Forest Ecology and Management 563 (2024) 121967

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Diminishing legacy effects from forest fertilization on stand structure, vegetation community, and soil function

Marcus Larsson [a,*], Joachim Strengbom [c], Michael J. Gundale [b], Annika Nordin [a]

[a] Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology, 901 83 Umeå, Sweden
[b] Swedish University of Agricultural Sciences, Department of Forest Ecology and Management, Umeå 901 83, Sweden
[c] Swedish University of Agricultural Sciences, Department of Ecology, Uppsala 750 07, Sweden

ARTICLE INFO

Keywords:
Forest fertilization
Forest growth
Vegetation community composition
Mineralization
Soil organic carbon
Ion-exchange resin

ABSTRACT

While there is consensus that fertilization with nitrogen (N) is a cost-effective way of increasing both forest biomass yield and timber harvest profitability, the strength and longevity of legacy effects are debated. To quantify legacy effects of past fertilization, we analysed 21 mixed *Pinus sylvesteris* and *Picea abies* stands. The stands, on average 23 years old at the time of this study, were either unfertilized (n=7), fertilized with 150 kg N ha^{-1} once 36 years ago (n=7), or twice, 45 and 36 years ago, respectively (n=7), during the previous stand rotation. We performed measurements on soil N mineralisation and N availability, forest growth, ground vegetation community composition, soil and vegetation C/N ratios and soil C and N stocks, many of which responded to legacy N fertilization earlier in stand development. Our results show that the legacy effects of fertilization during the previous stand rotation have diminished through time, indicating an eventual convergence of stand properties. Specifically, all significant effects present in the previous measurement period (over a decade ago), were weaker or completely absent in the current study (i.e. 36 years after fertilization and 23 years after initiation of the new stands). None-the-less, this indicates a longer legacy effect of N fertilization than what is normally considered and suggests that care should be taken to mitigate unwanted, long-term effects when utilizing N addition to promote tree growth in boreal forests.

1. Introduction

Plant growth in northern boreal forest ecosystems is generally limited by low availability of N (Binkley and Högberg, 2016). This makes fertilization with N an attractive way of increasing forest biomass yield (Nohrstedt, 2001), which can increase timber harvest profitability by up to 15 % (Jacobson and Pettersson, 2010). About 40 000 ha of Swedish forest is fertilized annually ("measures in forestry", 2023) and while this area only represents a small part of the available productive forest land (> 20 million ha) in Sweden, there is potential for a more widespread and/or intensive use of forest fertilization (Bergh and Hedwall, 2013). The standard fertilization dose utilized in Nordic forestry is 150 kg N ha^{-1}, added once or twice late in the forest rotation, which often results in an approximately 30 % increase in biomass growth, increased N concentrations in needles, and potential effects on N leaching, changes in understory diversity, and alterations to soil C cycling processes (Mayer et al., 2020; Nohrstedt, 2001). While the impacts from standard doses normally are considered to last no more than 10 years, long term changes (i.e. > 10 years) usually only occur under more intensive fertilization (Nohrstedt, 2001). However, a few studies have reported that even standard forest fertilization practices can have legacy effects that impact the forest ecosystem properties and processes at the start of the next rotation. For example From et al., (2015) showed increased growth of young trees in stands fertilized with standard N doses during the previous forest generation, as well as changes in the species composition of the ground vegetation (Strengbom and Nordin, 2012, 2008). Furthermore, extractable soil ammonium (NH_4-N) and nitrate (NO_3-N) were found to be higher in previously fertilized stands, indicating higher rates of N mineralization and mobile soil NH_4-N and NO_3-N, than in stands that were not previously fertilized (From et al., 2015). Hence, these studies suggested that standard fertilizer additions in boreal forests may induce legacy effects on vegetation growth and N cycling.

While the potential to increase forest growth is attractive, N addition also has the potential to induce vegetation changes that negatively affect biodiversity (Bobbink et al., 2010, 1998; Midolo et al., 2019). The N

* Corresponding author.
E-mail addresses: marcus.j.larsson@slu.se (M. Larsson), michael.gundale@slu.se (M.J. Gundale).

https://doi.org/10.1016/j.foreco.2024.121967
Received 9 February 2024; Received in revised form 3 April 2024; Accepted 2 May 2024
Available online 14 May 2024

enrichment levels which an ecosystem can tolerate without suffering significant harmful effects according to present knowledge (i.e. the N critical load; Nilsson and Grennfelt, 1988) is suggested to occur in boreal forest understory vegetation at levels as low as 6 kg N ha^{-1} yr^{-1} (Nordin et al., 2005) and the effects often intensify with increasing N loads (Midolo et al., 2019). Rare species (Suding et al., 2005) such as orchids, (e.g., *Calypso bulbosa*), or areas with low background N deposition are also often impacted to a larger degree than common species or areas exposed to comparatively higher rates of background N deposition (Hedwall et al., 2013). Changes in species composition could also arise through indirect N addition-effects such as changes in the light environment (Strengbom et al., 2004), or altered susceptibilities to natural enemies such as pathogenic fungi (Nordin et al., 2006; Strengbom et al., 2002).

The increase in forest productivity following fertilizer additions can also lead to increased soil carbon accumulation, beneficial for the mitigation of atmospheric CO_2 (Friedlingstein et al., 2020; Hyvönen et al., 2008; Johnson and Curtis, 2001; Jörgensen et al., 2021). This effect is mainly due to the increased production of above and below-ground plant litter, and shifts in the soil microbial community, hampering soil organic matter decomposition (Forsmark et al., 2021; Haas et al., 2018; Jörgensen et al., 2022; Maaroufi et al., 2019, 2015). However, the majority of results demonstrating impacts of N additions on soil carbon accumulation in boreal forests stem from experiments using either large doses of N applied a single time, or small doses added repeatedly during long periods of time (Forsmark et al., 2020; Huang et al., 2011; Hyvönen et al., 2008; Maaroufi et al., 2015; Olsson et al., 2005). It remains unclear whether standard forest fertilization regimes used by the forest industry, (i.e., one or two "standard" dose applications during late rotation) result in long-term increases in soil carbon storage. Therefore, to make informed decisions regarding fertilization practices, there is a need for improved understanding of the strength and longevity of any unintended legacy effects that may arise from it.

In this study we utilize a study system situated in the boreal forest of mid-Sweden, designed to represent standard fertilization practices in accordance with the guidelines recommended by the Swedish Forest Agency ("measures in forestry" 2023). We evaluated whether a one or two-time application of 150 kg N ha^{-1} at the end of the previous stand rotation resulted in long term legacy effects on both above and below-ground forest properties 36 years since fertilization and 23 years into the current forest rotation. Legacy effects in this study system were initially reported by Strengbom and Nordin, (2012, 2008), and (From et al., 2015), approximately 10 years after the new stands were initiated. At c. 23 years of age, the stands have now reached canopy closure, which may have consequences for how forest properties and processes are affected by legacy N. In addition to follow up measurements of tree growth, N mineralization and extractable soil N, and ground vegetation species composition, effects on soil carbon were also examined.

