved inorganic nitrogen leaching in European forests using two independent databases. Sci. Total Environ. 407, 1798–1808. https://doi.org/10.1016/j.scitotenv.2008.11.003.

Dise, N.B., Rothwell, J.J., Gauci, V., Van der Salm, C., De Vries, W., 2009b. Predicting dissolved inorganic nitrogen leaching in European forests using two independent databases. Sci. Total Environ. 407, 1798–1808.

Dise, N.B., Wright, R.F., 1995. Nitrogen leaching from European forests in relation to nitrogen deposition. For. Ecol. Manag., Nitrex 71, 153–161. https://doi.org/10.1016/0378-1127(94)06092-W.

Dong, D., Du, E., Sun, Z., Zeng, X., de Vries, W., 2017. Non-linear direct effects of acid rain on leaf photosynthetic rate of terrestrial plants. Environ. Pollut. 231, 1442–1445.

Draaijers, G.P.J., Erisman, J.W., Van Leeuwen, N.F.M., Römer, F.G., Te Winkel, B.H., Veltkamp, A.C., Vermeulen, A.T., Wyers, G.P., 1997. The impact of canopy exchange on differences observed between atmospheric deposition and throughfall fluxes. Atmos. Environ. 31, 387–397.

Du, E., Clark, C.M., De Vries, W., 2024a. Forest remediation options in the face of excess nitrogen deposition. In: Du, E., De Vries, W. (Eds.), Atmospheric Nitrogen Deposition to Global Forests. Cambridge, MA: Academic Press, pp. 263–271. https://doi.org/10.1016/B978-0-323-91140-5.00004-X.

Du, E., de Vries, W., 2018. Nitrogen-induced new net primary production and carbon sequestration in global forests. Environ. Pollut. 242, 1476–1487. https://doi.org/10.1016/j.envpol.2018.08.041.

Du, E., de Vries, W. (Eds.), 2023. Atmospheric Nitrogen Deposition to Global Forests: Spatial Variation, Impacts and Management Implications. Elsevier Academic Press.

Du, B., Pang, J., Hu, B., Allen, D.E., Bell, T.L., Pfautsch, S., Netzer, F., Dannenmann, M., Zhang, S., Rennenberg, H., 2019. N$_2$-fixing black locust intercropping improves ecosystem nutrition at the vulnerable semi-arid Loess Plateau region, China. Sci. Total Environ. 688, 333–345.

Du, E., Xia, N., Cai, R., Bai, W., de Vries, W., 2024b. Impacts of nitrogen deposition on soil nitrous oxide emissions in global forests. In: Du, E., De Vries, W. (Eds.), Atmospheric Nitrogen Deposition to Global Forests. Cambridge, MA: Academic Press, pp. 169–179. https://doi.org/10.1016/B978-0-323-91140-5.00014-2.

Du, E., Xia, N., Guo, Y., Tian, Y., Li, B., Liu, X., De Vries, W., 2022. Ecological effects of nitrogen deposition on urban forests: an overview. Front. Agric. Sci. Eng. 9, 445–456.

Duquesnay, A., Dupouey, J.-L., Clement, A., Ulrich, E., Le Tacon, F., 2000. Spatial and temporal variability of foliar mineral concentration in beech (*Fagus sylvatica*) stands in northeastern France. Tree Physiol. 20, 13–22.

(EFI) European Forest Institute, 2021. EFI Network Fund, Towards A Harmonised European Forest Monitoring System [WWW Document]. URL ⟨https://efi.int/grants-training/grants/G-01-2021⟩ (accessed 9.9.24).

Eklund, L., Eliasson, L., 1990. Effects of calcium ion concentration on cel wall synthesis. J. Exp. Bot. 41, 863–867. https://doi.org/10.1093/jxb/41.7.863.

Elvir, J.A., Wiersma, G.B., Day, M.E., Greenwood, M.S., Fernandez, I.J., 2006. Effects of enhanced nitrogen deposition on foliar chemistry and physiological processes of forest trees at the Bear Brook Watershed in Maine. For. Ecol. Manag. 221, 207–214.

EMEP, 2023. Transboundary particulate matter, photo-oxidants, acidifying and eutrophying components (No. EMEP Status Report 1/2023). West Norwegian Meteorological Institute, Blindern, Norway.

Emmett, B.A., 2007. Nitrogen saturation of terrestrial ecosystems: some recent findings and their implications for our conceptual framework. Water Air Soil Pollut.: Focus 7, 99–109. https://doi.org/10.1007/s11267-006-9103-9.

Etzold, S., Ferretti, M., Reinds, G.J., Solberg, S., Gessler, A., Waldner, P., Schaub, M., Simpson, D., Benham, S., Hansen, K., Ingerslev, M., Jonard, M., Karlsson, P.E., Lindroos, A.-J., Marchetto, A., Manninger, M., Meesenburg, H., Merilä, P., Nöjd, P., Rautio, P., Sanders, T.G.M., Seidling, W., Skudnik, M., Thimonier, A., Verstraeten, A., Vesterdal, L., Vejpustkova, M., de Vries, W., 2020. Nitrogen deposition is the most important environmental driver of growth of pure, even-aged and managed European forests. For. Ecol. Manag. 458, 117762. https://doi.org/10.1016/j.foreco.2019.117762.

Etzold, S., Waldner, P., Thimonier, A., Schmitt, M., Dobbertin, M., 2014. Tree growth in Swiss forests between 1995 and 2010 in relation to climate and stand conditions: Recent disturbances matter. For. Ecol. Manag. 311, 41–55.

Fan, J., Luo, R., McConkey, B.G., Ziadi, N., 2020. Effects of nitrogen deposition and litter layer management on soil CO$_2$, N$_2$O, and CH$_4$ emissions in a subtropical pine forestland. Sci. Rep. 10, 8959. https://doi.org/10.1038/s41598-020-65952-8.

Feller, U., Anders, I., Mae, T., 2008. Rubiscolytics: fate of Rubisco after its enzymatic function in a cell is terminated. J. Exp. Bot. 59, 1615–1624.

Felton, A., Lindbladh, M., Brunet, J., Fritz, Ö., 2010. Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe. For. Ecol. Manag. 260, 939–947. https://doi.org/10.1016/j.foreco.2010.06.011.

Ferm, M., Granat, L., Engardt, M., Pihl Karlsson, G., Danielsson, H., Karlsson, P.E., Hansen, K., 2019. Wet deposition of ammonium, nitrate and non-sea-salt sulphate in Sweden 1955 through 2017. Atmos. Environ.: X 2, 100015. https://doi.org/10.1016/j.aeaoa.2019.100015.

Ferraretto, D., Nair, R., Shah, N.W., Reay, D., Mencuccini, M., Spencer, M., Heal, K.V., 2022. Forest canopy nitrogen uptake can supply entire foliar demand. Funct. Ecol. 36, 933–949. https://doi.org/10.1111/1365-2435.14005.

Ferretti, M., Gessler, A., Cools, N., Fleck, S., Guerrieri, R., Jakovljević, T., Nicolas, M., Nieminen, T.M., Pitar, D., Potočić, N., Raspe, S., Schaub, M., Schwärzel, K., Timmermann, V., Vejpustková, M., Vesterdal, L., Vanninen, P., Waldner, P., Zimmermann, L., Sanders, T.G., 2024. Perspectives: resilient forests need joint forces for better inventorying and monitoring. For. Ecol. Manag. 561, 121875. https://doi.org/10.1016/j.foreco.2024.121875.

Fink, A.H., Brücher, T., Krüger, A., Leckebusch, G.C., Pinto, J.G., Ulbrich, U., 2004. The 2003 European summer heatwaves and drought-synoptic diagnosis and impacts. Weather 59, 209–216.

Flechard, C.R., Ibrom, A., Skiba, U.M., de Vries, W., van Oijen, M., Cameron, D.R., Dise, N.B., Korhonen, J.F.J., Buchmann, N., Legout, A., Simpson, D., Sanz, M.J., Aubinet, M., Loustau, D., Montagnani, L., Neirynck, J., Janssens, I.A., Pihlatie, M., Kiese, R., Siemens, J., Francez, A.-J., Augustin, J., Varlagin, A., Olejnik, J., Juszczak, R., Aurela, M., Berveiller, D., Chojnicki, B.H., Dämmgen, U., Delpierre, N., Djuricic, V., Drewer, J., Dufrêne, E., Eugster, W., Fauvel, Y., Fowler, D., Frumau, A., Granier, A., Gross, P., Hamon, Y., Helfter, C., Hensen, A., Horváth, L., Kitzler, B., Kruijt, B., Kutsch, W.L., Lobo-do-Vale, R., Lohila, A., Longdoz, B., Marek, M.V., Matteucci, G., Mitosinkova, M., Moreaux, V., Neftel, A., Ourcival, J.-M., Pilegaard, K., Pita, G., Sanz, F., Schjoerring, J.K., Sebastià, M.-T., Tang, Y.S., Uggerud, H., Urbaniak, M., van Dijk, N., Vesala, T., Vidic, S., Vincke, C., Weidinger, T., Zechmeister-Boltenstern, S., Butterbach-Bahl, K., Nemitz, E., Sutton, M.A., 2020. Carbon–nitrogen interactions in European forests and semi-natural vegetation–Part 1: Fluxes and budgets of carbon, nitrogen and greenhouse gases from ecosystem monitoring and modelling. Biogeosciences 17, 1583–1620.

