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Effects of nitrogen fertilization on stand growth and ground vegetation dynamics in boreal Scots pine and Norway spruce stands

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Academic dissertation

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ABSTRACT

Boreal forests are typically nitrogen (N) limited. Therefore, N fertilization may substantially affect carbon (C) sequestration and biomass production of trees and ground vegetation, which contribute to climate change mitigation. The aim of this study was to evaluate the effects of N fertilization on stand growth and ground vegetation dynamics in boreal Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) stands. Systematic quantitative literature synthesis was conducted to analyze the effects of N fertilization on stand growth (Study **I**). The short-term impacts of N fertilization on the cover of ground vegetation were studied in a field experiment in Eastern Finland (Study **II**). Nitrogen fertilization increased the stand growth 0.2–2.7 m^3 ha^{-1} yr^{-1}. The amount of applied N was the most important factor predicting the stand volume growth response. The growth response increased linearly with increasing fertilizer dose until 208 kg N ha^{-1}. The volume growth response depended also on the site type, annual precipitation, and time since fertilization. When studying ground vegetation dynamics, we found that the total cover of ground vegetation tended to decrease with increasing N fertilizer dose, due to decrease in the moss cover. Site fertility and climatic conditions should be considered when making fertilization decisions. The results suggest that a single N fertilization using recommended N doses increases stand growth but has no substantial impact on the ground vegetation.

Keywords: forest fertilization, tree growth response, understory vegetation, upland forests, vegetation cover

PREFACE

I started my journey to the world of nutrients in Joensuu in the spring of 2021, when Professor Heli Peltola offered me a job as a research assistant for the summer. This resulted in a master's thesis on the topic of nitrogen fertilization one year later. After graduation, I was granted an opportunity to continue research on the same topic. Now I have accumulated five years' worth of knowledge about forests, nutrients and nutrient management, and yet I feel like I have only scraped the mor humus layer of the knowledge on the topic.

First, I want to thank my supervisors Associate Professor Marjo Palviainen, Professor Annamari Laurén, and Professor Heli Peltola. They have introduced me to the secrets of academic work, eagerly shared their wisdom and knowledge, and firmly guided me through my doctoral studies. Second, I want to thank my pre-examiners Associated Professor Jürgen Aosaar, Professor Line Nybakken, and Associate Professor Per-Ola Hedwall for their valuable feedback on the thesis manuscript. Also, thanks to Associated Professor Jürgen Aosaar for his willingness to act as my opponent.

I had the privilege to collaborate with great people, and I want to thank my co-authors Samuli Launiainen, Professor Eeva-Stiina Tuittila, Katariina Laurén, Elisa Männistö, Associate Professor Antti Kilpeläinen, Nicola Kokkonen, Olli Muhonen, Juha Nevalainen, and Veli-Pekka Ikonen who have given their valuable input to the manuscripts and aided in the data collection. Special thanks to Elisa Männistö for always helping me in my statistical endeavors.

Thanks to my thesis committee Soili Haikarainen, Sakari Sarkkola, and Jori Uusitalo for their guidance and comments. The speedy completion of my thesis would not have been possible without funding. The Research Council of Finland funded PREFER-project provided me with a salary for three years and enabled full-time work on my thesis.

Thanks to all old and new members of the research group. Especially Mikko Kesälä and Oona Hillgén with whom I have been able to share the ups and downs of the PhD journey from the beginning. I am grateful for the existence of people in room 410; Hannah O'Sullivan, Ville Laamanen, Annastina Saari, and Oili. They have provided a daily dose of laughter and enlightening discussions. Thanks to all the people in the forestry department for the moments and puzzles we have shared in the coffee room, as well as all the interesting lunch companies I have had throughout the years. Thanks to Theater Vuosaari and all the lovely people there for balancing the science with creativity. My warmest thanks to my family and friends for their patience, love, and support throughout good and bad times over the years. Special thanks to Lauri for understanding the long evenings and always being there when I needed you.

Helsinki, April 21st, 2026
Johanna Jetsonen

LIST OF ORIGINAL ARTICLES

I: Jetsonen J, Laurén A, Peltola H, Laurén K, Launiainen S, Palviainen M (2025) Volume growth responses of Scots pine and Norway spruce to nitrogen fertilization: quantitative synthesis of fertilization experiments in Finland. Silva Fenn 59(1), article id 24041. https://doi.org/10.14214/sf.24041.

II: Jetsonen J, Laurén A, Peltola H, Muhonen O, Nevalainen J, Ikonen V.-P, Kilpeläinen A, Tuittila E-S, Männistö E, Kokkonen N, Palviainen M (2024) Effects of nitrogen fertilization on the ground vegetation cover and soil chemical properties in Scots pine and Norway spruce stands. Silva Fenn (58):1, article id 23058. https://doi.org/10.14214/sf.23058.

AUTHOR'S CONTRIBUTIONS

I: Jetsonen participated in planning the study design and data analysis together with her supervisors and data curation with her colleague. She conducted all the data analyses, wrote the first draft of the manuscript and edited it further with all the co-authors.

II: Jetsonen conducted the vegetation inventories and soil sampling in the field together with her colleagues. She planned and conducted all the data analyses, wrote the first draft of the manuscript, and edited it further with all the co-authors.

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1 INTRODUCTION

1.1 Forest fertilization: history and possibilities

Boreal forests account for 27% of the world's forests (FAO 2020). They are located in the Northern Hemisphere in cold climates and are typically dominated by coniferous tree species (Bonan and Shugart 1989). Boreal forests store large quantities of carbon (C) in the trees, soils, and ground vegetation (Mäkipää 1995; Ilvesniemi et al. 2002; Bradshaw and Warkentin 2015). Because of the large C stocks, substantial C sequestration, and vast area, boreal forests are important for global climate change mitigation (Bradshaw and Warkentin 2015). Additionally, the need to substitute non-renewable resources with renewable ones increases the demand for wood biomass (Kilpeläinen et al. 2016; Baul et al. 2017). However, the relatively slow tree growth in boreal forests (Nikolov and Helmisaari 1992) limits the possibilities to meet the increased demand for wood biomass and C sequestration.

Global warming and increased atmospheric CO_2 concentrations can potentially increase tree growth in boreal forests; however, the growth increment is likely limited by changed precipitation patterns, drought, and the length of photoperiod (Kauppi et al. 2014; Stinziano and Way 2014). Forest growth can be enhanced, for example, by afforestation of previously non-forested lands, by planting genetically enhanced seedlings, or by applying optimized harvesting regimes (Mäkinen and Isomäki 2004; Garcia-Gonzalo et al. 2007; Ruotsalainen 2014; Ménard et al. 2023). These management practices may increase tree growth, but the impacts are gradual and relatively slow. Tree growth in boreal forests on mineral soils is also limited by the low nitrogen (N) availability (Tamm 1991). Other, but less common growth limiting nutrients can be phosphorus (P), especially in the most fertile sites (Tamm 1999), and boron (B) (Lehto et al. 2010a). Fertilizing with these nutrients is, compared to other methods, a fast way to increase the stand growth (Kellomäki et al. 1982; Sikström et al. 1998).

The relationship between nutrients and tree growth in upland forests has been studied since the late 19th century (Ebermayer 1882). When the emphasis of forest management shifted towards increasing wood production in the 20th century, nutrient management became a regular part of forest management especially in the boreal region (Tamm 1995). In the 1960s, there was a need to quickly increase the wood production in Finland because the annual harvest of growing stock had been higher than the annual forest growth from 1955 to 1964 (Official Statistics of Finland 2018). Large quantities of forest resources were used as energy and wood material supply during the second World War in the 1940s, afterwards in the 1950s to rebuild destroyed houses and infrastructure, and as war reparations for the Soviet Union (Lounasmeri 1952; Erickson 2024). The efforts to increase forest growth to replace the depleted forest resources were encouraged at the government level. As one of the policy instruments, the government provided financial incentives for forest owners to fertilize their forests (Siiskonen 2013), and the financial incentives were effective. As a result, there was a substantial increase in the annual fertilized land area between the years 1965 and 1975; fertilized land area increased from 6600 ha^{-1} yr^{-1} to 250 000 ha^{-1} yr^{-1} (Fig. 1). Forests in Finland were estimated to have grown 56 million m^3 more than they would have grown without fertilization between the 1950s and 1990s (Moilanen 1998; Kukkola and Nöjd 2000).

The annually fertilized land area has sharply decreased from the levels of 1975 because the financial incentives ceased, cost of fertilizers increased, and concerns about possible negative environmental effects, such as surface water eutrophication and changes in biodiversity, emerged (Kellner 1993; Binkley et al. 1999; Kukkola and Nöjd 2000).

Currently, the Finnish government subsidizes only fertilization for ameliorating severe nutrient deficiencies that impede normal stand growth. Forest owners have the full responsibility for investments in the growth fertilization when the aim is to enhance normal stand growth (Finlex 2023). The recommended fertilization dose in growth fertilization in Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) forests are 100–200 kg N ha^{-1} applied from one to three times with ten years intervals close to the end of rotation period (Äijälä et al. 2019). Even without the financial incentives, investment in forest fertilization is typically profitable for the forest owner (Saarsalmi and Mälkönen 2001; Pukkala 2017).

Large-scale fertilization can increase the forest C stocks in Finland (Hynynen et al. 2024), thus it has been recognized as one of the tools for climate change mitigation in the National Forest Strategy 2035 of Finland (Ministry of Agriculture and Forestry 2023). Hynynen et al. (2024) estimated that increasing the annual fertilized land area from 58 000 ha to 95 000 ha would increase the annual forest growth by over a million cubic meters. This increase in tree volume growth would translate to an additional 917 500 tonnes of CO_2 stored into the tree biomass annually (IPCC 2006). The increase in stand growth and financial gains encourage forest owners to utilize forest fertilization (Hedwall et al. 2014), and therefore, potentially increase the C stocks of Finnish forests.

The environmental concerns can be better considered when forestry shifts towards more site-specific forest management with development of precision forestry (Fardusi et al. 2017; Castro et al. 2021). The advances in geospatial information, remote sensing technologies, and ecosystem modeling provide increasingly detailed information of forest stands that can be used to support forest management planning.

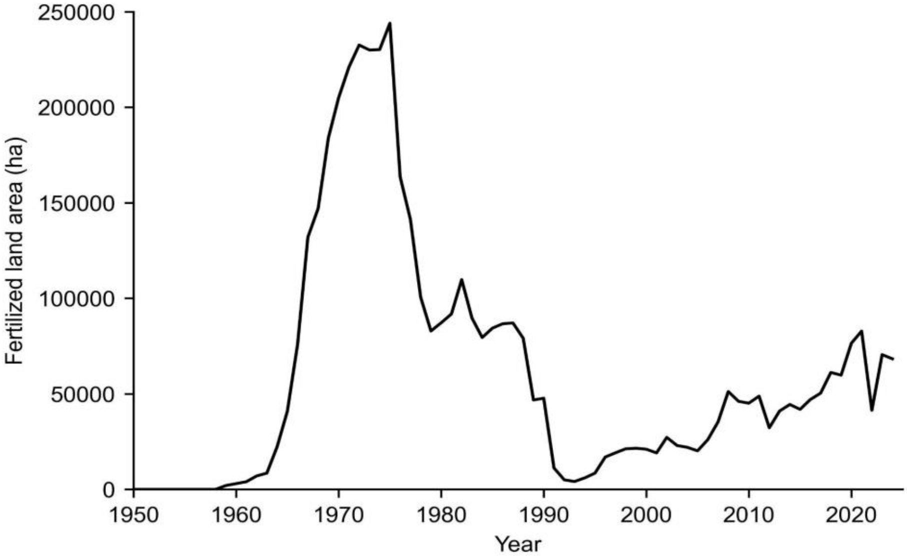

Figure 1. Annually fertilized land area (ha) in Finland from 1950 to 2024. Information of fertilized land area from 1950–1973 is from Kukkola and Nöjd (2000) and data from 1974–2024 is retrieved from the Statistics database of Natural Resources Institute Finland (Official Statistics of Finland 2015).