We tested the following hypotheses:

That fertilization would have a legacy effect on:

1. soil N cycling process, such that previously fertilized stands would exhibit higher net mineralization rates and higher amounts of mobile soil NH_4-N and NO_3-N. We expected this because a previous study from the same experimental system showed nearly four times higher soil N mineralization rates on fertilized sites compared to the control (From et al., 2015).
2. tree growth during the current stand rotation, where fertilized stands would exhibit larger basal area, height growth, and volume. We expected this because a previous study from the same experimental system showed on average 25 % higher trees on fertilized sites compared to the controls (From et al., 2015).
3. understory plant community composition and foliar N content, such that previously fertilized stands would show greater abundance of nitrophilic species (e.g., graminoids), and higher foliar N contents. We expected this because a previous study from the same experimental system showed that species composition and foliar N content of stands that had been fertilized were separated from the controls (Strengbom and Nordin, 2008).
4. soil C and N, such that previously fertilized stands would exhibit larger soil C and N stocks.

Testing these hypotheses in combination will provide valuable information regarding the persistence of legacy effects stemming from standard N fertilization practises in boreal forests, which may help optimise future forest management practises to maximise biomass growth, while simultaneously avoiding unwanted side-effects.

2. Materials and method

2.1. Study area

Data used in this analysis was gathered from 21 forest stands, each sized between 4.7 and 22.4 ha spread out over an 8500 ha forest land area in the middle boreal zone (Ahti et al., 1968) in central Sweden (62°58 "N, 16°40"E). The studied stands either had, or had not, been subjected to N fertilization before harvest and regeneration. Control (C) stands ($n = 7$) were never fertilized, N1 stands ($n = 7$) were fertilized with 150 kg N ha^{-1} once in 1985, and N2 stands ($n = 7$) were repeatedly fertilized with 150 kg N ha^{-1} in 1977 and 1985; thus, our study included 7 stands for each treatment (Table 1). Fertilizer N was added as granules of ammonium nitrate (NH_4NO_3) spread by tractor or aircraft. The forest land, currently owned by the forest company SCA (*Svenska Cellulosa Aktiebolaget*) was at the time of stand selection owned by the Swedish state-owned company, Sveaskog. The initial stand selection done in 2008, see From et al., (2015) was based on information describing the stands before clear-cut, originating from Sveaskog's forest inventory. Care was taken to select the stands with similar initial productivity indices, elevation, temperature sum (growing degree days; Womach, 2005), slope (forest floor incline from 1 (<10 % inclination) to 5 (>50 %), tree species composition, soil conditions and stand age at the time of site selection. Further details of the study system are found in (From et al., 2015; Strengbom and Nordin, 2008).

The annual precipitation in the area is between 500 and 600 mm per year, and the atmospheric background N deposition ranges from 1.6 to 2.4 kg ha^{-1} $year^{-1}$ (Karlsson and Hellsten, 2022). All stands used in the study had mesic site conditions with Udic moisture regime and soil were Typic Haplocryods developed on glacial till with an organic surface

Table 1
Number of stands per treatment, site index (SI), elevation (above sea level, a.s.l.), temperature sum (GDD) and forest floor slope. The stands were fertilized once in 1985 (N1) with 150 kg N Ha-1, twice (N2), both in 1977 and 1985 with 150 kg N Ha-1 or never fertilized (C).

Stands (n)	Control 7	N1 7	N2 7	*F*-value	*p*-value
Site index (H100), m)	20.6 ± 0.2	19.7 ± 0.3	20.4 ± 0.3	3.00	0.08
Elevation a.s.l (m)	334 ± 21	358 ± 20	334 ± 17	0.54	0.59
Temperature sum (GDD)	937 ± 6	900 ± 22	923 ± 11	1.59	0.23
Slope (1−5)	2.00 ± 0.22	1.86 ± 0.26	1.72 ± 0.18	0.41	0.67

Note. Table adapted from (From et al., 2015).

layer (O-horizon), sometimes also referred to as plant litter layer, where the upper part is relatively undecomposed and the lower parts were strongly humified (Driessen, 2001; From et al., 2015; Strengbom and Nordin, 2008). The relative abundance of the two dominant species (*Pinus sylvesteris and Picea abies*) prior to clear-felling ranged from 25 % to 75 % with no difference between fertilized and unfertilized stands (Mann–Whitney U-test: $U = 83.5$, $p = 0.348$) (From et al., 2015), and the forest field layer was dominated by dwarf shrubs such as *Vaccinium myrtillus* and *Vaccinium vitis-idaea.,* i.e., all stands were classified as spruce forest of bilberry type (Påhlsson, 1995). All stands were harvested by clear-felling between 1997 and 2000, subjected to soil scarification, and then planted with identical seedling stock of either *Pinus sylvestris* or *Picea abies* at a density of 2200–2300 seedlings ha^{-1}. Today the majority of stands contain a combination of both species and a mix of planted and naturally regenerated trees. Some areas have also been pre-commercially thinned, removing mainly spontaneously regenerated birches that have mixed into the planted conifer seedlings.

2.2. Buried bags and ion capsules

The buried bag technique (Eno, 1960; Gundale et al., 2011) was used to investigate N mineralization in all stands. Between June 15–18, 2021, seven samples from the entire O-horizon in each replicate stand (i.e. 147 samples in total) were collected with a cylindrical (diameter 10 cm) soil corer along 45 m transects passing through the centre of each stand. The depth of the O-horizon (ca. 5–15 cm) made sampling of the entire horizon possible for all 49 samples. After gently removing large roots and the top layer of easily identifiable plant material, half of each sample was put in a plastic bag, put into a cooler and transported back to the lab for analysis. The other half was put into another plastic bag and buried in the organic horizon *in situ*. The buried cores were then collected 85 days later (14–15 of September), transported them to the lab in a cooler, and processed them for analysis. All samples were sieved (2 mm mesh) and then extracted in 1 mol KCL and analysed for NH_4 and NO_3 using an Auto Analyzer 3 spectrophotometer (OmniProcess, Solna, Sweden). Net mineralization was calculated as the difference in NH_4-N and NO_3-N (mg g^{-1} dry weight [DW] soil) between the June and September sample times. Any damaged bags were excluded before estimating mineralization, and before statistical analyses, sub-replicate samples of NH_4-N and NO_3-N from the same stands were pooled to obtain one single value of mineralization per stand, with these stand level values serving as true replicates.

Resin ion-exchange capsules (PST-1, Universal Bioavailability Environment/Soil Test, MT, USA) were used to estimate the amount of soil mobile NH_4-N and NO_3-N (mg/capsule) in all stands. Between the 15–18 of June 2021, six capsules were buried just beneath the bottom of the organic horizon along a transect through each stand center. Later the same year, between the 14–15 of September, all capsules were retrieved, put in plastic bags, and transported to the lab for analysis. In the lab, the ion-exchange capsules were brushed off to get them as clean as possible, and then placed in 50 ml Falcon tubes. Ten ml of 1 mol KCl was then pipetted into the tubes, followed by 30 min agitation. This process was repeated 3 times, resulting in a total of 30 ml sample extracts. The NH_4-N and NO_3-N concentration on these extracts were analysed using an Auto Analyzer 3 spectrophotometer (OmniProcess, Solna, Sweden). Before statistical analysis sub-replicate samples from the same stands were pooled to obtain one single value per stand.