Flechard, C.R., van Oijen, M., Cameron, D.R., de Vries, W., Ibrom, A., Buchmann, N., Dise, N.B., Janssens, I.A., Neirynck, J., Montagnani, L., Varlagin, A., Loustau, D., Legout, A., Ziemblińska, K., Aubinet, M., Aurela, M., Chojnicki, B.H., Drewer, J., Eugster, W., Francez, A.-J., Juszczak, R., Kitzler, B., Kutsch, W.L., Lohila, A., Longdoz, B., Matteucci, G., Moreaux, V., Neftel, A., Olejnik, J., Sanz, M.J., Siemens, J., Vesala, T., Vincke, C., Nemitz, E., Zechmeister-Boltenstern, S., Butterbach-Bahl, K., Skiba, U.M., Sutton, M.A., 2020. Carbon–nitrogen interactions in European forests and semi-natural vegetation – Part 2: Untangling climatic, edaphic, management and nitrogen deposition effects on carbon sequestration potentials. Biogeosciences 17, 1621–1654. https://doi.org/10.5194/bg-17-1621-2020.

Flückiger, W., Braun, S., 1999. Nitrogen and its effect on growth, nutrient status and parasite attacks in beech and Norway spruce. Water Air Soil Pollut. 116, 99–110.

Formánek, P., Vranova, V., 2003. A contribution to the effect of liming on forest soils: review of literature. J. For. Sci. 49, 182–190.

Forrester, D.I., Bauhus, J., Cowie, A.L., Vanclay, J.K., 2006. Mixed-species plantations of Eucalyptus with nitrogen-fixing trees: a review. For. Ecol. Manag., Improv. Product. Mixed-Species Plant. 233, 211–230. https://doi.org/10.1016/j.foreco.2006.05.012.

Forstner, S.J., Wechselberger, V., Müller, S., Keibinger, K.M., Díaz-Pinés, E., Wanek, W., Scheppi, P., Hagedorn, F., Gundersen, P., Tatzber, M., Gerzabek, M.H., Zechmeister-Boltenstern, S., 2019. Vertical Redistribution of Soil Organic Carbon Pools After Twenty Years of Nitrogen Addition in Two Temperate Coniferous Forests. Ecosystems 22, 379–400. https://doi.org/10.1007/s10021-018-0275-8.

Forzieri, G., Girardello, M., Ceccherini, G., Spinoni, J., Feyen, L., Hartmann, H., Beck, P.S.A., Camps-Valls, G., Chirici, G., Mauri, A., Cescatti, A., 2021. Emergent vulnerability to climate-driven disturbances in European forests. Nat. Commun. 12, 1081. https://doi.org/10.1038/s41467-021-21399-7.

Foyer, C.H., Rennenberg, H., 2000. Regulation of glutathione synthesis and its role in abiotic and biotic stress defence. In: Brunold, C., Rennenberg, H., De Kok, L.J., Stulen, I., Davidian, J.C. (Eds.), Sulfur Nutrition and Sulfur Assimilation in Higher Plants: Molecular, Biochemical and Physiological Aspects. Paul Haupt Verlag, Paul Haupt, Bern, pp. 127–153.

Futter, M.N., Dirnböck, T., Forsius, M., Bäck, J.K., Cools, N., Diaz-Pines, E., Dick, J., Gaube, V., Gillespie, L.M., Högbom, L., Laudon, H., Mirtl, M., Nikolaidis, N., Poppe Terán, C., Skiba, U., Vereecken, H., Villwock, H., Weldon, J., Wohner, C., Alam, S.A., 2023. Leveraging research infrastructure co-location to evaluate constraints on terrestrial carbon cycling in northern European forests. Ambio 52, 1819–1831. https://doi.org/10.1007/s13280-023-01930-4.

Ganatsios, H.P., Tsioras, P.A., Pavlidis, T., 2010. Water yield changes as a result of silvicultural treatments in an oak ecosystem. For. Ecol. Manag. 260, 1367–1374.

Gasche, R., Butterbach-Bahl, K., Papen, H., 2002. Development and application of a method for determination of net nitrification rates. Plant Soil 240, 57–65. https://doi.org/10.1023/A:1015855506539.

Gasche, R., Papen, H., 1999. A 3-year continuous record of nitrogen trace gas fluxes from untreated and limed soil of a N-saturated spruce and beech forest ecosystem in Germany: 2. NO and NO$_2$ fluxes. J. Geophys. Res. 104, 18505–18520. https://doi.org/10.1029/1999JD900294.

Gessler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H., 2006. Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. Trees 21, 1–11. https://doi.org/10.1007/s00468-006-0107-x.

Gessler, A., Kopriva, S., Rennenberg, H., 2004. Regulation of nitrate uptake at the whole-tree level: interaction between nitrogen compounds, cytokinins and carbon metabolism. Tree Physiol. 24, 1313–1321.

Gessler, A., Schneider, S., Von Sengbusch, D., Weber, P., Hanemann, U., Huber, C., Rothe, A., Kreutzer, K., Rennenberg, H., 1998a. Field and laboratory experiments on net uptake of nitrate and ammonium by the roots of spruce (*Picea abies*) and beech (*Fagus sylvatica*) trees. N. Phytol. 138, 275–285. https://doi.org/10.1046/j.1469-8137.1998.00107.x.

Gessler, A., Schneider, S., Weber, P., Hanemann, U., Rennenberg, H., 1998b. Soluble N compounds in trees exposed to high loads of N: a comparison between the roots of Norway spruce (*Picea abies*) and beech (*Fagus sylvatica*) trees grown under field conditions. N. Phytol. 138, 385–399. https://doi.org/10.1046/j.1469-8137.1998.00134.x.

Gillespie, L.M., Hättenschwiler, S., Milcu, A., Wambsganss, J., Shihan, A., Fromin, N., 2021. Tree species mixing affects soil microbial functioning indirectly via root and litter traits and soil parameters in European forests. Funct. Ecol. 35, 2190–2204.

Gilliam, F.S., 2006. Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. J. Ecol. 94, 1176–1191. https://doi.org/10.1111/j.1365-2745.2006.01155.x.

Gilliam, F.S., Burns, D.A., Driscoll, C.T., Frey, S.D., Lovett, G.M., Watmough, S.A., 2019. Decreased atmospheric nitrogen deposition in eastern North America: Predicted responses of forest ecosystems. Environ. Pollut. 244, 560–574.

Göttlein, A., Weis, W., Ettl, R., Raspe, S., Rothe, A., 2023. Long-term effects of clearcut and selective cut on seepage chemistry in a N-saturated spruce stand – Case study Höglwald. For. Ecol. Manag. 533, 120831. https://doi.org/10.1016/j.foreco.2023.120831.

Gundersen, P., Christiansen, J.R., Alberti, G., Brüggemann, N., Castaldi, S., Gasche, R., Kitzler, B., Klemedtsson, L., Lobo-do-Vale, R., Moldan, F., Rütting, T., Schleppi, P., Weslien, P., Zechmeister-Boltenstern, S., 2012. The response of methane and nitrous oxide fluxes to forest change in Europe. Biogeosciences 9, 3999–4012. https://doi.org/10.5194/bg-9-3999-2012.

Gundersen, P., Schmidt, I.K., Raulund-Rasmussen, K., 2006. Leaching of nitrate from temperate forests effects of air pollution and forest management. Environ. Rev. 14, 1–57. https://doi.org/10.1139/a05-015.

Gundersen, P., Sevel, L., Christiansen, J.R., Vesterdal, L., Hansen, K., Bastrup-Birk, A., 2009. Do indicators of nitrogen retention and leaching differ between coniferous and broadleaved forests in Denmark? For. Ecol. Manag. 258, 1137–1146. https://doi.org/10.1016/j.foreco.2009.06.007.