This enables more precise forest management even at the scale of individual trees (Holopainen et al. 2014). Because fertilization affects the whole ecosystem, not just trees, precision management tools require a comprehensive understanding of the nutrient balances and cycles of the forest ecosystem (Laurén et al. 2021). Multiple factors and their interactions affect the end result of fertilization; therefore, development of the precision forestry tools should incorporate these factors and their interactions to be able to properly simulate the impacts of fertilization on the forest ecosystem. Data from field experiments is required to calibrate the models to better describe the reality (Janssen and Heuberger 1995).

1.2 Nitrogen cycle and effects of nitrogen fertilization

To understand the impacts of N fertilization one must first understand the nutrient cycles of the forest ecosystem. In boreal ecosystems the most abundant plant nutrients are N, P and potassium (K). Their fluxes in the ecosystem between soil, plants, water, and atmosphere are essential for sustaining plant growth (Foster 1974). Boreal forest soils have low pH, and most of the soil biological processes are performed by fungi (McLaren and Turkington 2013). A thin organic layer, mor or moder that has formed on top of the soil profile is characteristic of boreal mineral soils (Laurén 1999). A large amount of N is stored in the boreal soils; in Finland mineral soils contain on average 1707 kg N ha^{-1} from which 595 kg N ha^{-1} resides in the mor layer (Tamminen 1998). In nutrient-poor sites soil N stock is around 900 kg ha^{-1}, whereas in the most fertile site type, soil N stock can be more than 2740 kg N ha^{-1} (Tamminen 1998). Although the forest stands and soils store large quantities of N, the cycling of N within the forest ecosystem is slow in the cold climate (Van Cleve and Alexander 1981).

Nitrogen fixation of cyanobacteria mediates the transfer of gaseous N_2 from atmosphere into the soil (Cleveland et al. 1999; DeLuca et al. 2002). The cyanobacteria-feather moss symbiosis can fix 2 kg N ha^{-1} yr^{-1} in boreal forests (DeLuca et al. 2002). Another input of N and other macronutrients to the ecosystem is atmospheric dry and wet deposition (Korhonen et al. 2013; Schwede et al. 2018). In Finland, the N input with atmospheric deposition is small, ranging from 2–8 kg N ha^{-1} yr^{-1} (Korhonen et al. 2013). Nitrogen fixation and atmospheric deposition are thus important components of forest nutrient balance. Trees and ground vegetation store large quantities of nutrients. In seedling stands more nutrients are stored in ground vegetation than in the tree seedlings, but during the succession, the nutrient stock in trees increases (Helmisaari 1995). Trees and ground vegetation uptake N from soil in the form of nitrate (NO_3^-), ammonium (NH_4^+), amino acids and other small organic compounds (Virtanen 1935, Nordin et al. 2001). Leaves contain a significant share of plant N, and N content of leaves affects the photosynthetic capacity (Grassi et al. 2001; Warren et al. 2003). Plants can retranslocate nutrients from old and dying leaves and fine roots to new plant tissues (Helmisaari 1995). Therefore, only part of the nutrients are returned back to the soil through litterfall (Helmisaari 1995).

Microbes decompose organic matter and release N from the organic compounds (Berg 1986). Nitrogen is transformed into inorganic form through ammonification and nitrification processes (Killham 1990; Schimel and Bennett 2004). This mineralization process transforms only one percent of the total soil N stock into plant available form annually (Tamminen 1998). The nutrients in boreal forest ecosystems are tightly recycled, and the majority of the nutrients remain in the ecosystem. However, some natural outflows exist. Typically, about 2 kg N ha^{-1}yr^{-1} is exported to water courses from forested catchments in Finland (Kortelainen et al. 2006; Aaltonen et al. 2021). The gaseous N losses in the form of nitrous oxide (N_2O)

and nitrogen oxide (NO) are small, the order of magnitude being about 0.2 kg N $ha^{-1}yr^{-1}$ (Korhonen et al. 2013). The largest outflow of nutrients in managed boreal forest is tree harvesting (Paré et al. 2002). Especially harvesting of logging residues from a clearcut site removes large quantities of N. For instance, whole-tree harvesting from Norway spruce site removes 200–250 kg N ha^{-1} (Palviainen and Finér 2012), which is more than the recommended N dose in forest fertilization in Finland (Äijälä et al. 2019).

Nitrogen fertilization does not just increase the amount of available nutrients but has a more comprehensive impact on the functioning of the ecosystem. Increase in N input alters the nutrient cycling, nutrient stocks, and allocation of nutrients in forest ecosystems (From et al. 2015; Gao et al. 2016). Nitrogen fertilizers typically contain ammonium nitrate, ammonium sulfate, or urea, so that the applied N is easily available for trees (Lehto and Ilvesniemi 2023). Typical practice in Nordic slow-growing coniferous-dominated forests is to apply N as a mixture with P and K (Smethurst 2010). The fertilizer application is commonly done with a forwarder or a helicopter for larger areas at the time. However, this is not reflected in the previous fertilization experiments, where the fertilizer has been applied manually using exact N doses (Laakkonen et al. 1983; Saarsalmi et al. 2014). For instance, Muhonen et al. (2025) observed that the helicopter and forwarder application produces uneven distribution of N over the site. This may bring up some inconsistencies when the results of N fertilization research and the results of practical N fertilization are compared.

Nitrogen fertilization increases nutrient supply, which consequently changes ratios between different nutrients and lowers soil pH (Mäkipää 1994; Yan et al. 2025). These changes further affect the soil microbial communities and their functioning (Högberg et al. 2006; Demoling et al. 2008). For instance, Zackrisson et al. (2004) observed that increased N supply affects the functioning of N fixing cyanobacteria, and consequently, N fixation almost ceases. Maaroufi et al. (2015) also observed decrease in soil respiration and fungal and microbial biomass following increased N amount in soil. Forest N fertilization increases C accumulation both in the tree stand and soil (Mäkipää 1995). Carbon accumulates in the soil after N fertilization because litter production increases and simultaneously soil organic matter decomposition rate decreases resulting in increased mass of the organic layer (Fog 1988; Mäkipää 1994; Olsson et al. 2005). Particularly lignin decomposition slows down after N fertilization (Carreiro et al. 2000; Marshall et al. 2021) probably because the abundance of lignolytic fungi decreases (Entwistle et al. 2018). Nitrogen fertilization can also increase the N export to surface waters as well as gaseous N_2O emissions (Binkley et al. 1999; Håkansson et al. 2021).

Alterations in nutrient dynamics are reflected in the ground vegetation species composition and tree growth (Turkington et al. 1998; Saarsalmi and Mälkönen 2001). Nitrogen fertilization also increases the N concentration in tree leaves and ground vegetation (Grassi et al. 2001; Warren et al. 2003; Palmroth et al. 2014) and potentially reduces resource allocation to fine roots in Scots pine and Norway spruce stands (Axelsson and Axelsson 1986). Changes in leaf and root nutrient concentrations are reflected in the litter quality that further affects the organic matter decomposition rate and nutrient release (Allison et al. 2007; Lehto et al. 2010b).

1.3 Responses of trees and ground vegetation to nitrogen fertilization

Nitrogen fertilization increases stand growth in the boreal forests by 1–2 m^3 ha^{-1} yr^{-1} for a period of 6–10 years (Kukkola and Saramäki 1983; Valinger et al. 2000). Stand growth increases because N fertilization increases leaf area and leaf N concentration, and consequently the photosynthetic capacity increases (Kellomäki and Wang 1997). Multiple factors affect the intensity and duration of the growth response. Several studies have observed that the magnitude of the growth response is affected by climatic conditions. Stand growth increases more in the southern parts of Fennoscandia; whereas the growth response lasts longer in the north (Laakkonen et al. 1983; Pettersson 1994; Saarsalmi and Mälkönen 2001). Stand characteristics also have an impact on the growth response. In sites with higher initial fertility, the trees can utilize the increased N supply more efficiently (Pettersson 1994). Norway spruce and Scots pine, the most common commercially utilized tree species in Finland, have slightly different growth responses to N fertilization. The impacts of N fertilization can be observed earlier in Scots pine stands; however, the growth response of Norway spruce lasts longer (Kukkola and Saramäki 1983). Comprehensive synthesis on the magnitude, length, and explaining factors of growth responses is lacking. The order of importance between the different factors influencing growth response and their interactions are not well described. Thus, more information is needed to form a more thorough understanding of the mechanisms behind the growth response.

Ground vegetation is an important part of the nutrient cycle of the forest ecosystem. The ground vegetation uptakes high amounts of nutrients, and the majority of the ground vegetation biomass, renews annually (Mälkönen 1974; Helmisaari 1995). Each plant species has characteristic nutrient requirements, and therefore, increase in nutrient supply may either benefit or hinder plant species growth (Turkington et al. 1998; Rajaniemi 2002; Salemaa et al. 2008). At the same time, fertilizer-induced changes in soil properties, tree stand, and the availability of light may also change the ground vegetation growing conditions (Rajaniemi 2002; Skrindo and Øland 2002).

In previous studies vascular plant cover has increased after N fertilization, whereas moss cover tends to decrease (Olsson and Kellner 2006; Strengbom and Nordin 2008). Especially grasses, such as *Deschampsia flexuosa* (L.) Trin. and *Agrostis ssp.* as well as *Rubus idaeus* L., benefit from increased N supply and their abundance can increase substantially following N fertilization (van Dobben et al. 1999). In contrast, feather moss carpets, consisting of *Pleurozium schreberi* (Willd. ex Brid.) and *Hylocomium splendens* (Hedw.), decrease after N addition (Dirkse and Martakis 1992). Some litter dwelling moss species like *Brachythecium sp.* may benefit from the N fertilization as the litter input to ground increases (Strengbom and Nordin 2008). Dwarf shrubs, such as *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L., have had mixed responses to N fertilization (Sullivan and Sullivan 2018).

N fertilization shifts the plant composition of ground vegetation to resemble vegetation of more fertile site types; although the change might be long lasting, the change is not permanent (Kellner 1993). Although many previous studies have reported the effects of N fertilization on ground vegetation, most of them either report results of repeated fertilizations or emulate elevated atmospheric N deposition (Kellner 1993; Mäkipää 1994; Olsson and Kellner 2006). In these studies, the applied N doses exceed the N doses recommended in forest management guidelines in Finland (Äijälä et al. 2019). Knowledge about the effects of forest fertilization on ground vegetation in a practical setting is lacking.