2.3. Tree growth

Data on tree species composition and tree growth were gathered in June 2022. The stands were inventoried by using a square grid randomly positioned over the entire 8500 ha forest area on the map. Each grid cell was 100 × 100 m in size and all grid cell intersections contained within each of the 21 stands on the map were inventoried using circular ($r = 5.64$ m) plots, located during the inventory process with GPS. If a plot randomly landed on a nature conservation set-aside patch originating from the previous stand, it was excluded from sampling. After the removal of these specific sub-plots, a total of 253 sub-plots were inventoried across the whole experiment, divided among the different stands. Each stand was thus inventoried using the same "resolution" but the number of inventoried plots per stand varied depending on the size of the stand (4 plots in the 2.34 ha smallest stand, and 25 plots in the 26.4 ha biggest stand). In every plot, tree species and diameter at breast height (1.3 m.) was measured for all trees taller than 1.3 m. We also measured the height of the tree closest to the plot centre, and one tree in every cardinal direction closest to half the radius of the plots, i.e., 5 samples trees in total within each plot (Gundale et al., 2014). If two trees were equally close to the cardinal points, the clockwise positioned trees were used. As the stands used in this study are actively managed forests, pre-commercial thinning's had been performed in some of the stands since the last measurement in 2010. Pre-commercial thinning is a regular part of the forest management regime in Sweden, performed when the stand height is about 2–6 m (Pettersson et al., 2012) and involves removing selected, mainly young trees that have spontaneously regenerated and serve as competition for the planted cohort. This is done with a handheld motorized brush cutter to allow more development space for the remaining trees. The practice is not to be confused with commercial thinning, which is performed much later in stand development with the aid of a harvester and forwarder-group, and removes a substantial portion of stand basal area. At the time of our measurements, 5 stands in the C-treatment, 4 stands in the N1-treatment, and 3 stands in the N2-treatment had been subjected to pre-commercial thinning, while the rest remained un-thinned. For all variables, sub-replicate values from the same stands were pooled to obtain one true replicate value of average DBH and height per stand. Thus, for all statistical analysis, the stand was considered the unit of replication.

2.4. Ground vegetation and plant foliar chemistry

In July 2021 the vegetation was scored using a modified version of the point intercept method (Jonasson, 1988). We analysed the ground vegetation (vascular plants, bryophytes and lichens) at 200 random points along a 45 m transect through the centre of each stand. At each point we placed a stick (4 mm in diameter) and counted the number of contacts each species made with the stick. In addition, fresh foliage material from 4 different plant species, *Vaccinium myrtillus*, *Picea abies*, *Deschampsia flexuosa* and *Pleurozium scheberi* were also collected along the transects. These four species are common and represent four different groups of plants, i.e., dwarf shrubs, trees, grasses and mosses. For *Vaccinium myrtillus*, *Deschampsia flexuosa*, and *Pleurozium scheberi* fresh foliage material (leaves) were collected from seven random places along each transect while current year shoots from *Picea abies* were gathered from five different trees on or close to the transects. The material was immediately dried in paper bags in room temperature and then dried at 40 C° for 48 h in the lab. The material was then milled and analysed for total N and C concentrations (g/g dry mass) using a Isotope ratio mass spectrometer (DeltaV,Thermo Fisher Scientific, Bremen, Germany) and an Elemental analyser (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). Three samples of *Vaccinium myrtillus* were not included in the final analysis due to processing errors. Before statistical analyses, replicate samples from the same stands and species were pooled to obtain one value of foliar N content per stand and species.

2.5. Soil C and N

The soil C and N content (g g^{-1} dry mass) was sampled in each stand between the 15–18 of June 2021 at seven regular intervals along the same transects used to sample the ground vegetation. The organic horizon was sampled with a cylindrical (diameter 10 cm) soil corer, and the top 10 and 20 cm layers of the mineral soil was collected with a

Table 2
The means (±1 SE, N=7) for total soil N mineralization rates (NH4-N and NO3-N mg g−1 DW soil), total capture of N on ion capsules (NH4-N and NO3-N), tree diameter (cm) at breast height (DBH), and tree height (m), for each treatment. Results for p-values are based on a mixed-effects model ANOVA with treatment used as fixed factor and pre-commercial thinning as a random effects factor.

Treatment	Total mineralization *(N mg g^{-1} DW soil)*	Total soil mobile N *(N mg $capsule^{-1}$)*	DBH *(cm)*	Tree height *(m)*
C	0.188 ± 0.037	0.109 ± 0.009	5.11 ± 0.592	4.41 ± 0.362
N1	0.170 ± 0.030	0.111 ± 0.008	5.71 ± 0.320	5.30 ± 0.259
N2	0.220 ± 0.060	0.133 ± 0.015	5.18 ± 0.511	5.57 ± 0.370
p-value	0.747	0.356	0.386	0.095

metal core sampler (diameter 1.59 cm). The material was put in paper bags and after transport to the lab sieved (2 mm mesh) and then dried at 70 C° for at least 36 h, then stored in room temperature awaiting analyses. The samples where later milled, and total C and N concentration analysed using an Isotope ratio mass spectrometer (DeltaV,Thermo Fisher Scientific, Bremen, Germany) and an Elemental analyser (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). Before statistical analysis, replicate samples of C and N were pooled to obtain one value of concentration per element and stand. We upscaled C and N stocks only for the soil organic layer because many previous studies have shown that mineral soil C and N stocks are unresponsive to N fertilization (Blasko et al., 2022; Forsmark et al., 2020; Maaroufi et al., 2015; Xu et al., 2021). Carbon and N stocks in the organic layer were thus calculated by multiplying the C and N concentrations with the combined dry weight of the pooled samples from each stand, and then upscaled to Mg ha^{-1} using the combined cross-sectional area of the subsamples in each stand. For mineral soils we only analysed C:N ratios.

2.6. Experimental design and statistical analysis

For all statistical analyses the experiment is regarded as a completely randomized design, with each stand serving as the unit of replication. To test for difference in total net mineralization rates (ammonification plus nitrification, N mg g^{-1} DW soil), total soil exchangeable N (NH_4-N + NO_3-N, mg per ion capsule), tree diameter (cm), tree height (m), vegetation C and N status (g g^{-1} dry mass), soil C/N concentrations (g g^{-1} dry mass), and soil C and N stock (Mg/ha) analyses with a linear mixed-effects model ANOVA were performed. Using the fertilization treatments as a fixed factor and the pre-commercial thinning as a random effect accounted for any variation this activity may have caused. If the analysis of variance showed any significant (α=0.05) main effects from the fertilization treatments, Tukey's post hoc test for pairwise comparison was used to further the analysis. Response variables were checked for normality and homoscedasticity with the aid of residual plots, no data transformations were necessary. The analysis of variance (ANOVA) was preformed using the R. lme4-package (Bates et al., 2015).

To describe the differences in ground vegetation community structure between the different fertilization regiments, we used non-metric multidimensional scaling based on Bray-Curtis dissimilarities, using the R-vegan-package (Oksanen et al., 2022) with k=3 and no data transformations. The NMDS was followed by a PERMANOVA based on 9999 permutations using the fertilization treatments as factors. R-studio (version 1.3.1093) software was used for all statistical analyses (R Core Team, 2020).