Hartmann, A., Kobler, J., Kralik, M., Dirnböck, T., Humer, F., Weiler, M., 2016. Model-aided quantification of dissolved carbon and nitrogen release after windthrow disturbance in an Austrian karst system. Biogeosciences 13, 159–174.

Hashimoto, S., Suzuki, M., 2004. The impact of forest clear-cutting on soil temperature: a comparison between before and after cutting, and between clear-cut and control sites. J. For. Res. 9, 125–132. https://doi.org/10.1007/s10310-003-0063-x.

He, N., Cen, X., Sundert, K.V., Terrer, C., Yu, K., Li, M., Xu, L., He, L., Butterbach-Bahl, K., 2024. Global patterns of nitrogen saturation in forests. One Earth, in press.

Hedĕnec, P., Zheng, H., Siqueira, D.P., Lin, Q., Peng, Y., Schmidt, I.K., Frøslev, T.G., Kjøller, R., Rousk, J., Vesterdal, L., 2023. Tree species traits and mycorrhizal association shape soil microbial communities via litter quality and species mediated soil properties. For. Ecol. Manag. 527, 120608.

Hell, R.ü, Rennenberg, H., 1998. The Plant Sulphur Cycle. In: Schnug, E. (Ed.), Sulphur in Agroecosystems. Springer Netherlands, Dordrecht, pp. 135–173. https://doi.org/10.1007/978-94-011-5100-9_5.

Herschbach, C., Gessler, A., Rennenberg, H., 2012. Long-distance transport and plant internal cycling of N-and S-compounds. In: Progress in Botany, 73. Springer, pp. 161–188.

Hirano, Y., Mizoguchi, T., Brunner, I., 2007. Root parameters of forest trees as sensitive indicators of acidifying pollutants: a review of research of Japanese forest trees. J. For. Res. 12, 134–142. https://doi.org/10.1007/s10310-006-0263-2.

Hlásny, T., König, L., Krokene, P., Lindner, M., Montagné-Huck, C., Müller, J., Qin, H., Raffa, K.F., Schelhaas, M.-J., Svoboda, M., Viiri, H., Seidl, R., 2021. Bark beetle outbreaks in europe: state of knowledge and ways forward for management. Curr. For. Rep. 7, 138–165. https://doi.org/10.1007/s40725-021-00142-x.

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. Glob. Change Biol. 12, 489–499. https://doi.org/10.1111/j.1365-2486.2006.01102.x.

Horn, K.J., Thomas, R.Q., Clark, C.M., Pardo, L.H., Fenn, M.E., Lawrence, G.B., Perakis, S.S., Smithwick, E.A., Baldwin, D., Braun, S., Nordin, A., 2018. Growth and survival relationships of 71 tree species with nitrogen and sulfur deposition across the conterminous US. PloS One 13, e0205296. https://doi.org/10.1371/journal.pone.0205296.

Huber, C., Aherne, J., Weis, W., Farrell, E.P., Göttlein, A., Cummins, T., 2010. Ion concentrations and fluxes of seepage water before and after clear cutting of Norway spruce stands at Ballyhooly, Ireland, and Höglwald, Germany. Biogeochemistry 101, 7–26. https://doi.org/10.1007/s10533-010-9459-9.

Huber, C., Baier, R., Göttlein, A., Weis, W., 2006. Changes in soil, seepage water and needle chemistry between 1984 and 2004 after liming an N-saturated Norway spruce stand at the Höglwald, Germany. For. Ecol. Manag. 233, 11–20. https://doi.org/10.1016/j.foreco.2006.05.058.

Huber, C., Weis, W., Baumgarten, M., Göttlein, A., 2004. Spatial and temporal variation of seepage water chemistry after femel and small scale clear-cutting in a N-saturated Norway spruce stand. Plant Soil 267, 23–40. https://doi.org/10.1007/s11104-005-2573-0.

Huettl, R.F., Zoettl, H.W., 1993. Liming as a mitigation tool in Germany's declining forests—reviewing results from former and recent trials. For. Ecol. Manag. 61, 325–338. https://doi.org/10.1016/0378-1127(93)90209-6.

James, J., Page-Dumroese, D., Busse, M., Palik, B., Zhang, J., Eaton, B., Slesak, R., Tirocke, J., Kwon, H., 2021. Effects of forest harvesting and biomass removal on soil carbon and nitrogen: Two complementary meta-analyses. For. Ecol. Manag. 485, 118935. https://doi.org/10.1016/j.foreco.2021.118935.

Jansone, L., von Wilpert, K., Hartmann, P., 2020. Natural recovery and liming effects in acidified forest soils in SW-Germany. Soil Syst. 4, 38. https://doi.org/10.3390/soilsystems4030038.

Janssens, I.A., Dieleman, W., Luyssaert, S., Subke, J.-A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A.J., Grace, J., Matteucci, G., Papale, D., Piao, S.L., Schulze, E.-D., Tang, J., Law, B.E., 2010. Reduction of forest soil respiration in response to nitrogen deposition. Nat. Geosci. 3, 315–322. https://doi.org/10.1038/ngeo844.

Jerabkova, L., Prescott, C.E., Titus, B.D., Hope, G.D., Walters, M.B., 2011. A meta-analysis of the effects of clearcut and variable-retention harvesting on soil nitrogen fluxes in boreal and temperate forests. Can. J. For. Res. 41, 1852–1870. https://doi.org/10.1139/x11-087.

Ji, X., Wang, S., Guo, S., Zhao, S., Dong, Q., Yun, C., Zhang, X., Yang, Y., Wang, W., Wang, H., 2023. Tree species richness and arbuscular mycorrhizal tree fraction of leaf litter increase carbon and nitrogen retention in soil with macroaggregate and glomalin accrual. Plant Soil 488, 377–392. https://doi.org/10.1007/s11104-023-05980-1.

Johnson, J., Graf Pannatier, E., Carnicelli, S., Cecchini, G., Clarke, N., Cools, N., Hansen, K., Meesenburg, H., Nieminen, T.M., Pihl-Karlsson, G., Titeux, H., Vanguelova, E., Verstraeten, A., Vesterdal, L., Waldner, P., Jonard, M., 2018. The response of soil solution chemistry in European forests to decreasing acid deposition. Glob. Change Biol. 24, 3603–3619. https://doi.org/10.1111/gcb.14156.

Jonard, M., Fürst, A., Verstraeten, A., Thimonier, A., Timmermann, V., Potočić, N., Waldner, P., Benham, S., Hansen, K., Merilä, P., Ponette, Q., de la Cruz, A.C., Roskams, P., Nicolas, M., Croisé, L., Ingerslev, M., Matteucci, G., Decinti, B., Bascietto, M., Rautio, P., 2015. Tree mineral nutrition is deteriorating in Europe. Glob. Change Biol. 21, 418–430. https://doi.org/10.1111/gcb.12657.

Jönsson, A.M., Rosengren, U., Nihlgård, B., 2004. Excess nitrogen affects the frost sensitivity of the inner bark of Norway spruce. Ann. For. Sci. 61, 293–298.

Jung, H., Senf, C., Beudert, B., Krueger, T., 2021. Bayesian Hierarchical Modeling of Nitrate Concentration in a Forest Stream Affected by Large-Scale Forest Dieback. Water Resour. Res. 57, e2020WR027264. https://doi.org/10.1029/2020WR027264.

Kauppi, P., Hanewinkel, M., Lundmark, T., Nabuurs, G.J., Peltola, H., Trasobares, A., Hetemäki, L., 2018. Climate Smart Forestry in Europe | European Forest Institute. European Forest Institute.

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A., Lindquist, E., 2015. Dynamics of global forest area: results from the FAO Global Forest Resources Assessment 2015. For. Ecol. Manag. 352, 9–20.

Kellaway, E.J., Eimers, M.C., Watmough, S.A., 2022. Liming legacy effects associated with the world's largest soil liming and regreening program in Sudbury, Ontario, Canada. Sci. Total Environ. 805, 150321. https://doi.org/10.1016/j.scitotenv.2021.150321.

Kelly, C.N., Schwaner, G.W., Cumming, J.R., Driscoll, T.P., 2021. Metagenomic reconstruction of nitrogen and carbon cycling pathways in forest soil: influence of different hardwood tree species. Soil Biol. Biochem. 156, 108226.

Keskitalo, E.C.H., Legay, M., Marchetti, M., Nocentini, S., Spathelf, P., 2015. The role of forestry in national climate change adaptation policy: cases from Sweden, Germany, France and Italy. Int. For. Rev. 17, 30–42.

Kjønaas, O.J., Bárcena, T.G., Hylen, G., Nordbakken, J.-F., Økland, T., 2021. Boreal tree species change as a climate mitigation strategy: impact on ecosystem C and N stocks and soil nutrient levels. Ecosphere 12, e03826. https://doi.org/10.1002/ecs2.3826.