1.4 Objectives

The aim of this thesis was to study how N fertilization affects stand growth and ground vegetation cover in Scots pine and Norway spruce dominated forests in Finland. The effect of N fertilization on stand volume growth was studied using quantitative literature synthesis of previous fertilization studies (**I**). The short-term effects of N fertilization on ground vegetation were investigated in a field experiment in Eastern-Finland (**II**). More specifically the objectives and the hypotheses were:

1) To investigate how much different N fertilization intensities increase the stand volume growth (**I**), and which site, climate, fertilizer, and stand characteristics affect the volume growth response of Scots pine and Norway spruce (**I**). Assumption was that the growth response depends most strongly on N dose, whereas site, stand climate characteristics have a smaller impact.
2) To study the changes in the covers of functional plant groups (**II**) with different N fertilization doses, which arise from the unevenness of practical forest fertilization. Hypothesis was that changes are greatest with the highest N dose and that grasses and herbs benefit, whereas mosses suffer from the increased N dose.

The novelty of this study is that it quantifies the effects of N fertilization on ground vegetation dynamics on sites where fertilizer dose and application methods (forwarder and helicopter) are similar to that in practical forestry. The application of N fertilization with helicopter or forwarder leads to uneven distribution of N fertilizer. In this study, the effect of the uneven fertilizer distribution is considered (**II**). Based on a summary of a large number of studies, this thesis also provides new, quantitative information on the effects of stand characteristics, climate conditions, site fertility, N dose and tree species on growth responses induced by N fertilization (**I**).

2 MATERIALS AND METHODS

2.1 Stand growth responses

To analyze the effects of N fertilization on stand volume growth, a systematic literature search was carried out (**I**). The search for eligible published, peer-reviewed articles and gray literature, such as work reports of government organizations, was started by using keywords “nitrogen fertilization,” “Scots pine,” and “Norway spruce.” After the initial search, a pearl growing method was used to find more eligible articles from the references of the already found articles (Schlosser et al. 2006). Articles reporting results of N fertilization experiments located in Finland were considered eligible, if detailed information about applied fertilizer and the obtained growth response in terms of stand volume, height, or breast height diameter were reported. All the eligible articles were available in Library databases of the Universities of Oulu, Eastern Finland, and Helsinki, Google Scholar, or the open repository of the Natural Resources Institute Finland (Jukuri). Based on these criteria, 22 articles were initially included in the dataset.

All available information of the research design was extracted, such as location of research sites, mean effective temperature sum, mean annual precipitation, characteristics of the stand before fertilization, along with information on the fertilizer treatments and the growth response, as well as the duration of the experiment. Data reported in graphs were extracted using PlotDigitiser-program version 3.1.5 (https://plotdigitizer.com/app). If information on a variable was not available, the data entry was left empty. Long-term mean annual precipitation and effective temperature sums were retrieved from the open data repository of Finnish Meteorological Institute (2024) using the measurement period from 1961 to 1990 (https://en.ilmatieteenlaitos.fi/open-data).

Volume growth was selected as the response variable because it was the most commonly reported growth-related variable among the articles. Other variables describing stand characteristics, such as basal area and age of the stand, were inadequately reported in the articles, and therefore, these variables were not used in the analysis. After the data extraction 13 articles were excluded from the dataset (**I**). Three articles reporting repeated fertilization and three articles where sites were fertilized with mixture of N and ash were excluded from the dataset. In addition, one study with a small initial stand volume was excluded because young stands are typically not fertilized in practical forestry. Furthermore, four articles were removed because they did not report initial stand volume or volume growth response, and two articles were excluded because they added only one observation to the dataset. Total of 9 studies were included into the final dataset in study **I** (Table 1).

The Scots pine datasets contained 108 observations and the Norway spruce dataset contained 57 observations. The observations were from 97 different locations ranging from south to north of Finland (Fig. 2). The majority of the Scots pine stands were located in sub-xeric heath forest sites (*Vaccinium*-type), and all Norway spruce stands in mesic heath forest sites (*Myrtillus*- type, Cajander, 1949). Typical fertilization dose in the included studies was 120 kg N ha^{-1}; however, the applied N amounts ranged from 54 to 208 kg N ha^{-1} in Scots pine sites and from 60 to 180 kg N ha^{-1} in Norway spruce sites (Table 2).

Variables containing enough observations were selected from the compiled dataset for statistical analyses for study **I** (Table 2). The response variable was the annual volume growth response compared to the unfertilized control (m^3 ha^{-1} yr^{-1}). Data was cleaned from missing observations and divided into two datasets based on the dominant tree species, Scots pine (n = 108) and Norway spruce (n = 57). Statistical analyses for both tree species were conducted separately using R 4.2.2 (R Core Team 2022). Differences in stand volume growth responses to N fertilization between different geographical locations were analyzed using parametric one-way ANOVA. Nonparametric ANOVA using Kruskal–Wallis test and Wilcoxon rank sum test were utilized to investigate differences in volume growth responses between site types. Linear mixed models were used to analyze how the N fertilizer dose and other variables affect the stand volume growth response (**I**).

$$y = \boldsymbol{\beta}^{\mathbf{T}}\ \mathbf{X}+\mathbf{Z}+\varepsilon, \qquad \text{(Eq. 1)}$$

where y is the mean annual volume growth response obtained by N fertilization (m^3 ha^{-1} yr^{-1}), βT is a transpose of a coefficient vector (β1, β2, β3, … β10), X is a vector of explanatory fixed variables, Z is the vector of article identification number (A_{id}) as random factors, and ε is the residual (Table 2). The models were composed using lme-function from nlme-package (Pinheiro and Bates 2024).

Several models were compiled to investigate which variables and variable combinations best explained the variation in the volume growth responses. First, we analyzed which single variables (Table 2) best explained the variation in volume growth response. Next, we selected the best-performing variable and added a second variable to the model. Then, we continued adding explanatory variables one at a time and evaluated how the model goodness-of-fit improved. Finally, we started with a full set of explanatory variables and applied backward stepwise regression using the *dredge* function from the MuMIn package (Bartoń 2024) to identify the best combination of variables. In all models, the article identification number (A_{id}) was included as a random factor. In both the Scots pine and Norway spruce datasets, effective temperature sum (T_{sum}) and mean annual precipitation (P_a) were highly correlated and showed a decreasing trend toward the North. To avoid multicollinearity, only one variable representing the site's climate and growing conditions (G_{lat}, T_{sum}, or P_a) was included in each model. Multicollinearity was assessed using the variance inflation factor (VIF). The models were compared based on Akaike Information Criteria (AIC), R^2, RMSE, and p-values. The best model for both Scots pine and Norway spruce was selected based on the lowest AIC-value.

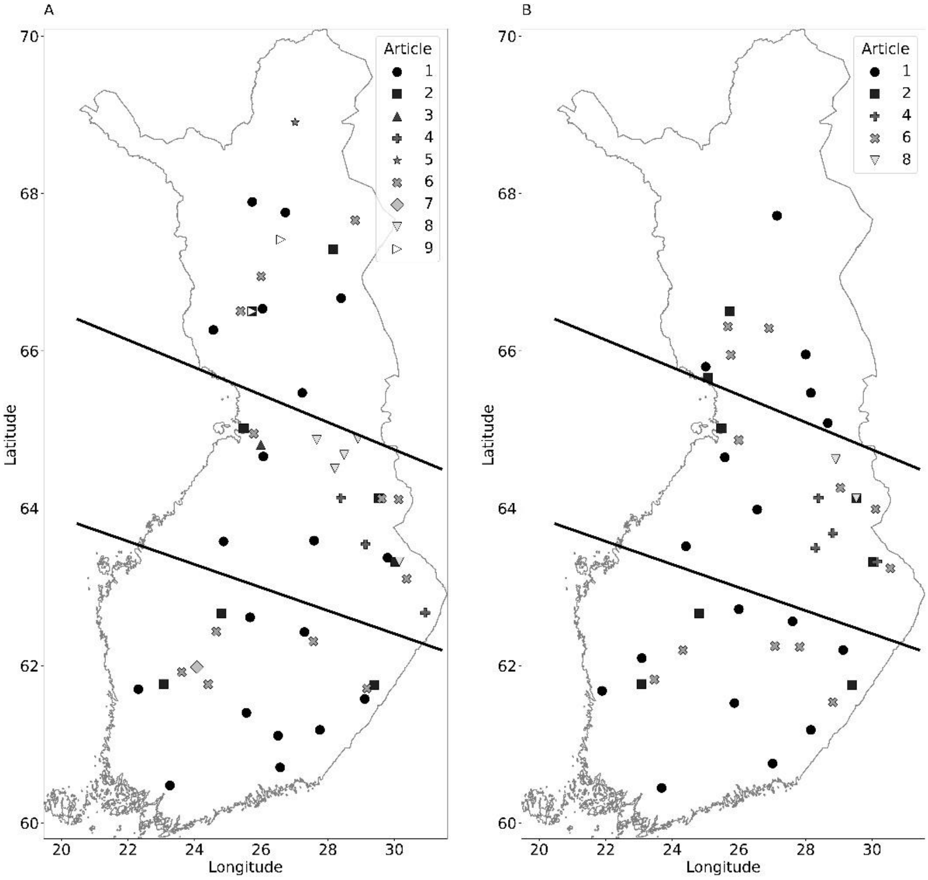

Figure 2. Locations of the nitrogen fertilization experiments used in study **I**. Map A contains the locations of Scots pine research sites and map B the Norway spruce sites. Information on the studies are presented in Table 1. The article numbers correspond to the article identification numbers in the study **I**. Lines represent division to Northern, Middle, and Southern Finland. In Northern Finland the temperature sum (threshold +5°C) is <1000 d.d., in Middle Finland 1000–1200 d.d. and in Southern Finland >1200 d.d.

Table 1. Description of articles which were included in the dataset and used in the quantitative synthesis on stand volume growth responses after nitrogen fertilization in Finland (**I**). F_N is the range of applied N fertilizer doses. V_{ini} is the initial stand volume before fertilization. The annual precipitation (P_a), and the effective temperature sum (T_{sum}) are the long-term averages from 1961 to 1990. The site type classification followed the Cajander's (1949) site classification system. S_F is the time since fertilization in years and n is the number of observations in the dataset.