For all statistical tests we used a terminology suggested in Muff et al., (2022), where different ranges of p-values are reported on a continuum from "little or no evidence" to "very strong evidence". A p-value of 0.0001–0.001 subsequently was interpreted as very strong evidence, a value of 0.001–0.01 as strong evidence, 0.01–0.05 as moderate evidence, 0.05–0.1 as weak evidence, and p-values > 0.1 as no evidence.

3. Results

3.1. Soil nitrogen and forest growth

Our results showed no evidence of any significant legacy effect from the previous forest fertilization on the soil N mineralization rates or mobile N. However, the trees in stands exposed to fertilization twice (N2) during the preceding stand rotation (150 kg N ha $^{-1}$ in 1977 and 1985) were on average 20 % higher than trees in the control stands, suggesting weak evidence of a legacy effect of past N fertilization on tree growth > 35 years after the last fertilization event *($p = 0.095$*; Table 2).

3.2. Ground vegetation

Our results showed no evidence, with one exception of weak evidence, that the ground vegetation was still affected by the previous fertilization(s). The NMDS showed considerable species community overlap between treatments (Fig. 1a), and a related PERMANOVA also provided no evidence (*p=0.636*) that vegetation composition differed between the fertilizer treatments. A complete species inventory list is provided in supplementary Table 1. We did, however, find weak evidence of a difference in foliar N values in dwarf shrubs ($p = 0.09$), but no evidence that the foliar N values in the three other functional groups of plants differed, including trees ($p = 0.32$), grasses ($p = 0.42$), and mosses ($p = 0.55$), (Fig. 1b).

3.3. Soil metrics

We found strong evidence *(p=0.008)* that soil C stocks differed in the organic layer, with lower C stock in the N1 treatment compared to the control and N2-treatment (Fig. 2a). However, no evidence of this effect was found comparing the control and N2-treatment. We also found strong evidence *(p=0.006)* that soil N stocks differed in the organic layer (Fig. 2b). With lower N stock in the N1 treatment compared to the control and higher N stock in the N2 treatment compared to both the N1 treatment and the control stands. Comparison of the soils' C/N-ratios, which was measured at three different depths (organic, 0–10 cm, and 10–20 cm depth; Fig. 2c), indicated no evidence of any effect between treatments.

4. Discussion

The purpose of this study was to assess legacy effects from forest fertilization in rotational forestry. Particularly the focus was to determine whether fertilizer induced effects on some key variables relating to forests productivity and understory species composition persisted following harvest of the fertilized forest stands, i.e. c. 23 years into the new forest rotation. Our data together with the existence of older measurements has given us the opportunity to follow the effects from the original fertilization event in 1977 and 1985 through the forest rotation boundary, and into the canopy closure of the new stand. Previous studies in the same study system had revealed that legacy effects from forest fertilization were present c. 10 years into the new stand rotation.

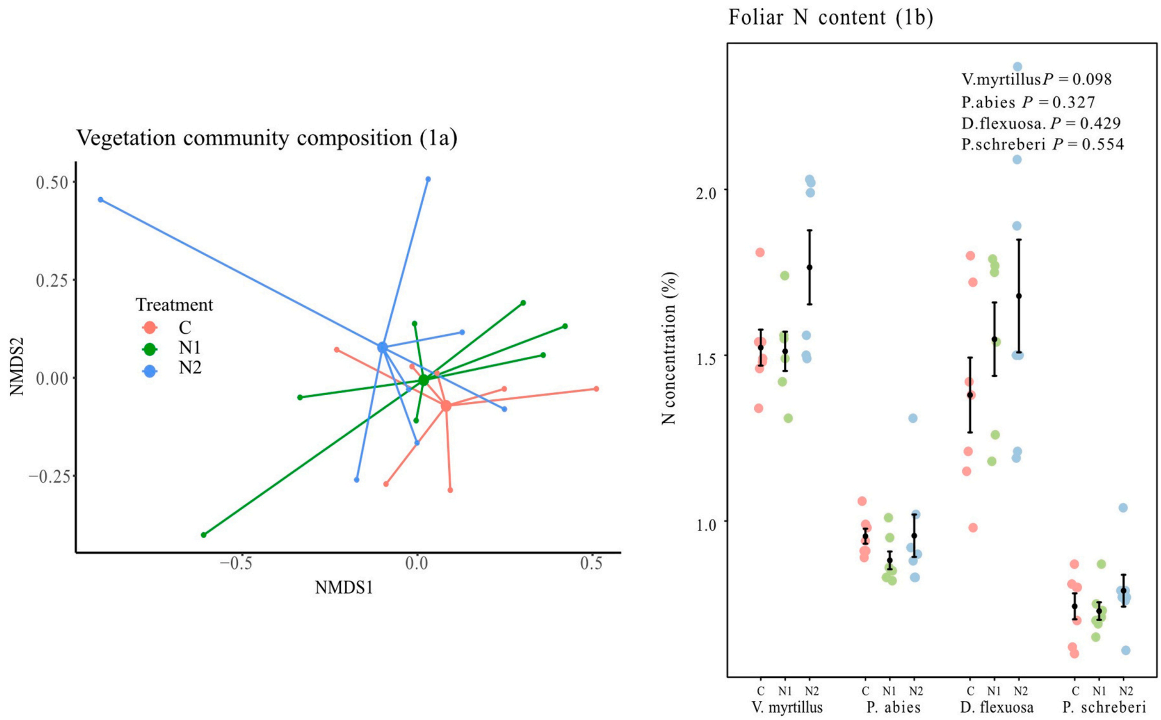

Fig. 1. Left (graph 1a.): Visualization of the NMDS ordination for the ground vegetation community composition among the different treatments. Each coloured "spider" represents a treatment (red = control, green = single nitrogen application, and blue = two nitrogen applications). Data were analysed using PERMANOVA based on 9999 permutations, where no evidence of any effect were present from the fertilization treatments (*p=0.636*). Right *(graph 1b.)* Foliar N content in four different functional groups of plants, bars represent the mean (±1 SE, N=7) for each treatment.

Specifically, the ground vegetation species composition differed due to the fertilization (Strengbom and Nordin, 2008 and 2012), and trees in the fertilized stands had grown higher than those in stands not fertilized (From et al. 2015). Here we revisited the same forest stands > 35 years after the last application of fertilizer, and well into the next forest generation as the trees had become c. 23 years old. We measured the same variables as in previous studies, as well as the carbon and nitrogen stock in the organic soil horizon, which was not measured previously. The combined body of data suggests that subsequent legacy effects from standard forest fertilization both have the potential to last much longer than originally assumed, and also confirms that legacy can persist (> 10 years), but that they appear to diminish over time.

In contrast to our first hypothesis, we detected no differences in mineralization rate between fertilized stands and non-fertilized stands (Table 1). This lack of difference diverges from measurements made earlier in the stand rotation, where mineralization was nearly four times higher in the N2 treatment compared to the control (From et al., 2015). Other long-term studies have also shown a significant decrease in gross N mineralization rate over time, but under much higher N application rates compared to our experiment (Högberg et al., 2014).