Kolström, M., Lindner, M., Vilén, T., Maroschek, M., Seidl, R., Lexer, M.J., Netherer, S., Kremer, A., Delzon, S., Barbati, A., 2011. Reviewing the science and implementation of climate change adaptation measures in European forestry. Forests 2, 961–982.

Korkiakoski, M., Tuovinen, J.-P., Penttilä, T., Sarkkola, S., Ojanen, P., Minkkinen, K., Rainne, J., Laurila, T., Lohila, A., 2019. Greenhouse gas and energy fluxes in a boreal peatland forest after clear-cutting. Biogeosciences 16, 3703–3723.

Kovács, B., Tinya, F., Németh, C., Ódor, P., 2020. Unfolding the effects of different forestry treatments on microclimate in oak forests: results of a 4-yr experiment. Ecol. Appl. 30, e02043. https://doi.org/10.1002/eap.2043.

Krejza, J., Cienciala, E., Světlík, J., Bellan, M., Noyer, E., Horáček, P., Štěpánek, P., Marek, M.V., 2021. Evidence of climate-induced stress of Norway spruce along elevation gradient preceding the current dieback in Central Europe. Trees 35, 103–119. https://doi.org/10.1007/s00468-020-02022-6.

Kreutzer, K., 1995. Effects of forest liming on soil processes. Plant Soil 168 447–470. https://doi.org/10.1007/BF00029358.

Kreutzer, K., Butterbach-Bahl, K., Rennenberg, H., Papen, H., 2009. The complete nitrogen cycle of an N-saturated spruce forest ecosystem. Plant Biol. 11, 643–649. https://doi.org/10.1111/j.1438-8677.2009.00236.x.

Kreutzweiser, D.P., Hazlett, P.W., Gunn, J.M., 2008. Logging impacts on the biogeochemistry of boreal forest soils and nutrient export to aquatic systems: a review. Environ. Rev. 16, 157–179. https://doi.org/10.1139/A08-006.

Lafuente, A., Recio, J., Ochoa-Hueso, R., Gallardo, A., Pérez-Corona, M.E., Manrique, E., Durán, J., 2020. Simulated nitrogen deposition influences soil greenhouse gas fluxes in a Mediterranean dryland. Sci. Total Environ. 737, 139610. https://doi.org/10.1016/j.scitotenv.2020.139610.

Lang, C., Polle, A., 2011. Ectomycorrhizal fungal diversity, tree diversity and root nutrient relations in a mixed Central European forest. Tree Physiol. 31, 531–538. https://doi.org/10.1093/treephys/tpr042.

Li, Z., Wang, Y., Liu, Y., Guo, H., Li, T., Li, Z.-H., Shi, G., 2014. Long-term effects of liming on health and growth of a Masson pine stand damaged by soil acidification in Chongqing, China. PLoS One 9, e94230.

Lin, N., Bartsch, N., Heinrichs, S., Vor, T., 2015. Long-term effects of canopy opening and liming on leaf litter production, and on leaf litter and fine-root decomposition in a European beech (*Fagus sylvatica* L.) forest. For. Ecol. Manag. 338, 183–190. https://doi.org/10.1016/j.foreco.2014.11.029.

Liu, C.L.C., Kuchma, O., Krutovsky, K.V., 2018. Mixed-species versus monocultures in plantation forestry: Development, benefits, ecosystem services and perspectives for the future. Glob. Ecol. Conserv. 15, e00419.

Long, R.P., Bailey, S.W., Horsley, S.B., Hall, T.J., 2022. Thirty-year effects of liming on soil and foliage chemistry and growth of northern hardwoods in Pennsylvania, USA. Can. J. For. Res. 52, 539–552. https://doi.org/10.1139/cjfr-2021-0246.

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. https://doi.org/10.1007/s10021-011-9432-z.

Lu, X., Mao, Q., Gilliam, F.S., Luo, Y., Mo, J., 2014. Nitrogen deposition contributes to soil acidification in tropical ecosystems. Glob. Change Biol. 20, 3790–3801. https://doi.org/10.1111/gcb.12665.

Lundmark, H., Josefsson, T., Östlund, L., 2013. The history of clear-cutting in northern Sweden – driving forces and myths in boreal silviculture. For. Ecol. Manag. 307, 112–122. https://doi.org/10.1016/j.foreco.2013.07.003.

Luo, G.J., Brüggemann, N., Wolf, B., Gasche, R., Grote, R., Butterbach-Bahl, K., 2012. Decadal variability of soil CO_2, NO, N_2O, and CH_4 fluxes at the Höglwald Forest, Germany. Biogeosciences 9, 1741–1763. https://doi.org/10.5194/bg-9-1741-2012.

Luo, Y., El-Madany, T., Ma, X., Nair, R., Jung, M., Weber, U., Filippa, G., Bucher, S.F., Moreno, G., Cremonese, E., Carrara, A., Gonzalez-Cascon, R., Cáceres Escudero, Y., Galvagno, M., Pacheco-Labrador, J., Martín, M.P., Perez-Priego, O., Reichstein, M., Richardson, A.D., Menzel, A., Römermann, C., Migliavacca, M., 2020. Nutrients and water availability constrain the seasonality of vegetation activity in a Mediterranean ecosystem. Glob. Change Biol. 26, 4379–4400. https://doi.org/10.1111/gcb.15138.

Ma, Y., Geng, Y., Huang, Y., Shi, Y., Niklaus, P.A., Schmid, B., He, J.-S., 2013. Effect of clear-cutting silviculture on soil respiration in a subtropical forest of China. J. Plant Ecol. 6, 335–348.

MacDonald, J.A., Dise, N.B., Matzner, E., Armbruster, M., Gundersen, P., Forsius, M., 2002. Nitrogen input together with ecosystem nitrogen enrichment predict nitrate leaching from European forests. Glob. Change Biol. 8, 1028–1033. https://doi.org/10.1046/j.1365-2486.2002.00532.x.

Maehara, N., Kikuchi, J., Futai, K., 1993. Mycorrhizae of Japanese black pine (*Pinus thunbergii*): protection of seedlings from acid mist and effect of acid mist on mycorrhiza formation. Can. J. Bot. 71, 1562–1567. https://doi.org/10.1139/b93-190.

Magill, A.H., Aber, J.D., Currie, W.S., Nadelhoffer, K.J., Martin, M.E., McDowell, W.H., Melillo, J.M., Steudler, P., 2004. Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. For. Ecol. Manag., Harv. For. (USA) Nitrogen Satur. Exp.: Results First 15 Years 196, 7–28. https://doi.org/10.1016/j.foreco.2004.03.033.

Marschner, B., Waldemar Wilczynski, A., 1991. The effect of liming on quantity and chemical composition of soil organic matter in a pine forest in Berlin, Germany. Plant Soil 137, 229–236. https://doi.org/10.1007/BF00011201.

Mason, R.E., Craine, J.M., Lany, N.K., Jonard, M., Ollinger, S.V., Groffman, P.M., Fulweiler, R.W., Angerer, J., Read, Q.D., Reich, P.B., Templer, P.H., Elmore, A.J., 2022. Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems. Science 376, eabh3767. https://doi.org/10.1126/science.abh3767.

Mason, W.L., Diaci, J., Carvalho, J., Valkonen, S., 2022. Continuous cover forestry in Europe: usage and the knowledge gaps and challenges to wider adoption. For.: Int. J. For. Res. 95, 1–12.

Matejek, B., Huber, C., Dannenmann, M., Kohlpaintner, M., Gasche, R., Papen, H., 2010. Microbial N turnover processes in three forest soil layers following clear cutting of an N saturated mature spruce stand. Plant Soil 337, 93–110. https://doi.org/10.1007/s11104-010-0503-2.

Mayer, M., Prescott, C.E., Abaker, W.E.A., Augusto, L., Cécillon, L., Ferreira, G.W.D., James, J., Jandl, R., Katzensteiner, K., Laclau, J.P., 2020. Influence of forest management activities on soil organic carbon stocks: a knowledge synthesis. Ecol. Manag. 466: 118127. For. Ecol. Manag. 466. https://doi.org/10.1016/j.foreco.2020.118127.

Mazza, G., Agnelli, A.E., Cantiani, P., Chiavetta, U., Doukalianou, F., Kitikidou, K., Milios, E., Orfanoudakis, M., Radoglou, K., Lagomarsino, A., 2019. Short-term effects of thinning on soil CO_2, N_2O and CH_4 fluxes in Mediterranean forest ecosystems. Sci. Total Environ. 651, 713–724.