Article	F_N (kg ha^{-1})	V_{ini} (m^3 ha^{-1})	P_a (mm)	T_{sum} (d.d.)	Tree species	Site type	S_F (yrs.)	n	Reference
1	120	130–200	470–590	900–1180	*Pinus sylvestris, Picea abies*	MT, VT, CT	10	12	Laakkonen et al. (1983)
2	120	122–175	430–640	790–1280	*Pinus sylvestris, Picea abies*	MT, VT	5	68	Lipas & Levula (1980)
3	156–208	81–123	596	990	*Pinus sylvestris*	MT, VT	11	10	Moilanen & Meriluoto (1984)
4	100	50–230	630	1090	*Pinus sylvestris, Picea abies*	MT, VT, CT	4	12	Salonen (1973)
5	54–200	62–70	400–540	740–880	*Pinus sylvestris*	VT	4–10	6	Lipas et al. (1983)
6	120	103–180	520–610	800–1190	*Pinus sylvestris, Picea abies*	MT, VT	10	32	Lipas (1988)
7	180	112	714	1130	*Pinus sylvestris*	VT	5	4	Levula (1991)
8	60–180	106	590–600	910–1020	*Pinus sylvestris, Picea abies*	MT, VT	5	18	Gustavsen & Lipas (1975)
9	170	65–74	500–540	797–840	*Pinus sylvestris*	MT, VT	7	3	Hirvelä & Hynynen (1990)

Table 2. Description of variables and their range of values in the dataset compiled from fertilization studies conducted in Finland. Data was used in modeling N fertilizer-induced volume growth responses of Scots pine and Norway spruce in study **I**.

Variables	Coefficients	Description	Range of values in Scots pine data	Range of values in Norway spruce data
y		Annual mean volume growth response obtained by N fertilization (m^3 ha^{-1} yr^{-1})	0.18–2.7	0.36–2.3
F_N	β1	Applied dose of nitrogen (kg ha^{-1})	54–208	59.8–180
P_a	β2	Mean annual precipitation (mm)	396–714	472–630
$G_{fertility}$	β3	Site fertility group: boolean, 1 when Site type ∈ [MT], else 0	0, 1	0, 1
T_{sum}	β4	Effective temperature sum (d.d.)	743–1282	884–1283
G_{south}	β5	Area group: Boolean, 1 when in Southern Finland, else 0	0, 1	0,1
G_{middle}	β6	Area group: Boolean, 1 when in Middle Finland, else 0	0, 1	0, 1
G_{north}	β7	Area group: Boolean, 1 when in Northern Finland, else 0	0, 1	0, 1
G_{lat}	β8	Latitude of the stand in decimal degree	61.76–68.91	61.76–66.50
V_{ini}	β9	Initial stand volume (m^3 ha^{-1})	50–173	60–200
S_F	β10	Time since fertilization	4–15	4–15
A_{id}	β11	Article identification number	1–9	1,2,4,6,8

2.2 Ground vegetation response to N fertilization

Field measurements for study **II** were conducted in four research sites in Eastern-Finland (Table 3). Sites in Liperi (62° 33.5076' N, 29° 3.7590' E) and Ilomantsi (62° 51.3258' N, 30° 40.623' E) were Scots pine-dominated, and Juuka (63° 3.9719' N, 28° 52.4784' E) and Savonranta (62° 8.3417' N, 29° 8.9452' E) sites were dominated by Norway spruce (Fig. 3). The long term (1991–2020) mean annual air temperature was 2.8–3.5 °C and long-term annual precipitation 640–670 mm. The warmest month was July and the coldest January (Finnish Meteorological Institute 2023). During the experiment the growing seasons were either warmer or drier than the long-term average in the area (Table 4). The soil was Haplic podzol according to FAO/WRB classification, and the organic layer consisted of mor humus. The thickness of mor humus layer was 4.6 and 3.0 cm in Liperi and Ilomantsi respectively, 4.0 cm in Juuka and 3.0 cm in Savonranta. Soil pH was similar in all research sites; in the mor humus layer pH was 4, and 5 in depth of 0–20 cm in the mineral soil. All the research sites represented mesic heath forest site type (*Myrtillus*-type; MT; Cajander 1949).

The experiment was established as a randomized block design with three treatments and three replicate blocks of each treatment (Fig. 3). Target levels for different treatments were 150 kg N ha^{-1} and 200 kg N ha^{-1} following the practical forestry recommendations in Finland (Äijälä et al. 2019), and 0 kg N ha^{-1} for unfertilized control. Treatments for each block were randomly selected. Three circular plots (200 m^2) were randomly located and marked in each replicate block (n = 108) (Fig. 3 and 4). All the trees with diameter at breast height (DBH) more than 8 cm were measured from the plots. Inside each plot, three circular subplots were established (n = 324) (Fig. 4).

The fertilizer application was made with a forwarder and a centrifugal spreader in Scots pine-dominated sites and with a helicopter in the Norway spruce-dominated sites (Table 3). Ponsse Gazelle forwarder with an Amazon centrifugal spreader was used for the ground spreading. Spreading was done from skid tracks located with 20 m spacing. For aerial spreading, an Airbus H125 Ecureuil was used with a centrifugal spreader attached by a cable beneath the helicopter. Flying speed was 28-40 knots and the spreading width was 40–45 m. YaraBela Metsäsalpietari was used as fertilizer in Scots pine sites and YaraMila Metsän NP in Norway spruce sites. YaraBela Metsäsalpietari contains 26.8% N (as 12.2% nitrate N, 14.6% ammonium N), 1% potassium (K), 1% magnesium (Mg), 4% sulfur (S) and 0.15% boron (B). YaraMila Metsän NP contains 25% N (as 12% nitrate N, 13% ammonium N), 2% phosphorus (P), 1% Mg, 0.3% B and 0.1% zinc (Zn). The amount of applied fertilizer was measured using three funnel traps (diameter 0.5 m) located at every plot. The funnel traps were placed three meters from the plot center towards the subplots (Fig. 3). In the Ilomantsi research site three additional funnel traps were installed in each plot. The funnel trap measurements were used to quantify the realized fertilizer dose (kg N ha^{-1}). The mean realized fertilizer dose in each plot was used in statistical analyses instead of the nominal target levels in the treatments (150 kg N ha^{-1} and 200 kg N ha^{-1}), and from here on are referred as N fertilizer dose.

Table 3. Description of the research sites of study **II**. The mean annual air temperature and the annual precipitation are the 30-year average from 1990–2020 (Finnish Meteorological Institute 2023). Stand characteristics were calculated as averages of 27 plots (200 m^2).

Research site	Liperi	Ilomantsi	Juuka	Savonranta
Dominant tree species	*P. sylvestris*	*P. sylvestris*	*P. abies*	*P. abies*
Altitude (m a.s.l.)	160	180	170–200	120–140
Mean annual air temperature (°C)	3.5	3.0	2.8	3.4
Effective temperature sum (d.d.)	1200–1300	1100–1200	1100–1200	1200–1300
Annual precipitation (mm)	640	644	661	670
Stand density (stems ha^{-1})	513	687	619	455
Mean diameter at breast height (cm)	23	18	21	21
Mean basal area (m^2 ha^{-1})	19	20	20	17
Initial volume (m^3 ha^{-1})	167	170	187	159
Date of N application	27.06.2018	20.07.2018	25.-27.07.2019	10.08.2019
Means of application	Forwarder	Forwarder	Helicopter	Helicopter
Range of the N fertilizer dose (kg N ha^{-1})[a]	110–288	109–369	48–441	50–426

[a] Due to problems in fertilizing, the measured N fertilizer dose was zero in one plot in Ilomantsi and two plots in Savonranta and these plots were excluded from range values.

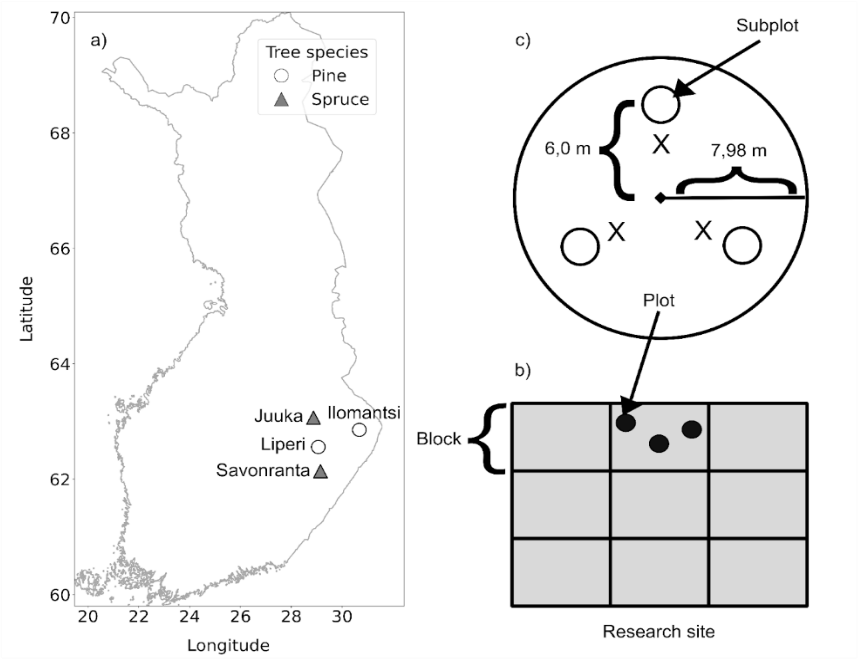

Figure 3. Location of the four research sites (a) and study design (b, c) in study **II**. In the map (a) the circles represent Scots pine sites and the triangles Norway spruce sites. Each research site had nine blocks (b) with an area of 1 ha. The blocks were allocated into three fertilization treatments (target levels 0, 150 and 200 kg N ha^{-1}), each with three replicates. Each block included three circular plots (200 m^2) from where tree characteristics were measured. Within each plot, there were three subplots (0.5 m^2) for determining covers of ground vegetation species (c). Each plot included funnel traps used for measuring N fertilizer dose. The three funnel traps were placed 3 m from the center of the plot towards the subplots and are indicated with X in (c). Ilomantsi research site had three additional funnel traps placed in each plot.

Table 4. Mean air temperature and mean precipitation for the growing season (April–September) for each research site over the measurement years and as the 30-year average from 1991–2020 (Finnish Meteorological Institute 2023). The first measurement year at Liperi and Ilomantsi was 2018, while at Juuka and Savonranta, the measurements were started in 2019.