In partial support of our second hypothesis, we found weak evidence, but a relatively large effect size (20 % increase), of a legacy effect from N addition on tree height between the control and N2 stands. In the previous study using the same sites, N fertilization showed a similar average effect size of ca. 20 % in tree height between the control and N2-stands, but as the variation among sites then was much smaller, the effect of past fertilization also ended up as statistically significant ($p = 0.026$; From et al., 2015). However, in accordance with the earlier study there was no effect on tree diameter (DBH). Few other studies have evaluated legacy effects of past N addition using N doses that are comparable to the ones used in operational forest fertilization, and to our knowledge, no other study in the northern boreal zone has evaluated the growth response of trees this far in time from the fertilization event. Pettersson and Högbom, (2004) reported an overall (although non-significant) tendency of increased residual tree growth from standard fertilization application rates (150 kg N ha^{-1}), 14–28 years after the last fertilization event but within the same forest generation. Other studies have in contrast reported decreased growth approximately 20 years after cessation of N fertilization compared to controls (Högberg et al., 2014, 2006), however it is worth noting that these results were based on a more intensive fertilization regimen (1350–2160 kg N ha^{-1}) than the standard application rates used in this study. While many factors may help explain the persistent effect of the N2-treatment on growth, and increased foliar N content in dwarf shrubs present, one such factor could be that fertilization offsets the immobilization of N that is often caused by the mycelial biomass and necromass production in N poor soils (Näsholm et al., 2013). This phenomenon has the potential to open up the N cycle to plants (Högberg et al., 2017) and could therefore serve as an explanation for both the still measurable tree growth and the absence of detectable N relative to the control stands in many other measurements. There is however also a possibility that the "excess" N is lost from the system or present in an ecosystem compartment we have not measured.

In contrast to our third hypothesis, we found no difference in ground vegetation community structure or foliar N content, with the exception of weak evidence for a difference in foliar N content in *Vaccinium myrtillus*. Our NMDS showed a considerable overlap in the species composition of the ground vegetation between the treatments (Fig. 1a), and the following PERMANOVA indicated no significant effect. This result contrasts Strengbom and Nordin, (2008) who found a clear distinction in ground vegetation community composition between fertilized and non-fertilized stands in the same study system, as they noted a higher abundance of more N-demanding species on fertilized stands nine years after clear-felling. The following analysis of foliar N content in four functional groups of plants i.e., dwarf shrubs, trees, grasses, and mosses indicated a trend where stands exposed to fertilization showed a higher N content in plant foliage compared to the plants present in the control stands for all functional groups except trees. However, we found no

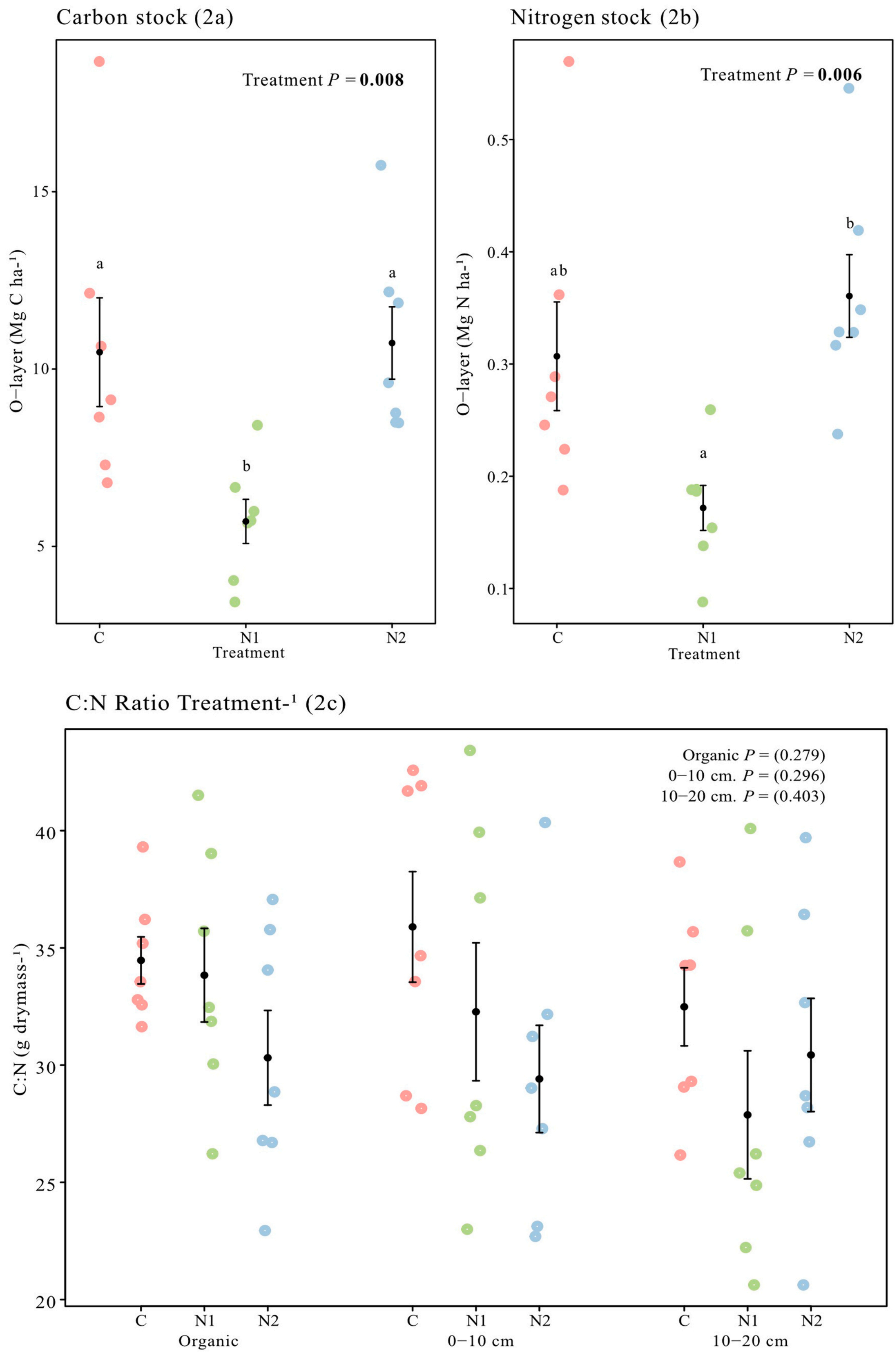

Fig. 2. The left *(graph 2a.)* shows the C stock within the organic layer. The right, *(graph 2b.)* shows the N stock within the organic layer. The bottom figure *(graph 2c)* shows C/N-ratios in three different soil layers for each treatment (organic, 0–10 cm mineral soil depth and 10–20 cm mineral soil depth. Bars represent the different means (±1 SE, N=7).

significant differences, with the exception of weak tendency for a higher foliar N content of the dwarf shrubs. This result differs compared to the analysis made on plant material collected in 2007 (approximately 10 years after clear-felling and 22 and/or 30 years after last fertilization event) where differences in foliar content between treatments could be detected in gathered plant material from all functional groups except mosses (Strengbom and Nordin, 2008). While there is a substantial body of evidence indicating that N enrichment effects terrestrial plant diversity (Bobbink et al., 2010; Sullivan and Sullivan, 2018), long term legacy measurements such as we provide are very rare. A result similar to our study was found by Jacobson, Högbom and Ring, (2020), who reported no effects of fertilizers on ground vegetation diversity 10–34 years after application, although significant differences in ground cover were detected. However their study did not measure legacy effects between subsequent forest rotations, such as we did in our study. The disappearance of a measurable legacy effect could also be due to the ongoing canopy closure. Even if N is the overall growth-limiting nutrient, the decrease in light availability might make the aboveground competition more important than any persisting legacy effect stemming from the N fertilization treatments (Strengbom et al., 2004).