McLaughlin, S.B., Tjoelker, M.G., Roy, W.K., 1993. Acid deposition alters red spruce physiology: laboratory studies support field observations. Can. J. For. Res. 23, 380–386. https://doi.org/10.1139/x93-055.

Medinets, S., Gasche, R., Kiese, R., Rennenberg, H., Butterbach-Bahl, K., 2019. Seasonal dynamics and profiles of soil NO concentrations in a temperate forest. Plant Soil 445, 335–348. https://doi.org/10.1007/s11104-019-04305-5.

Meiwes, K.J., Mindrup, M., Khanna, P.K., 2002. Retention of Ca and Mg in the forest floor of a spruce stand after application of various liming materials. For. Ecol. Manag. 159, 27–36.

Melvin, A.M., Lichstein, J.W., Goodale, C.L., 2013. Forest liming increases forest floor carbon and nitrogen stocks in a mixed hardwood forest. Ecol. Appl. 23, 1962–1975. https://doi.org/10.1890/13-0274.1.

Millard, P., Grelet, G., 2010. Nitrogen storage and remobilization by trees: ecophysiological relevance in a changing world. Tree Physiol. 30, 1083–1095.

Miller, J.D., Anderson, H.A., Cooper, J.M., Ferrier, R.C., Stewart, M., 1991. Evidence for enhanced atmospheric sulphate interception by Sitka spruce from evaluation of some Scottish catchment study data. Sci. Total Environ. 103, 37–46.

Mu, X., Chen, Q., Chen, F., Yuan, L., Mi, G., 2018. Dynamic remobilization of leaf nitrogen components in relation to photosynthetic rate during grain filling in maize. Plant Physiol. Biochem. 129, 27–34.

Muller, B., Touraine, B., Rennenberg, H., 1996. Interaction between atmospheric and pedospheric nitrogen nutrition in spruce (*Picea abies* L. Karst) seedlings. Plant Cell Environ. 19, 345–355. https://doi.org/10.1111/j.1365-3040.1996.tb00257.x.

Naudts, K., Chen, Y., McGrath, M.J., Ryder, J., Valade, A., Otto, J., Luyssaert, S., 2016. Europe's forest management did not mitigate climate warming. Science 351, 597–600. https://doi.org/10.1126/science.aad7270.

Netzer, F., Pozzi, L., Dubbert, D., Herschbach, C., 2019. Improved photosynthesis and growth of poplar during nitrogen fertilization is accompanied by phosphorus depletion that indicates phosphorus remobilization from older stem tissues. Environ. Exp. Bot. 162, 421–432.

Neumann, M., Ukonmaanaho, L., Johnson, J., Benham, S., Vesterdal, L., Novotný, R., Verstraeten, A., Lundin, L., Thimonier, A., Michopoulos, P., Hasenauer, H., 2018. Quantifying Carbon and Nutrient Input From Litterfall in European Forests Using Field Observations and Modeling. Glob. Biogeochem. Cycles 32, 784–798. https://doi.org/10.1029/2017GB005825.

Nordén, B., Rørstad, P.K., Magnér, J., Götmark, F., Löf, M., 2019. The economy of selective cutting in recent mixed stands during restoration of temperate deciduous forest. Scand. J. For. Res. 34, 709–717. https://doi.org/10.1080/02827581.2019.1679876.

Olsson, B.A., Kellner, O., 2002. Effects of soil acidification and liming on ground flora establishment after clear-felling of Norway spruce in Sweden. For. Ecol. Manag. 158, 127–139. https://doi.org/10.1016/S0378-1127(00)00713-1.

Oulehle, F., Goodale, C.L., Evans, C.D., Chuman, T., Hruška, J., Krám, P., Navrátil, T., Tesař, M., Ač, A., Urban, O., Tahovská, K., 2021. Dissolved and gaseous nitrogen losses in forests controlled by soil nutrient stoichiometry. Environ. Res. Lett. 16, 064025. https://doi.org/10.1088/1748-9326/ac007b.

Palokangas, P., Neuvonen, S., Haapala, S., 1995. The effects of simulated acid rain on growth and susceptibility to predation of *Phratora polaris* (Col., Chrysomelidae). Environ. Pollut. 89, 67–71.

Papen, H., Butterbach-Bahl, K., 1999. A 3-year continuous record of nitrogen trace gas fluxes from untreated and limed soil of a N-saturated spruce and beech forest ecosystem in Germany: 1. N_2O emissions. J. Geophys. Res. 104, 18487–18503. https://doi.org/10.1029/1999JD900293.

Papen, H., Geβler, A., Zumbusch, E., Rennenberg, H., 2002. Chemolithoautotrophic nitrifiers in the phyllosphere of a spruce ecosystem receiving high atmospheric nitrogen input. Curr. Microbiol. 44, 56–60. https://doi.org/10.1007/s00284-001-0074-9.

Papen, H., Von Berg, R., Hellmann, B., Rennenberg, H., 1991. Einfluß von saurer Beregnung und Kalkung auf chemolithotrophe und heterotrophe Nitrifikation in Böden des Höglwaldes. Forst Forsch. 39, 111–116.

Pardos, M., del Río, M., Pretzsch, H., Jactel, H., Bielak, K., Bravo, F., Brazaitis, G., Defossez, E., Engel, M., Godvod, K., Jacobs, K., Jansone, L., Jansons, A., Morin, X., Nothdurft, A., Oreti, L., Ponette, Q., Pach, M., Riofrío, J., Ruíz-Peinado, R., Tomao, A., Uhl, E., Calama, R., 2021. The greater resilience of mixed forests to drought mainly depends on their composition: Analysis along a climate gradient across Europe. For. Ecol. Manag. 481, 118687. https://doi.org/10.1016/j.foreco.2020.118687.

Patacca, M., Lindner, M., Lucas-Borja, M.E., Cordonnier, T., Fidej, G., Gardiner, B., Hauf, Y., Jasinevičius, G., Labonne, S., Linkevičius, E., Mahnken, M., Milanovic, S., Nabuurs, G.-J., Nagel, T.A., Nikinmaa, L., Panyatov, M., Bercak, R., Seidl, R., Ostrogović Sever, M.Z., Socha, J., Thom, D., Vuletic, D., Zudin, S., Schelhaas, M.-J., 2023. Significant increase in natural disturbance impacts on European forests since 1950. Glob. Change Biol. 29, 1359–1376. https://doi.org/10.1111/gcb.16531.

Peguero, G., Folch, E., Liu, L., Ogaya, R., Peñuelas, J., 2021. Divergent effects of drought and nitrogen deposition on microbial and arthropod soil communities in a Mediterranean forest. Eur. J. Soil Biol. 103, 103275. https://doi.org/10.1016/j.ejsobi.2020.103275.

Peichl, M., Arain, M.A., Ullah, S., Moore, T.R., 2010. Carbon dioxide, methane, and nitrous oxide exchanges in an age-sequence of temperate pine forests. Glob. Change Biol. 16, 2198–2212. https://doi.org/10.1111/j.1365-2486.2009.02066.x.

Persson, T., Andersson, S., Bergholm, J., Grönqvist, T., Högbom, L., Vegerfors, B., Wirén, A., 2021. Long-term impact of liming on soil C and N in a fertile spruce forest ecosystem. Ecosystems 24, 968–987. https://doi.org/10.1007/s10021-020-00563-y.

Persson, T., Rudebeck, A., Wirén, A., 1995. Pools and fluxes of carbon and nitrogen in 40-year-old forest liming experiments in Southern Sweden. Water Air Soil Pollut. 85, 901–906. https://doi.org/10.1007/BF00476944.

Piirainen, S., Finér, L., Mannerkoski, H., Starr, M., 2002. Effects of forest clear-cutting on the carbon and nitrogen fluxes through podzolic soil horizons. Plant Soil 239, 301–311. https://doi.org/10.1023/A:1015031718162.

Piirainen, S., Finér, L., Mannerkoski, H., Starr, M., 2007. Carbon, nitrogen and phosphorus leaching after site preparation at a boreal forest clear-cut area. For. Ecol. Manag. 243, 10–18.

Pilegaard, K., Skiba, U., Ambus, P., Beier, C., Brüggemann, N., Butterbach-Bahl, K., Dick, J., Dorsey, J., Duyzer, J., Gallagher, M., Gasche, R., Horvath, L., Kitzler, B., Leip, A., Pihlatie, M.K., Rosenkranz, P., Seufert, G., Vesala, T., Westrate, H., Zechmeister-Boltenstern, S., 2006. Factors controlling regional differences in forest soil emission of nitrogen oxides (NO and N_2O). Biogeosciences 3, 651–661. https://doi.org/10.5194/bg-3-651-2006.