	Mean temperature (°C)				Mean precipitation (mm)			
	30 years	2018/19	2021	2022	30 years	2018/19	2021	2022
Liperi	11.2	12.9	12.2	11.5	356	355	350	290
Ilomantsi	10.8	12.8	11.7	11.2	373	322	341	333
Juuka	10.4	10.5	11.2	10.7	370	264	377	332
Savonranta	10.8	10.9	11.7	11.1	362	304	362	254

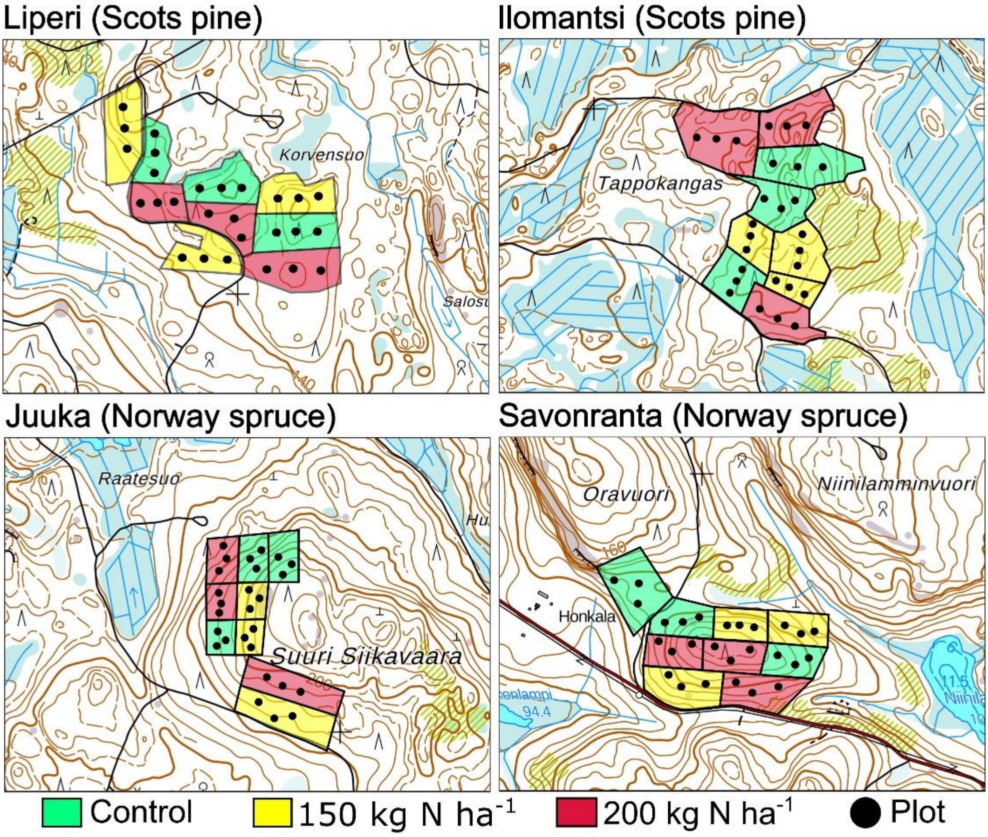

Figure 4. Set-up of the N-fertilization experiment with three target N-doses (0, 150 and 200 kg N ha^{-1}) in four research sites. Each site contained nine blocks, to which the target N-dose was randomly selected. The green color indicates control blocks, yellow indicates treatment of 150 kg N ha^{-1}, and red 200 kg N ha^{-1}. Three plots were randomly located inside each block. The base maps are retrieved from open data of the National land survey of Finland (https://asiointi.maanmittauslaitos.fi/karttapaikka/?lang=en).

Vegetation inventories were carried out first time before N fertilization in Scots pine dominated stands in 2018, and in Norway spruce dominated stands in 2019. Vegetation inventory was repeated two times after fertilization in 2021 and 2022, i.e. 2–4 years after fertilization depending on the research site. The percentage cover of each species was visually evaluated from circular subplots in size of 0.5 m^2 (with radius of 0.4 m). Each research site contained 81 subplots, 27 per target treatment, from which ground vegetation was surveyed. Visual estimation was selected as an inventory method because it enabled repeated measurements from the same subplot without disturbing the vegetation. To minimize the variation caused by subjectivity of different observers, the same observer carried out the vegetation inventories, except inventories made in 2018. In previous studies, visual species cover estimations have been effective for discovering the species present in the research area (Bergstedt et al. 2009). Because plants grow in multiple layers on top of each other, the total percentage cover of ground vegetation in the subplot may exceed 100%.

Table 5. The plant species found in ground vegetation inventories in nitrogen fertilized Scots pine and Norway spruce research sites in Finland in 2018–2022 (Study **II**).

Plant groups	Pine stands	Spruce stands
Grasses	*Agrostis* sp., *Calamagrostis arundinacea* (L.) Roth, *Calamagrostis phragmitoides* Hartm., *Deschampsia flexuosa* (L.) Trin., *Melica nutans* L., and *Poa nemoralis* L.	*Agrostis* sp., *C. arundinacea, C. phragmitoides, Calamagrostis* sp., *D. flexuosa, M. nutans,* and *P. nemoralis*
Herbs	*Carex brunnescens* (Pers.) Poir., *Carex digitata* L., *Carex globularis* L., *Carex leporina* L., *Convallaria majalis* L., *Epilobium angustifolium* L., *Fragaria vesca* L., *Galeopsis tetrahit* L., *Goodyera repens* (L.) R. Br., *Hierachium* sp., *Juncus effusus* L., *Luzula pilosa* (L.) Willd., *Maianthemum bifolium* (L.) F.W. Schmidt, *Melampyrum pratense* L., *Orthilia secunda* (L.) House, *Oxalis acetosella* L., *Potentilla erecta* (L.) Raeusch., *Rubus idaeus* L., *Rubus saxatilis* L., *Solidago virgaurea* L., *Stellaria media* (L.) Vill., *Trientalis europaea* L., *Veronica officinalis* L., *Viola palustris* L., and *Viola riviniana* Rchb.	*Angelica sylvestris* L., *C. brunnescens, C. digitata, C. globularis, Carex* sp., *C. majalis, E. angustifolium, F. vesca, G. tetrahit, Geranium sylvaticum* L., *G. repens, Hieracium* sp., *Lathyrus pratensis* L., *L. pilosa, M. bifolium, M. pratense, Melampyrum sylvaticum* L., *O. secunda, O. acetosella, Platanthera bifolia* (L.) Rich., *Pyrola minor* L., *R. idaeus, R. saxatilis, S. virgaurea, T. europaea, Veronica chamaedrys* L., *Viola* sp., *Viola canina* L., *V. palustris,* and *V. riviniana*
Pteridophytes	*Athyrium filix-femina* (L.) Roth, *Dryopteris carthusiana* (Vill.) H.P. Fuchs, *Equisetum sylvaticum* L., *Gymnocarpium dryopteris* (L.) Newman, *Lycopodium clavatum* L., and *Pteridium aquilinum* (L.) Kuhn	*D. carthusiana, G. dryopteris,* and *P. aquilinum*
Shrubs	*Calluna vulgaris* (L.) Hull, *Linnaea borealis* L., *Salix* sp., *Vaccinium myrtillus* L., and *Vaccinium vitis-idaea* L.	*C. vulgaris, L borealis, V. myrtillus,* and *V. vitis-idaea*
Mosses, Lichens	*Aulacomnium palustre* (Hedw.) Schwägr., *Brachythecium* sp., *Bryum* sp., *Dicranum* sp., *Hylocomium splendens* (Hedw.) Schimp., *Marchantiophyta* sp., *Plagiomnium* sp., *Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Pohlia nutans* (Hedw.) Lindb., *Polytrichum* sp., *Ptilium crista-castrensis* (Hedw.) De Not., *Rhodobryum roseum* (Hedw.) Limpr., *Sphagnum* sp., and *Cladonia* sp.	*A. palustre, Brachythecium* sp., *Bryum* sp., *Dicranum* sp., *H. splendens, Marchantiophyta* sp., *Plagiomnium cuspidatum* (Hedw.) T.J. Kop., *P. schreberi, P. nutans, Polytrichum* sp., *P. crista-castrensis., R. roseum, Hylocomiadelphus triquetrus* (Hedw.) Ochyra & Stebel, *Sphagnum* sp., *Cladonia* sp., and *Peltigera* sp.

The species recorded in vegetation inventories (Table 5) were sorted into three plant groups (Study **II**). The group of herbaceous species consisted of grass, herb, and pteridophyte species. The group of dwarf shrubs consisted mainly of *V. myrtillus* and *V. vitis-idaea*. The bottom layer group contained mosses and lichens (lichens had <0.1% cover). The dominant species in the bottom layer were *P. schreberi* and *H. splendens*. Ground vegetation cover data was arcsine-square-root transformed prior to the statistical analysis to meet the requirement of normal distribution. The cover of the species in a plant group were summed to obtain the total cover of each plant group. Difference in the cover of plant groups before and after fertilization (year 2022) was analyzed with two-sided T-test (in study **II,** Fig. 2). The changes between the years were calculated by subtracting cover before fertilization from the cover measurement after fertilization. Statistical analyses for study **II** were made with R 4.2.2 (R Core Team 2022) and all the research sites were analyzed separately.

Linear regression was used to study the relationship between changes in ground vegetation and the N fertilizer dose (Eq. 2).

$$y = \beta 0 + \beta 1 Nt + \varepsilon, \qquad \text{(Eq. 2)}$$

where y is the arcsine-square-root transformed ground vegetation cover change, Nt is the measured N fertilizer dose in a plot (kg N ha^{-1}), β0 is an intercept, and β1 is a slope describing the ground vegetation cover change per measured fertilizer N dose. Significance of the β1 term was used as a measure of the fertilizer impact. Because multiple linear regressions were made, p-values were corrected separately with two different methods described by Holm (1979) and Benjamini and Hochberg (1995). Holm (1979) corrects the family-wise error rate and Benjamini and Hochberg (1995) controls the false discovery rate.

The relationship between the N-dose and the plant cover was analyzed using linear regression in study **II.** For this summary, I reanalyzed the data considering the nested study design, where plots are located within the blocks. The analysis was done using a linear mixed model using lme-function from nlme-package (Pinheiro and Bates 2024). The mean cover of each vegetation group was calculated based on the three sub plots and the plot within a block was set as a random variable in the analysis.

To evaluate the impact of tree competition on the ground vegetation, measured tree data from the research sites was used to calculate competition indices (C_i) for each subplot using equation:

$$C_i = \sum_{i=1}^{n} \left(\arctan \left(\frac{d_i}{2dist_i} \right) \right) \qquad \text{(Eq. 3)}$$

where d_i is diameter at breast height (1.3 m) of a tree *I* and $dist_i$ is the distance between the tree and a center point of the subplot. All trees inside 2 m radius were accounted for and *n* is the number of these trees. The relationship of ground vegetation changes and competition indices was studied using linear regression (Eq. 2).

3 RESULTS

3.1 Fertilization-induced changes in stand volume growth

The annual volume growth response of Scots pine and Norway spruce to N fertilization varied from 0.2 to 2.7 $m^3 ha^{-1}$ (**I**). The volume growth response was linear when the N fertilizer dose was between 60 and 200 kg N ha^{-1} for both tree species (Fig. 5). Larger growth increments were reported from Scots pine sites compared to Norway spruce sites. The volume growth response of Scots pine was on average 1.1 m^3 ha^{-1} yr^{-1} and Norway spruces 0.9 m^3 ha^{-1} yr^{-1}. However, the average N fertilizer dose was higher (128 kg N ha^{-1}) in Scots pine stands than in Norway spruce stands (118 kg N ha^{-1}).

The most significant factor defining the magnitude of the volume growth response was the N fertilizer dose (kg N ha^{-1}). The N fertilizer dose alone explained 31% of the variation in the volume growth responses of Scots pine and 24% for Norway spruce (**I**). The best models based on AIC-value also contained annual precipitation, and time since fertilization in addition to N fertilizer dose. Increases in annual precipitation produced larger growth responses, whereas longer time elapsed since fertilization decreased the growth response (Table 6).