For our last hypothesis, we expected that fertilization would have a legacy effect on soil C and N stocks, with greater stocks occurring in previously fertilized stands. We unexpectedly found evidence of both lower C and N stocks in the organic horizon present in N1 stands (fertilized in 1985) compared to the control and N2-stands, but no difference between N2 stands (fertilized in 1977 and 1985) and the controls for C stocks. When measuring N stocks however the N2-stands showed higher stocks than both the control and N1 treatments, in line with our hypothesis. The reason for this variation in results is not clear but Hasselquist et al., (2012) suggested that responses in boreal forest to added N is not always linear, and that some initial level of N addition could stimulate microbial activity, whereas higher levels may suppress it. Comparing instead the C/N-ratios in three different soil layers (Fig. 2c) resulted in a similar pattern as the foliar N content with lower C/N in previously fertilized stands for all but the deepest soil layer, but despite these apparent trends, no evidence of significant differences was detected. While the soil C and N stock variables do not have an analogous set of older measurements present on the same stands to which we can compare, we note that other studies have shown that anthropogenic N enrichment can increase soil C stocks (Forsmark et al., 2021; Jörgensen et al., 2022; Mäkipää, 1995; Ring et al., 2011) and that higher N input rates appear to increase this effect (Forsmark et al., 2021, 2020; Ring et al., 2011). Studies from more southern latitudes that do report legacy effects between forest rotations also suggests that the forest floor and ground vegetation could act as a nutrient sink for added fertilizer, realising nutrients in subsequent forest rotation and thus increasing forest growth (Subedi et al., 2014). Destruction of the soil organic material instead appear to leave a legacy effect of declining productivity (O'Hehir and Nambiar, 2010). The same type of nutrient sink have been shown to occur in boreal areas (Gundale et al., 2014), and seems to subsists between forest rotations, as illustrated by the slightly higher N stock in the O-horizon in N2 stands present in our experiment. Our study thus addresses a key knowledge gap regarding N fertilization and soil C in northern boreal forests, where studies analysing long-term legacy effects from standard fertilizer application rates are very rare.

5. Conclusion

Based on the results in this study, and in comparison to previous inventories in the same study system (Strengbom and Nordin, 2008, 2012; From, Strengbom and Nordin, 2015), our results indicate that standard N fertilization application rates in boreal forests have the potential to persist much longer than previously reported (i.e., 10 years), but that these effects clearly diminish through time. Sponseller et al., (2016) noted that a disconnect remains between basic research focused on understanding N dynamics and balances in boreal forests, and the applied knowledge needed to sustainably manage these ecosystems. Our study contributes to this important knowledge gap regarding the time-spans over which N fertilization affects boreal forests and suggests that care should be taken when employing N fertilization, given that effects appear to be longer lasting than previously thought. Further research is needed to fully understand what mechanisms are responsible for retention of fertilizer N across stand rotations, and how these vary across forest types (Blasko et al., 2022). Such additional knowledge could be used to avoid applying fertilizers in areas at risk of prolonged legacy effects, and thereby mitigate unwanted long-term effects on the boreal forest ecosystem, while at the same time maintaining the benefits of forest fertilization for increasing biomass growth.

Funding

This work was supported by: Stora Enso AB and Knut and Alice Wallenberg foundation [no.2018.0259].

CRediT authorship contribution statement

Joachim Strengbom: Writing – review & editing, Resources, Methodology, Data curation, Conceptualization. **Marcus Larsson:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Annika Nordin:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Data curation, Conceptualization. **Michael J. Gundale:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Marcus Larsson reports financial support was provided by Stora Enso AB. Annika Nordin reports a relationship with Stora Enso AB that includes: employment. Co-author reports a previous relationship (2016–2020) with Sveaskog AB that included: board membership (A. N.).

Co-author declare no conflicts of interest, and do not have any commercial affiliations (M.J.G. and J.S.).

Data Availability

Data will be made available on request.

Acknowledgments

M.L. acknowledge Adam Björklund and Adreas Edholm for making the field measurements and lab-work possible, along with Jenny Ekman for making the lab-analysis. A.N. acknowledge Stora Enso AB for permitting her leave of absence from her current position with the company to take part in the reported research and supervision. We also want to acknowledge past and current landowners for letting us conduct the study on their land.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121967.

References

Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in northwestern Europe. Ann. Bot. Fenn. 5, 169–211.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 https://doi.org/10.18637/jss.v067.i01.