Piotto, D., 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. For. Ecol. Manag. 255, 781–786. https://doi.org/10.1016/j.foreco.2007.09.065.

Porter, E.M., Bowman, W.D., Clark, C.M., Compton, J.E., Pardo, L.H., Soong, J.L., 2013. Interactive effects of anthropogenic nitrogen enrichment and climate change on terrestrial and aquatic biodiversity. Biogeochemistry 114, 93–120. https://doi.org/10.1007/s10533-012-9803-3.

Prescott, C.E., 1997. Effects of clearcutting and alternative silvicultural systems on rates of decomposition and nitrogen mineralization in a coastal montane coniferous forest. For. Ecol. Manag. 95, 253–260. https://doi.org/10.1016/S0378-1127(97)00027-3.

Pretzsch, H., del Río, M., Arcangeli, C., Bielak, K., Dudzinska, M., Forrester, D.I., Klädtke, J., Kohnle, U., Ledermann, T., Matthews, R., Nagel, J., Nagel, R., Ningre, F., Nord-Larsen, T., Biber, P., 2023. Forest growth in Europe shows diverging large regional trends. Sci. Rep. 13, 15373. https://doi.org/10.1038/s41598-023-41077-6.

Pretzsch, H., Poschenrieder, W., Uhl, E., Brazaitis, G., Makrickiene, E., Calama, R., 2021. Silvicultural prescriptions for mixed-species forest stands. A European review and perspective. Eur. J. For. Res 140, 1267–1294. https://doi.org/10.1007/s10342-021-01388-7.

Pretzsch, H., Schütze, G., 2016. Effect of tree species mixing on the size structure, density, and yield of forest stands. Eur. J. For. Res 135, 1–22. https://doi.org/10.1007/s10342-015-0913-z.

Pukkala, T., Lähde, E., Laiho, O., 2009. Growth and yield models for uneven-sized forest stands in Finland. For. Ecol. Manag. 258, 207–216.

Quinn Thomas, R., Canham, C.D., Weathers, K.C., Goodale, C.L., 2010. Increased tree carbon storage in response to nitrogen deposition in the US. Nat. Geosci. 3, 13–17. https://doi.org/10.1038/ngeo721.

Ranger, J., Loyer, S., Gelhaye, D., Pollier, B., Bonnaud, P., 2007. Effects of the clear-cutting of a Douglas-fir plantation (*Pseudotsuga menziesii* F.) on the chemical composition of soil solutions and on the leaching of DOC and ions in drainage waters. Ann. For. Sci. 64, 183–200.

Ranta, H., Neuvonen, S., Ylimartimo, A., 1995. Interactions of Gremmeniella abietina and endophytic fungi in shoots of Scots pine trees treated with simulated acid rain. J. Appl. Ecol. 67–75.

Raven, J.A., Andrews, M., 2010. Evolution of tree nutrition. Tree Physiol. 30, 1050–1071. https://doi.org/10.1093/treephys/tpq056.

Rennenberg, H., Dannenmann, M., 2015. Nitrogen nutrition of trees in temperate forests—the significance of nitrogen availability in the pedosphere and atmosphere. Forests 6, 2820–2835.

Rennenberg, H., Gessler, A., 1999. Consequences of N deposition to forest ecosystems — recent results and future research needs. In: Sheppard, L.J., Cape, J.N. (Eds.), Forest Growth Responses to the Pollution Climate of the 21st Century. Springer Netherlands, Dordrecht, pp. 47–64. https://doi.org/10.1007/978-94-017-1578-2_3.

Rennenberg, H., Kreutzer, K., Papen, H., Weber, P., 1998. Consequences of high loads of nitrogen for spruce (*Picea abies*) and beech (*Fagus sylvatica*) forests. N. Phytol. 139, 71–86.

Rennenberg, H., Wildhagen, H., Ehlting, B., 2010. Nitrogen nutrition of poplar trees. Plant Biol. 12, 275–291.

Reverchon, F., Bai, S.H., Liu, X., Blumfield, T.J., 2015. Tree plantation systems influence nitrogen retention and the abundance of nitrogen functional genes in the Solomon Islands. Front. Microbiol. 6. https://doi.org/10.3389/fmicb.2015.01439.

Richards, A.E., Forrester, D.I., Bauhus, J., Scherer-Lorenzen, M., 2010. The influence of mixed tree plantations on the nutrition of individual species: a review. Tree Physiol. 30, 1192–1208. https://doi.org/10.1093/treephys/tpq035.

Rosenvald, R., Lõhmus, A., 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. For. Ecol. Manag. 255, 1–15.

Roth, D.R., Fahey, T.J., 1998. The effects of acid precipitation and ozone on the ectomycorrhizae of red spruce saplings. Water, Air, Soil Pollut. 103, 263–276. https://doi.org/10.1023/A:1004929801839.

Rothe, A., Binkley, D., 2001. Nutritional interactions in mixed species forests: a synthesis. Can. J. For. Res. 31, 1855–1870. https://doi.org/10.1139/x01-120.

Rothstein, D., 2018. Effect of fertilization on growth and mortality of jack pine growing on poor, sandy soils in Michigan, USA: Implications for sustainable management. Forests 9, 549.

Ruuhola, T., Rantala, L.M., Neuvonen, S., Yang, S., Rantala, M.J., 2009. Effects of long-term simulated acid rain on a plant–herbivore interaction. Basic Appl. Ecol. 10, 589–596.

Saarsalmi, A., Tamminen, P., Kukkola, M., Levula, T., 2011. Effects of liming on chemical properties of soil, needle nutrients and growth of Scots pine transplants. For. Ecol. Manag., Environ. Stress For. Ecosyst.: Case Stud. Est. 262, 278–285. https://doi.org/10.1016/j.foreco.2011.03.033.

Sant'Anna-Santos, B.F., da Silva, L.C., Azevedo, A.A., de Araujo, J.M., Alves, E.F., da Silva, E.A.M., Aguiar, R., 2006. Effects of simulated acid rain on the foliar micromorphology and anatomy of tree tropical species. Environ. Exp. Bot. 58, 158–168.

Sardans, J., Alonso, R., Janssens, I.A., Carnicer, J., Vereseglou, S., Rillig, M.C., Fernández-Martínez, M., Sanders, T.G.M., Peñuelas, J., 2016. Foliar and soil concentrations and stoichiometry of nitrogen and phosphorous across E uropean *P inus sylvestris* forests: relationships with climate, N deposition and tree growth. Funct. Ecol. 30, 676–689. https://doi.org/10.1111/1365-2435.12541.

Schiermeier, Q., 2018. Climate as culprit. Nature 560, 20–22.

Schleppi, P., Curtaz, F., Krause, K., 2017. Nitrate leaching from a sub-alpine coniferous forest subjected to experimentally increased N deposition for 20 years, and effects of tree girdling and felling. Biogeochemistry 134, 319–335. https://doi.org/10.1007/s10533-017-0364-3.

Schmitz, A., Sanders, T.G.M., Bolte, A., Bussotti, F., Dirnböck, T., Johnson, J., Peñuelas, J., Pollastrini, M., Prescher, A.-K., Sardans, J., Verstraeten, A., de Vries, W., 2019. Responses of forest ecosystems in Europe to decreasing nitrogen deposition. Environ. Pollut. 244, 980–994. https://doi.org/10.1016/j.envpol.2018.09.101.

Schneider, S., GEßLER, A., Weber, P., Von Sengbusch, D., Hanemann, U., Rennenberg, H., 1996. Soluble N compounds in trees exposed to high loads of N: a comparison of spruce (*Picea abies*) and beech (*Fagus sylvatica*) grown under field conditions. N. Phytol. 134, 103–114. https://doi.org/10.1111/j.1469-8137.1996.tb01150.x.

Schuler, L.J., Bugmann, H., Snell, R.S., 2017. From monocultures to mixed-species forests: is tree diversity key for providing ecosystem services at the landscape scale? Landsc. Ecol. 32, 1499–1516. https://doi.org/10.1007/s10980-016-0422-6.

Schulte-Uebbing, L.F., Ros, G.H., de Vries, W., 2022. Experimental evidence shows minor contribution of nitrogen deposition to global forest carbon sequestration. Glob. Change Biol. 28, 899–917.

Schwede, D.B., Simpson, D., Tan, J., Fu, J.S., Dentener, F., Du, E., deVries, W., 2018. Spatial variation of modelled total, dry and wet nitrogen deposition to forests at global scale. Environ. Pollut. 243, 1287–1301.