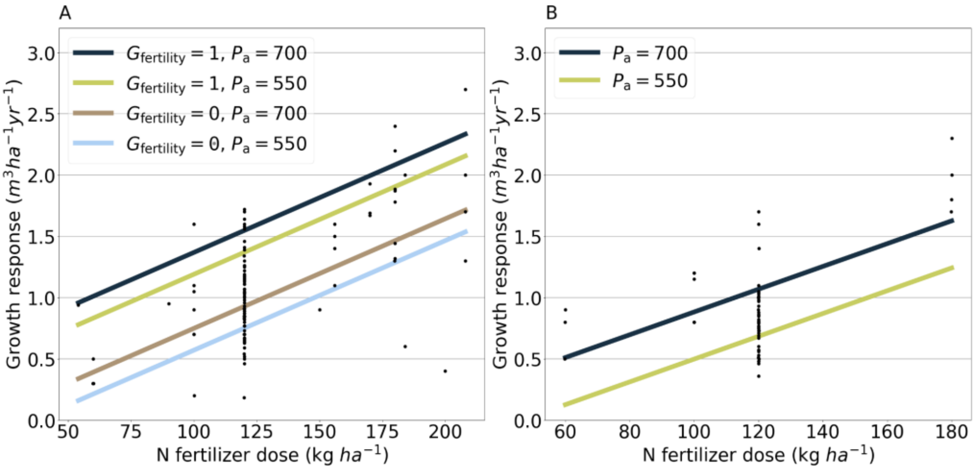

Figure 5. Mean annual volume growth responses to applied N fertilizer dose. Dots represent measured volume growth responses and lines are modelled volume growth responses (Study **I**, Table 5). Panel A shows volume growth responses of Scots pine in different annual precipitation (P_a) and site fertility levels ($G_{fertility}$). P_a values represent conditions in Northern Finland (green and light blue lines) and Southern Finland (blue and brown lines). $G_{fertility}$ value 1 (blue and green lines) indicates that the stand represents mesic heath forest (*Myrtillus*-type, MT) and 0 (brown and light blue lines) combined sub-xeric heath forest (*Vaccinium*-type, VT) and xeric heath forest (*Calluna*-type, CT) (Cajander 1949). Panel B shows Norway spruce volume growth responses in different annual precipitation (P_a) levels. Time since fertilization (S_F) was set to 10 years in the models for both tree species.

The model of Scots pine volume growth responses also included site fertility, which indicated that the volume growth responses of Scots pine were significantly higher in mesic heath forest (*Myrtillus*-type, MT) compared to the less fertile site types (Fig. 5). The best model for Scots pine explained 55% of the variation in volume growth responses and for Norway spruce 51% (**I**). Site type was not included in Norway spruce models because all the stands were from mesic heath forest (*Myrtillus*-type, MT) sites (Study **I**). The volume growth response in Norway spruce sites was of similar magnitude as the volume growth response in sub-xeric heath Scots pine forest sites (Fig. 6). There was no significant difference in the Scots pine and Norway spruce volume growth responses between Southern, Middle, and Northern parts of Finland (Fig. 6).

Table 6. Fixed and random effect parameters of linear mixed models in study **I** for Scots pine and Norway spruce volume growth responses (m^3 ha^{-1} yr^{-1}) to N fertilization. The models were selected based on smallest AIC-values. β is a coefficient representing the relationship between each variable and dependent variable, SE is standard error, and SD is standard deviation. Variables included in the models are N fertilizer dose (F_N), annual precipitation (P_a), site fertility ($G_{fertility}$), time since fertilization (S_F), and article identification number (A_{id}) as a random effect.

	Scots pine			Norway spruce		
Fixed effects	β	SE	p-value	β	SE	p-value
Intercept	-0.271	0.319	0.399	-1.254	0.598	0.041
F_N (kg N ha^{-1})	0.009	0.001	<0.001	0.009	0.001	<0.001
P_a (mm)	0.001	0.001	0.022	0.003	0.001	0.006
$G_{fertility}$	0.619	0.155	<0.001			
S_F (yrs.)	-0.071	0.013	<0.001	-0.059	0.023	0.086
Random effects	Variance	SD		Variance	SD	
A_{id}	<0.001	<0.001		0.012	0.107	
Residual	0.101	0.318		0.044	0.211	

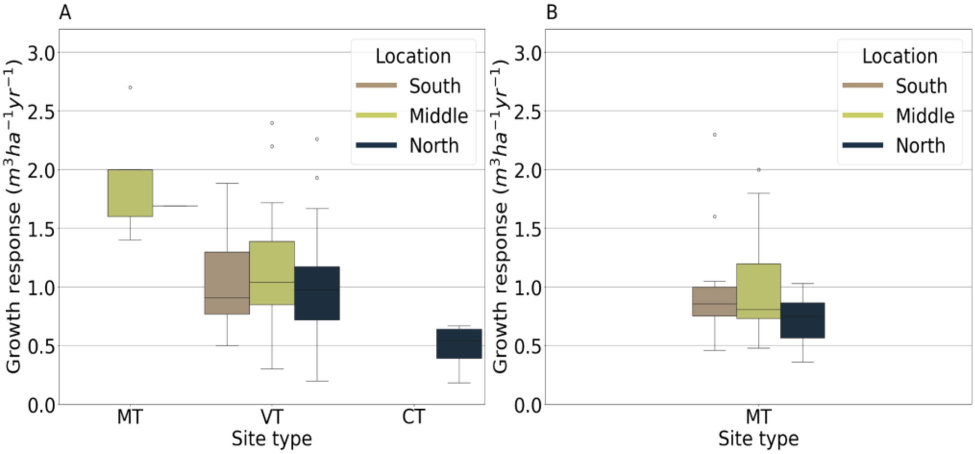

Figure 6. The volume growth response of Scots pine (A) to nitrogen fertilization in different geographical locations and site types in Finland. Site types are mesic heath forest (*Myrtillus*-type, MT), sub-xeric heath forest (*Vaccinium*-type, VT), and xeric heath forest (*Calluna*-type, CT) (Cajander 1949). The volume growth response of Norway spruce (B) in different geographical locations in Finland (data was only available from mesic heath forest (MT) sites).

3.2 Fertilization-induced changes in ground vegetation

Before fertilization the moss cover in all of the research sites (**II**) was on average 41–54% and the herbaceous species covered 16–21%. The dwarf shrub cover was larger in Scots pine sites, covering 19% and 31% of the area, than in Norway spruce sites, where the cover was on average 5–9%. In total, 76 different species were found during the study period. Before fertilization there were 45 different vascular plant and moss species in Liperi, 27 in Ilomantsi, 33 in Juuka, and 50 in Savonranta. After fertilization in 2021, one to four species less were observed from all research sites except from Liperi where the amount of species remained the same. In the final measurement year slightly more species were found in Scots pine stands (Liperi 46 species, Ilomantsi 29 species) after N fertilization, whereas the number of species slightly decreased or remained the same in the Norway spruce stands (Juuka 33 species, Savonranta 46 species). Although the number of the species remained almost the same after the fertilization, the species found from the research areas changed to some extent.

All the research sites represented mesic heath forest (*Myrtillus*-type, MT), however, there were differences in the species composition between the research sites. Liperi and Savonranta were more grass and herb dominated compared to Juuka and Ilomantsi. In Juuka, the dominant plant group was mosses, whereas in Ilomantsi the dwarf shrubs *V. myrtillus* and *V. vitis-idaea* dominated the research site.

The evenness of fertilization varied between the research sites (Table 3). In Scots pine dominated Liperi and Ilomantsi research sites the range of N fertilizer doses (109–369 kg N ha^{-1}) were closer to the target doses compared to the N fertilizer doses in Norway spruce dominated Juuka and Savonranta (48–441 kg N ha^{-1}).

The total cover of ground vegetation decreased after fertilization, however, the reactions to N fertilization were different between the plant groups (**II**). The cover of herbaceous plants increased; especially the cover of grasses increased with increasing N fertilizer dose. There were only minor changes in the cover of dwarf shrubs; only in Savonranta there was significant decrease in dwarf shrub cover with increase in N fertilizer dose (Table 7). Substantial decrease in moss and lichen cover was observed in all research sites, and the decrease was more evident with higher N fertilizer doses. However, the cover of mosses decreased also in the unfertilized control plots. According to the adjusted p-values, only statistically significant changes occurred in the herbaceous plant group (Table 7). In Ilomantsi and Savonranta the total cover of all herbaceous plants increased, whereas in Juuka only the increase in grass cover was statistically significant. The N fertilization did not cause changes in Liperi according to the adjusted p-values. Competition with the trees did not have an impact on the changes in ground vegetation cover.

Further analysis on the mean cover of the vegetation groups on a plot level using linear mixed models revealed similar statistically significant trends of increasing covers of herbaceous plants in Ilomantsi, Juuka and Savonranta as the simple linear regression models (Table 8). However, based on the adjusted p-values, N fertilization did not cause changes in any of the mean covers of ground vegetation on a plot level.

Table 7. The change in the covers of ground vegetation groups on a subplot level expressed as slopes (β1, Eq. 2) from linear regression analysis. The slope indicates how the arcsine square-root–transformed ground vegetation cover changes in relation to the amount of nitrogen applied (Mg ha^{-1}). Negative slopes indicate decreasing cover and positive slope increasing cover. Statistically significant slope values ($p<0.05$) are indicated with letters a, b and c. The different letters represent p-values adjusted with different methods.

Plant groups	Liperi (Pine)			Ilomantsi (Pine)			Juuka (Spruce)			Savonranta (Spruce)		
	2018–2021	2018–2022	2021–2022	2018–2021	2018–2022	2021–2022	2019–2021	2019–2022	2021–2022	2019–2021	2019–2022	2021–2022
Herbaceous plants	0.11	0.04	-0.08	0.56^{abc}	0.36^{a}	-0.08	0.12	0.21	0.09	0.39^{ac}	0.50^{ac}	0.11
Grasses	-0.42^{a}	-0.50^{a}	-0.08	0.35^{ac}	0.19^{a}	-0.08	0.32^{ac}	0.38^{a}	0.07	0.20^{a}	0.14	-0.06
Herbs	-0.08	0.18	0.26^{a}	0.32^{ac}	0.28^{a}	0.02	-0.12	-0.04	0.08	0.08	0.15	0.07
Pteridophytes	0.48	0.27	-0.21	0.03	-0.02	-0.02	-0.08	-0.08	0.00	0.22^{a}	0.38^{a}	0.16
Dwarf shrubs	-0.25	-0.39	-0.15	0.00	0.01	0.18	-0.04	-0.02	0.02	-0.05	-0.18^{a}	-0.12^{a}
Mosses	-0.39	-0.23	0.13	-0.55	-0.57	0.11	-0.60^{a}	-0.29	0.30^{a}	-0.08	-0.29	-0.21

[a] Significant un-adjusted p-value. [b] Significant adjusted p-value corrected with Holm (1979). [c] Significant adjusted p-value corrected with Benjamini and Hochberg (1995).

Table 8. The change in the mean covers of ground vegetation groups on a plot level expressed as slopes from linear mixed effect models. The slope indicates how the arcsine square-root–transformed ground vegetation cover changes in relation to the amount of nitrogen applied (Mg ha^{-1}). Negative slopes indicate decreasing cover and positive slope increasing cover. Bold text represents statistically significant slope values ($p<0.05$) are indicated with letters a, b and c. The different letters represent p-values adjusted with different methods.