Bergh, J., Hedwall, P.-O., 2013. Fertilization in Boreal and temperate forests and the potential for biomass production. In: Kellomäki, S., Kilpeläinen, A., Alam, A. (Eds.), Forest BioEnergy Production: Management, Carbon Sequestration and Adaptation. Springer, New York, NY, pp. 95–109. https://doi.org/10.1007/978-1-4614-8391-5_6.
Binkley, D., Högberg, P., 2016. Tamm Review: Revisiting the influence of nitrogen deposition on Swedish forests. For. Ecol. Manag. 368, 222–239. https://doi.org/10.1016/j.foreco.2016.02.035.
Blasko, R., Forsmark, B., Gundale, M.J., Lim, H., Lundmark, T., Nordin, A., 2022. The carbon sequestration response of aboveground biomass and soils to nutrient enrichment in boreal forests depends on baseline site productivity. Sci. Total Environ. 838 https://doi.org/10.1016/j.scitotenv.2022.156327.
Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., De Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecol. Appl. 20, 30–59. https://doi.org/10.1890/08-1140.1.
Bobbink, R., Hornung, M., Roelofs, J.G.M., 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural european vegetation. J. Ecol. 86, 717–738.
Measures in forestry (in Swedish) [WWW Document], 2023. URL ⟨http://pxweb.skogsstyrelsen.se/pxweb/sv/Skogsstyrelsens%20statistikdatabas/Skogsstyrelsens%20statistikdatabas_Atgarder%20i%20skogsbruket/JO16_05%20-%20Godsling%20per%20landsdel.px/table/tableViewLayout2/?rxid=03eb67a3-87d7-486d-acce-92fc8082735d⟩ (accessed 3.21.23).
Driessen, P., 2001. Lecture notes on the major soils of the world, World soil resources reports. Food and Agriculture Organization of the United Nations, Rome.
Eno, C.F., 1960. Nitrate production in the field by incubating the soil in polyethylene bags. Soil Sci. Soc. Am. J. 24, 277–279. https://doi.org/10.2136/sssaj1960.03615995002400040019x.
Forsmark, B., Nordin, A., Maaroufi, N.I., Lundmark, T., Gundale, M.J., 2020. Low and high nitrogen deposition rates in northern coniferous forests have different impacts on aboveground litter production, soil respiration, and soil carbon stocks. Ecosystems 23, 1423–1436. https://doi.org/10.1007/s10021-020-00478-8.
Forsmark, B., Nordin, A., Rosenstock, N.P., Wallander, H., Gundale, M.J., 2021. Anthropogenic nitrogen enrichment increased the efficiency of belowground biomass production in a boreal forest. Soil Biol. Biochem. 155, 108154 https://doi.org/10.1016/j.soilbio.2021.108154.
Friedlingstein, P., O'Sullivan, M., Jones, M.W., Andrew, R.M., Hauck, J., Olsen, A., Peters, G.P., Peters, W., Pongratz, J., Sitch, S., Le Quéré, C., Canadell, J.G., Ciais, P., Jackson, R.B., Alin, S., Aragão, L.E.O.C., Arneth, A., Arora, V., Bates, N.R., Becker, M., Benoit-Cattin, A., Bittig, H.C., Bopp, L., Bultan, S., Chandra, N., Chevallier, F., Chini, L.P., Evans, W., Florentie, L., Forster, P.M., Gasser, T., Gehlen, M., Gilfillan, D., Gkritzalis, T., Gregor, L., Gruber, N., Harris, I., Hartung, K., Haverd, V., Houghton, R.A., Ilyina, T., Jain, A.K., Joetzjer, E., Kadono, K., Kato, E., Kitidis, V., Korsbakken, J.I., Landschützer, P., Lefèvre, N., Lenton, A., Lienert, S., Liu, Z., Lombardozzi, D., Marland, G., Metzl, N., Munro, D.R., Nabel, J.E.M.S., Nakaoka, S.-I., Niwa, Y., O'Brien, K., Ono, T., Palmer, P.I., Pierrot, D., Poulter, B., Resplandy, L., Robertson, E., Rödenbeck, C., Schwinger, J., Séférian, R., Skjelvan, I., Smith, A.J.P., Sutton, A.J., Tanhua, T., Tans, P.P., Tian, H., Tilbrook, B., van der Werf, G., Vuichard, N., Walker, A.P., Wanninkhof, R., Watson, A.J., Willis, D., Wiltshire, A.J., Yuan, W., Yue, X., Zaehle, S., 2020. Global carbon budget 2020. Earth Syst. Sci. Data 12, 3269–3340. https://doi.org/10.5194/essd-12-3269-2020.
From, F., Strengbom, J., Nordin, A., 2015. Residual long-term effects of forest fertilization on tree growth and nitrogen turnover in Boreal forest. Forests 6, 1145–1156. https://doi.org/10.3390/f6041145.
Gundale, M.J., Deluca, T.H., Nordin, A., 2011. Bryophytes attenuate anthropogenic nitrogen inputs in boreal forests. Glob. Change Biol. 17, 2743–2753. https://doi.org/10.1111/j.1365-2486.2011.02407.x.
Gundale, M.J., From, F., Bach, L.H., Nordin, A., 2014. Anthropogenic nitrogen deposition in boreal forests has a minor impact on the global carbon cycle. Glob. Change Biol. 20, 276–286. https://doi.org/10.1111/gcb.12422.
Haas, J.C., Street, N.R., Sjödin, A., Lee, N.M., Högberg, M.N., Näsholm, T., Hurry, V., 2018. Microbial community response to growing season and plant nutrient optimisation in a Boreal Norway spruce forest. Soil Biol. Biochem. 125, 197–209. https://doi.org/10.1016/j.soilbio.2018.07.005.
Hasselquist, N.J., Metcalfe, D.B., Högberg, P., 2012. Contrasting effects of low and high nitrogen additions on soil CO_2 flux components and ectomycorrhizal fungal sporocarp production in a Boreal forest. Glob. Change Biol. 18, 3596–3605. https://doi.org/10.1111/gcb.12001.
Hedwall, P.O., Nordin, A., Strengbom, J., Brunet, J., Olsson, B., 2013. Does background nitrogen deposition affect the response of boreal vegetation to fertilization? Oecologia 173, 615–624. https://doi.org/10.1007/s00442-013-2638-3.
Högberg, M.N., Blaško, R., Bach, L.H., Hasselquist, N.J., Egnell, G., Näsholm, T., Högberg, P., 2014. The return of an experimentally N-saturated boreal forest to an N-limited state: observations on the soil microbial community structure, biotic N retention capacity and gross N mineralisation. Plant Soil 381, 45–60. https://doi.org/10.1007/s11104-014-2091-z.
Högberg, P., Fan, H., Quist, M., BINKLEY, D., TAMM, C., 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.
Högberg, P., Näsholm, T., Franklin, O., Högberg, M.N., 2017. Tamm review: on the nature of the nitrogen limitation to plant growth in Fennoscandian Boreal forests. For. Ecol. Manag. 403, 161–185. https://doi.org/10.1016/j.foreco.2017.04.045.
Huang, Z., Clinton, P.W., Baisden, W.T., Davis, M.R., 2011. Long-term nitrogen additions increased surface soil carbon concentration in a forest plantation despite elevated decomposition. Soil Biol. Biochem. 43, 302–307. https://doi.org/10.1016/j.soilbio.2010.10.015.
Hyvönen, R., Persson, T., Andersson, S., Olsson, B., Ågren, G.I., Linder, S., 2008. Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. Biogeochemistry 89, 121–137. https://doi.org/10.1007/s10533-007-9121-3.
Jacobson, S., Högbom, L., Ring, E., 2020. Long-term responses of understory vegetation in boreal Scots pine stands after nitrogen fertilization. Scand. J. For. Res. 35, 139–146. https://doi.org/10.1080/02827581.2020.1761996.
Jacobson, S., Pettersson, F., 2010. An assessment of different fertilization regimes in three Boreal coniferous stands. Silva Fenn. 44 https://doi.org/10.14214/sf.123.
Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta analysis. For. Ecol. Manag. 140, 227–238. https://doi.org/10.1016/S0378-1127(00)00282-6.
Jonasson, S., 1988. Evaluation of the point intercept method for the estimation of plant biomass. Oikos 52, 101–106. https://doi.org/10.2307/3565988.
Jörgensen, K., Granath, G., Lindahl, B.D., Strengbom, J., 2021. Forest management to increase carbon sequestration in boreal Pinus sylvestris forests. Plant Soil 466, 165–178. https://doi.org/10.1007/s11104-021-05038-0.
Jörgensen, K., Granath, G., Strengbom, J., Lindahl, B.D., 2022. Links between boreal forest management, soil fungal communities and below-ground carbon sequestration. Funct. Ecol. 36, 392–405. https://doi.org/10.1111/1365-2435.13985.
Karlsson, G., Hellsten, S., 2022. Totalt kvävenedfall till kommuner i Sverige. Data till VERA-programmet. 2022.
Maaroufi, N.I., Nordin, A., Hasselquist, N.J., Bach, L.H., Palmqvist, K., Gundale, M.J., 2015. Anthropogenic nitrogen deposition enhances carbon sequestration in boreal soils. Glob. Change Biol. 21, 3169–3180. https://doi.org/10.1111/gcb.12904.
Maaroufi, N.I., Nordin, A., Palmqvist, K., Hasselquist, N.J., Forsmark, B., Rosenstock, N.P., Wallander, H., Gundale, M.J., 2019. Anthropogenic nitrogen enrichment enhances soil carbon accumulation by impacting saprotrophs rather than ectomycorrhizal fungal activity. Glob. Change Biol. 25, 2900–2914. https://doi.org/10.1111/gcb.14722.
Mäkipää, R., 1995. Effect of nitrogen input on carbon accumulation of boreal forest soils and ground vegetation. For. Ecol. Manag. 79, 217–226. https://doi.org/10.1016/0378-1127(95)03601-6.
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., Laganière, J., Nouvellon, Y., Paré, D., Stanturf, J.A., Vanguelova, E.I., Vesterdal, L., 2020. Tamm Review: Influence of forest management activities on soil organic carbon stocks: a knowledge synthesis. For. Ecol. Manag. 466, 118127 https://doi.org/10.1016/j.foreco.2020.118127.
Midolo, G., Alkemade, R., Schipper, A.M., Benítez-López, A., Perring, M.P., De Vries, W., 2019. Impacts of nitrogen addition on plant species richness and abundance: a global meta-analysis. Glob. Ecol. Biogeogr. 28, 398–413. https://doi.org/10.1111/geb.12856.
Muff, S., Nilsen, E.B., O'Hara, R.B., Nater, C.R., 2022. Rewriting results sections in the language of evidence. Trends Ecol. Evol. 37, 203–210. https://doi.org/10.1016/j.tree.2021.10.009.
Näsholm, T., Högberg, P., Franklin, O., Metcalfe, D., Keel, S.G., Campbell, C., Hurry, V., Linder, S., Högberg, M.N., 2013. Are ectomycorrhizal fungi alleviating or aggravating nitrogen limitation of tree growth in boreal forests? N. Phytol. 198, 214–221. https://doi.org/10.1111/nph.12139.
Nilsson, J., Grennfelt, P., 1988. Critical loads for sulphur and nitrogen. Miljoerapport 1988, 15.
Nohrstedt, H.-Ö., 2001. Response of coniferous forest ecosystems on mineral soils to nutrient additions: a review of Swedish experiences. Scand. J. For. Res. 16, 555–573. https://doi.org/10.1080/02827580152699385.
Nordin, A., Strengbom, J., Ericson, L., 2006. Responses to ammonium and nitrate additions by boreal plants and their natural enemies. Environ. Pollut. 141, 167–174. https://doi.org/10.1016/j.envpol.2005.08.017.
Nordin, A., Strengbom, J., Witzell, J., Näsholm, T., Ericson, L., 2005. Nitrogen deposition and the biodiversity of boreal forests: implications for the nitrogen critical load. Ambio 34, 20–24.
O'Hehir, J.F., Nambiar, E.K.S., 2010. Productivity of three successive rotations of P. radiata plantations in South Australia over a century. For. Ecol. Manag. 259, 1857–1869. https://doi.org/10.1016/j.foreco.2009.12.004.
Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Ouellette, M.-H., Cunha, E.R., Smith, T., Stier, A., Braak, C.J.F.T., Weedon, J., 2022. vegan: Community Ecology Package.
Olsson, P., Linder, S., Giesler, R., Högberg, P., 2005. Fertilization of boreal forest reduces both autotrophic and heterotrophic soil respiration. Glob. Change Biol. 11, 1745–1753. https://doi.org/10.1111/j.1365-2486.2005.001033.x.
Påhlsson, L., 1995. Vegetationstyper i Norden. Nordiska Ministerrådet, Köpenhamn.
Pettersson, N., Fahlvik, N., karlsson, A., 2012. Skogsskötselserien nr 6, Röjning, in: Skogsskötselserien. Jönköping.
Pettersson, F., Högbom, L., 2004. Long-term growth effects following forest nitrogen fertilization in Pinus sylvestris and Picea abies stands in Sweden. Scand. J. For. Res. 19, 339–347. https://doi.org/10.1080/02827580410030136.
R Core Team, 2020. R: The R Project for Statistical Computing [WWW Document]. URL ⟨https://www.r-project.org/⟩ (accessed 6.14.22).