Senf, C., Pflugmacher, D., Zhiqiang, Y., Sebald, J., Knorn, J., Neumann, M., Hostert, P., Seidl, R., 2018. Canopy mortality has doubled in Europe's temperate forests over the last three decades. Nat. Commun. 9, 4978.

Shan, Y., Feng, Z., Izuta, T., Aoki, M., Totsuka, T., 1996. The individual and combined effects of ozone and simulated acid rain on growth, gas exchange rate and water-use efficiency of *Pinus armandi* Franch. Environ. Pollut. 91, 355–361. https://doi.org/10.1016/0269-7491(95)00039-9.

Shigihara, A., Matsumoto, K., Sakurai, N., Igawa, M., 2008. Leaching of cell wall components caused by acid deposition on fir needles and trees. Sci. Total Environ. 398, 185–195.

Shumejko, P., Ossipov, V., Neuvonen, S., 1996. The effect of simulated acid rain on the biochemical composition of Scots pine (*Pinus sylvestris* L.) needles. Environ. Pollut. 92, 315–321.

Silveira, R., de Mello, T., de, R.B., Silva, M.R.S.S., Krüger, R.H., Bustamante, M.M., da, C., 2021. Long-term liming promotes drastic changes in the composition of the microbial community in a tropical savanna soil. Biol. Fertil. Soils 57, 31–46. https://doi.org/10.1007/s00374-020-01504-6.

Smolander, A., Törmänen, T., Kitunen, V., Lindroos, A.-J., 2019. Dynamics of soil nitrogen cycling and losses under Norway spruce logging residues on a clear-cut. For. Ecol. Manag. 449, 117444.

Soukupová, J., Albrechtová, J., Svobodová, H., Opatrná, J., 2002. Anatomical and Histochemical Changes of Norway Spruce Buds Induced by Simulated Acid Rain. Biol. Plant 45, 77–84. https://doi.org/10.1023/A:1015140222412.

Sousa-Silva, R., Verbist, B., Lomba, A., Valent, P., Suškevičs, M., Picard, O., Hoogstra-Klein, M.A., Cosofret, V.-C., Bouriaud, L., Ponette, Q., 2018. Adapting forest management to climate change in Europe: linking perceptions to adaptive responses. For. Policy Econ. 90, 22–30.

Sridhar, B., Wilhelm, R.C., Debenport, S.J., Fahey, T.J., Buckley, D.H., Goodale, C.L., 2022. Microbial community shifts correspond with suppression of decomposition 25 years after liming of acidic forest soils. Glob. Change Biol. 28, 5399–5415. https://doi.org/10.1111/gcb.16321.

Tanaka, K., Hashimoto, S., 2006. Plant canopy effects on soil thermal and hydrological properties and soil respiration. Ecol. Model. 196, 32–44.

Tate, K.R., Ross, D.J., Scott, N.A., Rodda, N.J., Townsend, J.A., Arnold, G.C., 2006. Post-harvest patterns of carbon dioxide production, methane uptake and nitrous oxide production in a Pinus radiata D. Don plantation. For. Ecol. Manag. 228, 40–50.

Templer, P.H., Harrison, J.L., Pilotto, F., Flores-Díaz, A., Haase, P., McDowell, W.H., Sharif, R., Shibata, H., Blankman, D., Avila, A., Baatar, U., Bogena, H.R., Bourgeois, I., Campbell, J., Dirnböck, T., Dodds, W.K., Hauken, M., Kokorite, I., Lajtha, K., Lai, I.-L., Laudon, H., Lin, T.C., Lins, S.R.M., Meesenburg, H., Pinho, P., Robison, A., Rogora, M., Scheler, B., Schleppi, P., Sommaruga, R., Staszewski, T., Taka, M., 2022. Atmospheric deposition and precipitation are important predictors of inorganic nitrogen export to streams from forest and grassland watersheds: a large-scale data synthesis. Biogeochemistry 160, 219–241. https://doi.org/10.1007/s10533-022-00951-7.

Templer, P.H., Lovett, G.M., Weathers, K.C., Findlay, S.E., Dawson, T.E., 2005. Influence of tree species on forest nitrogen retention in the catskill mountains, New York, USA. Ecosystems 8, 1–16. https://doi.org/10.1007/s10021-004-0230-8.

Templer, P.H., Mack, M.C., Chapin, F.S., Christenson, L.M., Compton, J.E., Crook, H.D., Currie, W.S., Curtis, C.J., Dail, D.B., D'Antonio, C.M., Emmett, B.A., Epstein, H.E., Goodale, C.L., Gundersen, P., Hobbie, S.E., Holland, K., Hooper, D.U., Hungate, B.A., Lamontagne, S., Nadelhoffer, K.J., Osenberg, C.W., Perakis, S.S., Schleppi, P., Schimel, J., Schmidt, I.K., Sommerkorn, M., Spoelstra, J., Tietema, A., Wessel, W.W., Zak, D.R., 2012. Sinks for nitrogen inputs in terrestrial ecosystems: a meta-analysis of ^{15}N tracer field studies. Ecology 93, 1816–1829. https://doi.org/10.1890/11-1146.1.

Thelin, G., Rosengren, U., Callesen, I., Ingerslev, M., 2002. The nutrient status of Norway spruce in pure and in mixed-species stands. For. Ecol. Manag. 160, 115–125. https://doi.org/10.1016/S0378-1127(01)00464-9.

Thom, D., Rammer, W., Garstenauer, R., Seidl, R., 2018. Legacies of past land use have a stronger effect on forest carbon exchange than future climate change in a temperate forest landscape. Biogeosciences 15, 5699–5713. https://doi.org/10.5194/bg-15-5699-2018.

Tian, D., Du, E., Jiang, L., Ma, S., Zeng, W., Zou, A., Feng, C., Xu, L., Xing, A., Wang, W., Zheng, C., Ji, C., Shen, H., Fang, J., 2018. Responses of forest ecosystems to increasing N deposition in China: a critical review. Environ. Pollut. 243, 75–86. https://doi.org/10.1016/j.envpol.2018.08.010.

Tian, Y., Haibara, K., Toda, H., Ding, F., Liu, Y., Choi, D., 2008. Microbial biomass and activity along a natural pH gradient in forest soils in a karst region of the upper Yangtze River, China. J. For. Res. 13, 205–214. https://doi.org/10.1007/s10310-008-0073-9.

Tian, Y., Shi, C., Malo, C.U., Kwatcho Kengdo, S., Heinzle, J., Inselsbacher, E., Ottner, F., Borken, W., Michel, K., Schindlbacher, A., Wanek, W., 2023. Long-term soil warming decreases microbial phosphorus utilization by increasing abiotic phosphorus sorption and phosphorus losses. Nat. Commun. 14, 864. https://doi.org/10.1038/s41467-023-36527-8.

Törmänen, T., Kitunen, V., Lindroos, A.-J., Heikkinen, J., Smolander, A., 2018. How do logging residues of different tree species affect soil N cycling after final felling? For. Ecol. Manag. 427, 182–189.

Türk, S., Gülpen, M., Fink, S., 1993. Aufnahme, transport und verbleib von calcium und magnesium in fichten (*Picea abies* [L.] Karst.) und Kiefern (*Pinus silvestris* L.) bei unterschiedlicher ernährung und schadstoffbelastung. Forst Cbl 112, 191–208. https://doi.org/10.1007/BF02742148.

Tveite, B., Abrahamsen, G., Stuanes, A.O., 1990. Liming and wet acid deposition effects on tree growth and nutrition: experimental results. Water Air Soil Pollut. 54, 409–422. https://doi.org/10.1007/BF02385234.

Valipour, M., Johnson, C.E., Battles, J.J., Campbell, J.L., Fahey, T.J., Fakhraei, H., Driscoll, C.T., 2021. Simulation of the effects of forest harvesting under changing climate to inform long-term sustainable forest management using a biogeochemical model. Sci. Total Environ. 767, 144881. https://doi.org/10.1016/j.scitotenv.2020.144881.

Valipour, M., Johnson, C.E., Battles, J.J., Campbell, J.L., Fahey, T.J., Fakhraei, H., Driscoll, C.T., 2022. Response of biomass, hydrology and biogeochemistry to alternative approaches of cutting a northern forest: model comparisons. Biogeochemistry 157, 131–148. https://doi.org/10.1007/s10533-021-00862-z.

van der Linde, S., Suz, L.M., Orme, C.D.L., Cox, F., Andreae, H., Asi, E., Atkinson, B., Benham, S., Carroll, C., Cools, N., 2018. Environment and host as large-scale controls of ectomycorrhizal fungi. Nature 558, 243–248.

van Straaten, O., Kulp, L., Martinson, G.O., Zederer, D.P., Talkner, U., 2023. Forest liming in the face of climate change: the implications of restorative liming for soil organic carbon in mature German forests. Soil 9, 39–54. https://doi.org/10.5194/soil-9-39-2023.