Plant groups	Liperi (Pine)			Ilomantsi (Pine)			Juuka (Spruce)			Savonranta (Spruce)		
	2018–2021	2018–2022	2021–2022	2018–2021	2018–2022	2021–2022	2019–2021	2019–2022	2021–2022	2019–2021	2019–2022	2021–2022
Herbaceous plants	0.16	0.12	-0.05	0.58[a]	0.66[a]	0.02	0.26	0.38	0.15	0.45[a]	0.55[a]	0.09
Grasses	-0.40	-0.48	-0.07	0.47[a]	0.48	0.01	0.33[a]	0.45[a]	0.06	0.31a	0.23	-0.07
Herbs	0.14	0.36	0.21	0.29	0.39	0.07	-0.08	0.01	0.08	0.07	0.10	0.02
Pteridophytes	0.47	0.22	-0.27	0.05	0.03	-0.02	-0.12	-0.07	0.03	0.35[a]	0.57[a]	0.22
Dwarf shrubs	-0.23	-0.36	-0.10	0.02	-0.10	-0.05	-0.06	-0.05	0.004	-0.08	-0.21	-0.13
Mosses	-0.27	-0.20	0.08	-0.63	-0.43	0.27	-0.51	-0.13	0.25	0.005	-0.16	-0.15

[a] Significant un-adjusted p-value. [b] Significant adjusted p-value corrected with Holm (1979). [c] Significant adjusted p-value corrected with Benjamini and Hochberg (1995).

4 DISCUSSION

4.1 Stand volume growth after fertilization

It has been known for a long time that N fertilization increases stand growth (Viro 1965). Fertilization has been a part of forest management in Finland for decades, and over the years, the quality, production, and application logistics of fertilizers have developed and improved the profitability (Saarsalmi and Mälkönen 2001; Pukkala 2017; Muhonen et al. 2025). Increased stand growth after N fertilization was evident in study **I;** and the volume growth response increased with increasing N fertilizer dose. The relationship between the N fertilizer dose and volume growth response appeared to be linear up to 208 kg N ha^{-1}. Some previous studies indicate that the growth response saturates with N fertilizer doses exceeding 250 kg N ha^{-1} and additional fertilizer above this limit does not increase the stand growth anymore (Kukkola and Saramäki 1983). Higher N fertilizer doses were excluded from the study **I** because all the higher N fertilizer doses were achieved with multiple applications and study **I** focused on the effects of a single N fertilizer application.

As was hypothesized, the N fertilizer dose explained the majority of the variation in the volume growth responses. However, N fertilizer dose did not explain all the variation. The large variation in the volume growth responses was evident especially in the stands fertilized with 120 kg N ha^{-1}. There were 149 stands fertilized with 120 kg N ha^{-1}. The number of studies with 120 kg N ha^{-1} was high because it was the recommended fertilizer dose in practical forestry during the 1960s (Laakkonen et al. 1983). The substantial variation in the volume growth responses with one N fertilizer dose may be due to differences in stand characteristics and climate conditions. In addition to the N fertilizer dose, the best linear mixed models in study **I** included annual precipitation and time since fertilization as explanatory variables. The model for Scots pine volume growth response also included site fertility as an explanatory variable.

Selection of the mean annual precipitation over effective temperature sum in the best performing linear mixed models in study **I** was unexpected. Effective temperature sum describes the length of the growing season, which regulates the stand growth in the boreal region together with the length of the photoperiod (Jarvis and Linder 2000; Singh et al. 2017). However, precipitation and effective temperature sum are strongly interlinked environmental factors in Finland; and they both have negative correlation with latitude. The mean annual precipitation in our models likely acted as a proxy variable for geographical location. Precipitation best explained the variation in the data because there is also variation in the annual precipitation patterns between Eastern and Western Finland, and thus precipitation may have better described the location of the fertilized stands than effective temperature sum and latitude. However, because the latitude and effective temperature sum did not have a large impact on the volume growth responses, it is possible that the annual precipitation, and water availability, influence the magnitude of the volume growth response more than location. The N fertilization has been shown to increase stand growth more accompanied with higher precipitation and good water availability (Lim et al. 2015). Nitrogen fertilization increases the stand water use because N fertilization increases needle mass, which in turn increases transpiration and interception evaporation (Choi et al. 2005; Ge et al. 2011). Site-specific weather data covering the study period could have improved the explanatory power of the models, however, such detailed weather data was rarely reported in the studies predating the 1990s.

In Finland, N fertilization is recommended for mesic heath and sub-xeric heath forest (*Myrtillus*-type MT, and *Vaccinium*-type VT, Cajander 1949) sites with medium fertile to medium poor nutrient conditions (Äijälä et al. 2019). This has become established practice in forest management because fertilization is economically most profitable in these site types (Pukkala 2017). The volume growth responses in study **I** were highest in MT Scots pine stands, which may indicate that this type of forests are best suited for a single N fertilization following the current forest management recommendations (Äijälä et al. 2019). However, the relatively small sample size of Scots pine MT-sites may decrease the reliability of the comparison with other site types and Norway spruce. Positive but smaller volume growth responses were observed also from other less fertile site types (**I**) but the lack of data from different site types hindered the analysis. Nitrogen fertilization is known to significantly increase stand growth also in less fertile sites (Palvi et al. 2025); however, different N fertilizer doses and multiple application times may be required to achieve larger growth responses. The volume growth responses in MT Norway spruce forests were similar to volume growth responses of Scots pine forests in VT-sites. Similar results have been observed previously (Pettersson 1994). This implies that the volume growth responses of Scots pine and Norway spruce are different.

Nitrogen fertilization increases both Scots pine and Norway spruce volume growth, however, some differences in the duration and magnitude of the volume growth responses exist (Kukkola and Saramäki 1983). Although there were some differences between the Scots pine and Norway spruce datasets, the results of study **I** indicate that with the range of N fertilizer doses used in the study, the Norway spruce volume growth response was smaller than that of Scots pines. The reason behind the species-specific volume growth responses is probably different nutrient requirements of Scots pine and Norway spruce. Norway spruce requires more N than Scots pine to sustain the needle mass because the needle biomass and needle N concentrations of Norway spruce are higher than in Scots pine (Palviainen and Finér 2012). Therefore, Scots pine is likely able to increase the volume growth more efficiently with smaller N fertilizer doses. The canopy structure of Scots pine and Norway spruce stands are also different, which may, to some extent, explain differences in volume growth responses between the tree species. Canopy structure can affect the spatial evenness of fertilization (Muhonen et al. 2025). The spatial evenness of the N fertilizer dose in the stand should be considered when predicting the volume growth responses of practical forest fertilization because the N fertilizer dose had a significant impact on the magnitude of the volume growth response (**I**).

The initial stand volume was the only variable describing stand structure in the datasets because it was the most frequently reported stand variable. The growth response to N fertilization has been studied in both mature and seedling stands, and the results have shown that N fertilization in mature forest produces the most economically profitable results (Pukkala 2017; Hiltunen et al. 2021). The initial stand volume did not have an impact on the volume growth responses in study **I**. However, only stands with initial stand volume 50 m^3 ha^{-1} or greater were included in the statistical analyses, and our models are applicable only in stands with volume higher than that. Additionally, most of the articles included in the study **I** did not report detailed descriptions of the forest management history of the stands. This was considered by using the article identification number as a random variable in all of the models. The management history, for example, timing and intensity of thinnings, can produce different growth responses in combination with N fertilization. For instance, combination of N fertilization and thinning has been shown to produce higher growth responses (Haapanen et al. 1979). Thinning itself increases availability of water, light, and nutrients in the forest stand (Vesala et al. 2005), and if the remaining trees are fertilized, the combination of increased resource availability produces larger growth response.

In addition to N fertilizer dose, the properties of the fertilizer are known to affect the growth response. For instance, fertilizers with ammonium nitrate produce higher growth responses than urea fertilizers (Kukkola and Saramäki 1983; Laakkonen et al. 1983). According to Gustavsen and Lipas (1975) urea produces 1 $m^3 ha^{-1} yr^{-1}$ smaller volume growth response compared to other N fertilizers. Ammonium nitrate and urea are water-soluble and contain nitrate which is vulnerable to leaching (Binkley et al. 1999). Slow-release N fertilizers, such as urea-formaldehyde, have been developed to decrease N export to water courses after fertilization (Smolander et al. 2020). The growth responses induced by urea-formaldehyde last longer compared to the fast-releasing N fertilizers (Smolander et al. 2022). The volatilization and leaching of N from fertilizers cause N loss, and consequently, limits the growth responses (Marshall and DeBell 1980; Lundin and Nilsson 2014). The volatilization and leaching losses are influenced by the weather conditions, and therefore, the timing of the fertilization also affects the growth response. Fertilizer application in spring is known to produce higher growth responses than application in other times of year (Viro 1970; Salonen 1973). However, urea fertilizer may benefit from application in autumn or winter (Lipas 1988). The timing of fertilization and chemical fertilizer properties were not included in the study **I**. These variations in study designs may have caused some additional variation in the volume growth responses, and they are accounted for by adding the article identification number as a random variable.

The growth response following N fertilization is known to be transient in time; the N-induced growth response starts to decrease six years after fertilization and ceases after ten years (Kukkola and Saramäki 1983; Pettersson 1994). This was supported by the results of study **I** because the best models predicting volume growth responses included the time since fertilization as an explanatory variable. The parameter estimate for the time since fertilization was negative for both Scots pine and Norway spruce volume growth responses indicating the gradually decreasing growth response. This implies that a single N fertilization with the recommended dose does not transform the forest ecosystem permanently into a more fertile site type. This transient nature of N-induced volume growth response could be attributed to immobilization of the fertilizer N. The majority of the fertilizer N is stored in the needles for two to six years depending on the tree species (Melin et al. 1983). This time period corresponds to the observed peak in the volume growth response (Kukkola and Saramäki 1983; Kellomäki 2022). After the peak, N contained in needle litter, and further forest floor organic matter, becomes gradually available again through microbial mineralization processes, although a large share of N may remain immobilized in the soil for years (Prescott et al. 1992). This is supported by study **II**, where higher N stocks in mor humus layer were observed in the fertilized plots 4 years after fertilization. The fertilizer N can reside in the soil for decades immobilized in the organic matter, thus no longer being available for supporting the stand growth (Melin and Nômmik 1988; Ladanai et al. 2007). Although the stand volume growth response decreases, the residual effects of N fertilization can be observed in soil and ground vegetation of the fertilized stands for decades (Strengbom and Nordin 2008; From et al. 2015).