Ring, E., Jacobson, S., Högbom, L., 2011. Long-term effects of nitrogen fertilization on soil chemistry in three Scots pine stands in Sweden. Can. J. Res. 41, 279–288. https://doi.org/10.1139/X10-208.

Sponseller, R.A., Gundale, M.J., Futter, M., Ring, E., Nordin, A., Näsholm, T., Laudon, H., 2016. Nitrogen dynamics in managed boreal forests: recent advances and future research directions. Ambio 45, 175–187. https://doi.org/10.1007/s13280-015-0755-4.

Strengbom, J., Näsholm, T., Ericson, L., 2004. Light, not nitrogen, limits growth of the grass Deschampsia flexuosa in boreal forests. Can. J. Bot. 82, 430–435. https://doi.org/10.1139/b04-017.

Strengbom, J., Nordin, A., 2008. Commercial forest fertilization causes long-term residual effects in ground vegetation of boreal forests. For. Ecol. Manag. 256, 2175–2181. https://doi.org/10.1016/j.foreco.2008.08.009.

Strengbom, J., Nordin, A., 2012. Physical disturbance determines effects from nitrogen addition on ground vegetation in boreal coniferous forests. J. Veg. Sci. 23, 361–371. https://doi.org/10.1111/j.1654-1103.2011.01359.x.

Strengbom, J., Nordin, A., Näsholm, T., Ericson, L., 2002. Parasitic fungus mediates change in nitrogen-exposed boreal forest vegetation. J. Ecol. 90, 61–67. https://doi.org/10.1046/j.0022-0477.2001.00629.x.

Subedi, P., Jokela, E.J., Vogel, J.G., Martin, T.A., 2014. Inter-rotational effects of fertilization and weed control on Juvenile Loblolly Pine productivity and nutrient dynamics. Soil Sci. Soc. Am. J. 78, S152–S167. https://doi.org/10.2136/sssaj2013.08.0345nafsc.

Suding, K.N., Collins, S.L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L., Milchunas, D. G., Pennings, S., 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proc. Natl. Acad. Sci. U.S.A 102, 4387–4392. https://doi.org/10.1073/pnas.0408648102.

Sullivan, T.P., Sullivan, D.S., 2018. Influence of nitrogen fertilization on abundance and diversity of plants and animals in temperate and boreal forests. Environ. Rev. 26, 26–42. https://doi.org/10.1139/er-2017-0026.

Womach, J., 2005. Agriculture: A Glossary of Terms, Programs, and Laws, 2005 Edition [WWW Document]. UNT Digital Library. URL ⟨https://digital.library.unt.edu/ark:/67531/metacrs7246/⟩ (accessed 10.12.23).

Xu, C., Xu, X., Ju, C., Chen, H.Y.H., Wilsey, B.J., Luo, Y., Fan, W., 2021. Long-term, amplified responses of soil organic carbon to nitrogen addition worldwide. Glob. Change Biol. 27, 1170–1180. https://doi.org/10.1111/gcb.15489.