Venterea, R.T., Groffman, P.M., Verchot, L.V., Magill, A.H., Aber, J.D., Steudler, P.A., 2003. Nitrogen oxide gas emissions from temperate forest soils receiving long-term nitrogen inputs. Glob. Change Biol. 9, 346–357. https://doi.org/10.1046/j.1365-2486.2003.00591.x.

Verkerk, P.J., Costanza, R., Hetemäki, L., Kubiszewski, I., Leskinen, P., Nabuurs, G.J., Potočnik, J., Palahí, M., 2020. Climate-Smart Forestry: the missing link. For. Policy Econ. 115, 102164. https://doi.org/10.1016/j.forpol.2020.102164.

Verma, P., Sagar, R., 2020. Effect of nitrogen (N) deposition on soil-N processes: a holistic approach. Sci. Rep. 10, 10470. https://doi.org/10.1038/s41598-020-67368-w.

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. For. Ecol. Manag. 255, 35–48. https://doi.org/10.1016/j.foreco.2007.08.015.

Vet, R., Artz, R.S., Carou, S., Shaw, M., Ro, C.-U., Aas, W., Baker, A., Bowersox, V.C., Dentener, F., Galy-Lacaux, C., 2014. A global assessment of precipitation chemistry and deposition of sulfur, nitrogen, sea salt, base cations, organic acids, acidity and pH, and phosphorus. Atmos. Environ. 93, 3–100.

Vitousek, P.M., Howarth, R.W., 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13, 87–115. https://doi.org/10.1007/BF00002772.

Vuorenmaa, J., Augustaitis, A., Beudert, B., Bochenek, W., Clarke, N., de Wit, H.A., Dirnböck, T., Frey, J., Hakola, H., Kleemola, S., Kobler, J., Krám, P., Lindroos, A.-J., Lundin, L., Löfgren, S., Marchetto, A., Pecka, T., Schulte-Bisping, H., Skotak, K., Srybny, A., Szpikowski, J., Ukonmaanaho, L., Váňa, M., Åkerblom, S., Forsius, M., 2018. Long-term changes (1990–2015) in the atmospheric deposition and runoff water chemistry of sulphate, inorganic nitrogen and acidity for forested catchments in Europe in relation to changes in emissions and hydrometeorological conditions. Sci. Total Environ. 625, 1129–1145. https://doi.org/10.1016/j.scitotenv.2017.12.245.

Wambsganss, J., Beyer, F., Freschet, G.T., Scherer-Lorenzen, M., Bauhus, J., 2021. Tree species mixing reduces biomass but increases length of absorptive fine roots in European forests. J. Ecol. 109, 2678–2691. https://doi.org/10.1111/1365-2745.13675.

Wan, S., Liu, Z., Chen, Y., Zhao, J., Ying, Q., Liu, J., 2019. Effects of lime application and understory removal on soil microbial communities in subtropical eucalyptus L'Hér. plantations. Forests 10, 338. https://doi.org/10.3390/f10040338.

Wang, Y., Yao, Z., Zhan, Y., Zheng, X., Zhou, M., Yan, G., Wang, L., Werner, C., Butterbach-Bahl, K., 2021. Potential benefits of liming to acid soils on climate change mitigation and food security. Glob. Change Biol. 27, 2807–2821. https://doi.org/10.1111/gcb.15607.

Wang, P., Zhou, S., Zhang, M., 2020. Occurrence of endogenous hormones in the roots of Masson pine (*Pinus massoniana* Lamb.) seedlings subjected to aluminum stress under the influence of acid deposition. Plant Growth Regul. 92, 43–52. https://doi.org/10.1007/s10725-020-00618-z.

Warren, C.R., Dreyer, E., Adams, M.A., 2003. Photosynthesis-Rubisco relationships in foliage of Pinus sylvestris in response to nitrogen supply and the proposed role of Rubisco and amino acids as nitrogen stores. Trees 17, 359–366. https://doi.org/10.1007/s00468-003-0246-2.

Wellbrock, N., Bolte, A., Flessa, H., 2016. Dynamik und räumliche Muster forstlicher Standorte in Deutschland. Ergebnisse der Bodenzustandserhebung im Wald 2006 bis 2008, Thünen Report 43. Johann Heinrich von Thünen-Institut, Braunschweig, Deutschland, p. 550. https://doi.org/10.3220/REP1473930232000.

Wellbrock, N., Eickenscheidt, N., Grüneberg, E., Bögelein, R., 2019. Environmental settings and their changes in the last decades. Status Dyn. For. Ger.: Results Natl. For. Monit. 29–54.

Whitney, R.D., Ip, D.W., 1991. Necrotic spots induced by simulated acid rain on needles of *Abies balsamea* saplings. Eur. J. For. Pathol. 21, 36–48. https://doi.org/10.1111/j.1439-0329.1991.tb00300.x.

Wild, D., von Schulthess, R., Gujer, W., 1995. Structured modelling of denitrification intermediates. Water Sci. Technol., Model. Control Act. Sludge Process. 31, 45–54. https://doi.org/10.1016/0273-1223(95)00179-Q.

Wilpert, K. von, 2022. Forest soils—what's their peculiarity? Soil Syst. 6, 5. https://doi.org/10.3390/soilsystems6010005.

Wu, X., Brüggemann, N., Gasche, R., Papen, H., Willibald, G., Butterbach-Bahl, K., 2011. Long-term effects of clear-cutting and selective cutting on soil methane fluxes in a temperate spruce forest in southern Germany. Environ. Pollut., Nitrogen Depos., Crit. Loads Biodivers. 159, 2467–2475. https://doi.org/10.1016/j.envpol.2011.06.025.

Xia, N., Du, E., Wu, X., Tang, Y., Wang, Y., de Vries, W., 2020. Effects of nitrogen addition on soil methane uptake in global forest biomes. Environ. Pollut. 264, 114751.

Xing, A., Du, E., Shen, H., Xu, L., de Vries, W., Zhao, M., Liu, X., Fang, J., 2022. Nonlinear responses of ecosystem carbon fluxes to nitrogen deposition in an old-growth boreal forest. Ecol. Lett. 25, 77–88.

Yuan, Z.Y., Chen, H.Y.H., 2010. Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. Crit. Rev. Plant Sci. 29, 204–221. https://doi.org/10.1080/07352689.2010.483579.

Zerva, A., Mencuccini, M., 2005. Short-term effects of clearfelling on soil CO2, CH4, and N_2O fluxes in a Sitka spruce plantation. Soil Biol. Biochem. 37, 2025–2036.

Zhang, T., Chen, H.Y.H., Ruan, H., 2018. Global negative effects of nitrogen deposition on soil microbes. ISME J. 12, 1817–1825. https://doi.org/10.1038/s41396-018-0096-y.

Zhang, Y., Li, J., Tan, J., Li, W., Singh, B.P., Yang, X., Bolan, N., Chen, X., Xu, S., Bao, Y., Lv, D., 2023. An overview of the direct and indirect effects of acid rain on plants: Relationships among acid rain, soil, microorganisms, and plants. Sci. Total Environ. 873, 162388.

Zhang, Q., Li, Y., Wang, M., Wang, K., Meng, F., Liu, L., Zhao, Y., Ma, L., Zhu, Q., Xu, W., Zhang, F., 2021. Atmospheric nitrogen deposition: a review of quantification methods and its spatial pattern derived from the global monitoring networks. Ecotoxicol. Environ. Saf. 216, 112180. https://doi.org/10.1016/j.ecoenv.2021.112180.

Zhang, Z., Teng, Z., Wang, N., Zhang, M., Sun, G., Hu, Y., Zhang, X., 2021. Responses of photosynthesis and antioxidants to simulated acid rain in mulberry seedlings. Physiol. Plant. 172, 188–200. https://doi.org/10.1111/ppl.13320.

Zhou, Z., Wang, C., Zheng, M., Jiang, L., Luo, Y., 2017. Patterns and mechanisms of responses by soil microbial communities to nitrogen addition. Soil Biol. Biochem. 115, 433–441. https://doi.org/10.1016/j.soilbio.2017.09.015.

Zuccarini, P., Asensio, D., Sardans, J., Ogaya, R., Liu, L., Peñuelas, J., 2023. Effects of nitrogen deposition on soil enzymatic activity and soil microbial community in a Mediterranean holm oak forest. Geoderma 430, 116354. https://doi.org/10.1016/j.geoderma.2023.116354.