4.2 Ground vegetation after N fertilization

Ground vegetation covers did not change significantly after N fertilization in study **II**, contradicting results obtained from previous fertilization experiments (Kellner 1993; Mäkipää 1994; Turkington et al. 1998; Strengbom and Nordin 2008; Hedwall et al. 2010). However, the majority of the previous studies report changes in vegetation following repeated N fertilizations or are emulating N deposition, and thus exceeding the N doses recommended in forest management guidelines (Äijälä et al. 2019). The novelty of study **II** was that recommended N fertilizer doses were applied using commercial method of fertilizer application with helicopter and forwarder. Because the evenness of the application was measured, we obtained a range of different N fertilizer doses that actually were supplied to each plot. That enabled the assessment of the linear relationship between the N fertilizer dose and the changes in ground vegetation. The study **II** provided weak support to the hypothesis that changes in plant cover are greatest with the highest N fertilizer dose, and that grasses and herb benefit, whereas mosses suffer from the increased N fertilizer dose. The slopes indicating the cover change in relation to unit N applied (Table 7 and 8) show increase in cover of grasses and herbs and decrease in mosses. However, in the mixed effects models (Table 8), where the hierarchical structure of the data was considered and the adjusted p-values were used, none of the changes were statistically significant. Although the plant group cover changes were not statistically significant in the conservative tests, the direction of the changes deserve further discussion.

The cover of mosses decreased slightly (**II)**, which is in line with previous literature (Kellner 1993; Olsson and Kellner 2006; Strengbom and Nordin 2008). Excess N fertilizer dose may be toxic for mosses because mosses do not have cuticle (Kellner 1993; Salemaa et al. 2008). This could be observed in the research sites as dried patches of moss at locations which received high quantities of N. Another possible mechanism behind the changes in ground vegetation is N-induced competition (Hedwall et al. 2010). Mosses may have had competition disadvantage compared to other species when the N concentration in soil changed. The covers of grasses and herbs increased as well as pteridophytes in some plots in study **II**. This may have changed light, water, and nutrient availability and hindered the growth of mosses (Bergamini and Pauli 2001; van der Wal et al. 2005). Increases in the cover of herbaceous plants in study **II** was in line with previous research (Kellner 1993; van Dobben et al. 1999; Strengbom and Nordin 2008, 2012) as were the mixed responses of dwarf shrubs (Sullivan and Sullivan 2018; Jacobson et al. 2020).

Although there were changes in the covers of grasses, herbs, pteridophytes, dwarf shrubs, and mosses (**II**), these changes were highly dependent on the research site and measurement year. The changes in species covers were mainly caused by annual variation and high spatial variation between and within the research sites. The covers of the ground vegetation species changed similarly in both fertilized and unfertilized plots and the annual variation in weather conditions may have had an impact on the results (Fig. 2 in study **II**). Growing seasons of the measurement years 2018 and 2021 were drier and warmer than the 30-year average (Table 4). This might have had an effect especially on the uniform decline in the moss covers because they are sensitive to the drought (He et al. 2016; Koelemeijer et al. 2024; Zhang et al. 2025). Meteorological conditions from previous years have been also shown to influence the growth of ground vegetation alongside those of the current growing season (Zhang et al. 2025). Heat and drought periods in years before fertilization may have already altered species covers, making the ground vegetation responses in 2021 during the new drought more pronounced.

The optimum growing condition for plants varies based on their ecophysiology; therefore, changes in light, water, and nutrient availability causes alterations in the composition of the plant community (Lavorel and Garnier 2002). In addition to nutrient availability, N fertilization changes the light conditions in the ground vegetation due to the increased needle mass in the canopy (Skrindo and Øland 2002). The effect of increased shading was tested using a competition index calculated using the trees growing in each plot in study **II**, however, this did not have a significant effect on any of the plant group covers. Hedwall et al. (2010) obtained similar results of the effects of canopy cover on the cover of mosses, however, changes in canopy cover affected the covers of vascular plants. Because the effects of N fertilization on the stand growth are known to last at least six to eight years (Kukkola and Saramäki 1983), it is possible that the effect of shading could be seen later in the fertilized plots. However, Rajaniemi (2002) noted that changes in light conditions alone does not explain the changes in vegetation following N fertilization. The uniform changes in ground vegetation cover regardless of the N fertilizer dose can be partly explained by the thinnings made four to eight years prior to N fertilization. Because thinning improves the light conditions for ground vegetation (Lieffers et al., 1999), the ground vegetation at all research sites has likely responded to thinning and is now gradually shifting back as increasing canopy cover reduces light availability.

All research sites represented *Myrtillus*-type (MT) vegetation (Cajander 1949), but species composition varied both between research sites and at a smaller spatial scale within each research site. These differences already existed before fertilization, reflecting how fine-scale variation in microclimate and nutrient availability influences the composition and diversity of ground vegetation (De Frenne et al. 2021; Buness et al. 2025). Such small-scale heterogeneity highlights the need for longitudinal studies with vegetation inventories conducted both before and after fertilization and underlines the limitations of studies comparing fertilized and unfertilized sites only after fertilization treatment. Furthermore, the generalizability of the results of study **II** may be limited by the low number of research sites that are located in Eastern Finland only. However, the stand age, site types and tree species represent well the typical N fertilized forest stands in Finland.

4.3 Implications for forest management

Traditionally N fertilization in forests has been used to increase wood production in the boreal region (Saarsalmi and Mälkönen 2001; Hedwall et al. 2014), but in recent years, benefits of increased stand growth have been assessed from the climate change mitigation perspective (Hynynen et al. 2024). Currently, the standard fertilization practice in Finland is to apply 150 kg N ha^{-1} once or twice towards the end of the rotation period (Äijälä et al. 2019). The fertilized land area was 47 910 ha in 2024 (Fig. 1). Fertilized land area has increased in recent years compared to 1990s (Fig. 1), and Hynynen et al. (2024) calculated that increasing the annually fertilized land area further to 95 000 ha has potential to increase the annual forest volume growth by over million cubic meters. This would mean an additional 917 500 tonnes of CO_2 stored into the tree biomass annually (IPCC 2006). In addition to the tree stand growth related C benefits, N fertilization has been shown to increase the soil C stocks especially with high N fertilizer doses (Mäkipää 1995). Another option to increase forest growth and C sequestration would be to increase the N fertilizer dose. This was supported by the results of study **I** because increase in N fertilizer dose produced higher volume growth responses at least until 200 kg N ha^{-1}.

Although the N fertilizer production and application logistics produce CO_2 emissions, they are compensated by the increased C sequestration in the trees and soil following N fertilization (Sathre et al. 2010). Nitrous oxide emissions can negate the potential climate benefits, however, the increase in N_2O emissions is observed to be minimal after forest N fertilization (Håkansson et al. 2021). There has been a concern that N fertilization affects biodiversity (Kellner 1993; Strengbom and Nordin 2008). Study **II** indicated that N fertilization caused only minor changes in the cover of ground vegetation species. Thus, the effects of N fertilization on ground vegetation biodiversity were smaller than predicted in previous studies (Kellner 1993; Strengbom and Nordin 2008), when the fertilization was done with the current forest management recommendations (Äijälä et al. 2019). Because the changes in ground vegetation were more pronounced with higher N fertilizer doses (**II**), increasing fertilized land area instead of increasing the N fertilizer dose, to obtain the climate benefits, may be more beneficial for the ground vegetation. However, the duration of study **II** was only 3–4 years and the long-term effects are still unclear.

The majority of the previous forest fertilization research is based on the goal of N fertilization increasing the stand volume growth and the following economic benefits (Äijälä et al. 2019). Hiltunen et al. (2021) found that simultaneously maximizing both climate and economic benefits of N fertilization was not feasible; and the N fertilization in mature stands following the current fertilization recommendations produced the smallest climate benefits. Therefore, more research is needed to find the N fertilization practices able to maximize C sequestration and C stocks in boreal forests. The climate benefits of increased forest growth can be prolonged by using the wood to long lasting end-products and recycling the wood as long as possible (Pingoud et al. 2010; Hiltunen et al. 2021). Most of the long-lasting end products have certain requirements for wood quality (Malesza 2015). Because N fertilization increases the growth rate of trees (Kukkola and Saramäki 1983), the impacts of N fertilization on wood quality has been studied. Increased growth rate can be observed as wider growth rings and decreased wood density in late-wood (Akello et al. 2024). However, Mäkinen and Hynynen (2014) have shown that N fertilization did not substantially decrease the wood quality of Scots pine.

As described earlier, climate conditions affected the volume growth responses caused by N fertilization (**I**) and annual weather conditions may have substantial impact on the ground vegetation. This highlights the need to understand the interactions between N-fertilization-induced changes in the ecosystem and the climatic conditions. More research on the topic is needed because climate change causes drastic changes in the weather conditions, especially in higher latitudes (IPCC 2023). Fertilization as a climate change mitigation solution has been discussed (Hynynen et al. 2024); however, fertilization may have potential to be also used as an adaptation method in locations where the possible negative environmental effects are not a concern. Because low N availability in boreal soils limits the stand growth, N fertilization can be used to enable the stand growth to adapt to the higher atmospheric CO_2 concentrations (Norby et al. 2010). Additionally, frequency of disturbances is expected to increase because of climate change (IPCC 2023). Therefore, impacts of N fertilization on the forest resilience in boreal conditions should be investigated because nutrient management has been shown to shorten recovery time after disturbances (Herbert et al. 1999). However, the effects of N fertilization in changing climate may not all be beneficial. For example, the occurrence of dry periods is expected to increase with increasing temperatures (IPCC 2023), which together with the N-fertilization-induced increase in transpiration may increase drought susceptibility of Norway spruce stands (Nilsen 1990; Ge et al. 2010).

More targeted fertilization practices, tailored to specific site conditions, can help to minimize N leaching, greenhouse gas emissions as well as changes in biodiversity following N fertilization (Fardusi et al. 2017). While fertilization has the potential to significantly boost C sequestration (Mäkipää 1995; Jörgensen et al. 2021), its overall feasibility depends on economic, ecological, and operational factors. The balance between the costs of implementing N fertilization and the benefits, including increased stand growth and C stocks, must be carefully evaluated; but the information on the topic is currently lacking. More research is needed to understand small-scale variations in N cycling, retention and transport in soil, soil microbial responses, and their interaction with N fertilizer to enable more precise nutrient management. Because the research has traditionally focused on the economic feasibility of N fertilization, there is a lack of information on the effects of N fertilization on a wide range of different tree species and site conditions. For instance, only few studies report the effects of N fertilization from mixed-species stands (Niemistö 2022), or more, or less fertile sites where the N fertilization is currently recommended (Palvi et al. 2025). Therefore, more research is needed in order to evaluate the climate change mitigation potential of N fertilization in boreal forests.

5 CONCLUSIONS

Nitrogen fertilization significantly increases stand volume growth in boreal Scots pine and Norway spruce stands, and the magnitude of volume growth response varies with N fertilization intensity, site fertility, precipitation, and time since application. Nitrogen fertilization may slightly alter ground vegetation composition by decreasing moss cover while increasing herbaceous species, in areas receiving higher N fertilizer doses. The results indicate that a single N fertilization made following current management recommendation has a smaller impact on the ground vegetation than previously expected. Annual variation in meteorological conditions may have a larger effect on the ground vegetation than N fertilization shortly after fertilization. The results provide information for site-specific and ecologically informed fertilization practices that optimize stand growth benefits while minimizing the changes in biodiversity. The evenness of the N fertilization made with helicopter or forwarder should also be considered when the impacts of N fertilization is evaluated because variations in the applied N fertilizer doses are reflected in the ground vegetation and stand growth. More fertilization research from a wider range of different stands is needed to consider the viability of N fertilization as a climate change mitigation tool.

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