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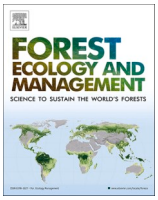

Grey alder at the regeneration stage: Long-term effects on soil nitrogen and carbon pools and Norway spruce growth

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ABSTRACT

Increasing soil N availability is an effective way to enhance soil organic carbon (SOC) sequestration and biomass production in N-limited ecosystems such as boreal Norway spruce forests. Alder has a root nodule symbiosis with *Frankia*, an N_2-fixing bacterium, and can thus add considerable amounts of N to soil mainly through its N-rich leaf litter. The objective of this study was to determine whether the presence of grey alder at the regeneration stage had any long-term effects on soil C and N cycling and stocks and spruce growth. The study sites were two relatively fertile 40-year-old Norway spruce stands (Luhdansuo and Porkkola) in Southern Finland. At both study sites, half the spruce stand had an admixture of grey alders for approximately 10–15 years after regeneration (alder treatment), but no alder had been present in the other half (control treatment). Alders were cut from the alder treatment 25 (Luhdansuo) or 30 (Porkkola) years before the measurements. At Porkkola, alder treatment received ash fertilisation 13 years ago. We observed no significant differences in the plant-available N fluxes, measured with a microdialysis technique, or SOC stocks between treatments. The total N stock (organic horizon + 0–30 cm mineral soil) and organic horizon thickness were larger, while the microbial biomass C:N and C mineralisation rate were lower in the alder versus the control treatment at Luhdansuo. The annual ring widths of spruces were larger in the alder versus the control treatment for up to six years after alder removal at both sites, but no differences were observed in the current tree diameters or diameter increments. In conclusion, most of the current soil or tree properties did not differ significantly between treatments, possibly because the effect of alder had faded out over the 25–30 years since its removal, and because the sites were initially relatively fertile.

1. Introduction

Boreal forests are a large C stock, and enhancing C sequestration to soil and trees is an important tool for mitigating climate change. Adding N to soil is an effective way to enhance C sequestration in these N-limited ecosystems (Prescott, 2010; Hedwall et al., 2014). Besides N fertilisation, one way to affect soil organic carbon (SOC) stock is to modify the tree species composition, as tree species differ in their litter inputs and quality, as well as soil organic matter decomposition rates (Vesterdal et al., 2013). Norway spruce is currently favoured in forest regeneration in Southern Finland, increasing the area of spruce-dominated forests. The problem is that spruce reduces soil fertility compared to broad-leaved trees by increasing C:N ratio and decreasing soil pH, microbial biomass C and N, and the concentrations of exchangeable nutrients, for example (Priha, 1999; Hagen-Thorn et al., 2004; Smolander and Kitunen, 2011; Augusto et al., 2015).

One option to improve soil fertility in Norway spruce stands could therefore be the introduction of broad-leaved trees, especially species capable of N fixation symbiosis such as grey alder, to the spruce stands. Grey alder can form a root nodule symbiosis with *Frankia*, an N_2-fixing actinomycete commonly occurring in our soils (Smolander and Sundman, 1987). Thus, alder litter is N-rich, and the annual litter yield of alders can add an average of 50–100 kg ha^{-1} of N to soil in pure alder stands (Mikola, 1966; Uri et al., 2014) and mixed alder-conifer stands (Binkley et al., 1992). The potential to improve soil by growing grey alder as an admixture in conifer stands in Finland was recognised as early as the 1930 s (Kalela, 1937). At that time, alder was a relatively common tree species, particularly in Eastern Finland, after slash-and-burn cultivation. The litter of grey alder increased the amount of organic matter, the concentrations of NH_4-N, Ca and K, and pH in the topsoil of Norway spruce stands (Mikola, 1966). The effects of alder on conifer growth appear to depend on site characteristics such as soil fertility and conifer species. For example, red alder as an admixture in conifer stands increased conifer growth on a site with low initial soil N

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content and reduced it on a site with high N content (Binkley, 2003).

Despite its soil-improving properties, alder has traditionally been considered a weed species in forestry due to its low commercial value and strong competitive capacity. Alder as a nurse tree after regeneration in spruce stands has also been associated with growth disorders in spruce trees due to boron deficiency (Rikala, 2004). However, grey alder is recognised as a promising species for bioenergy in the Nordic and Baltic countries, as it grows fast, regenerates efficiently by sprouting, and is not prone to herbivore damage (Aosaar, 2012; Hytönen and Saarsalmi, 2015). In recent decades, grey alder research has indeed focused on its use in short-rotation forestry to produce bioenergy (Aosaar, 2012) or improve soil on post-mining sites (Frouz et al., 2009).

Grey alder generally increases soil N availability and enhances SOC sequestration. The mechanisms behind SOC sequestration by N-fixing trees are not fully understood, but they may be similar to N fertilisation: increased litter inputs and reduced decomposition and C mineralisation rates (Mayer et al., 2020). For example, Resh et al. (2002) observed higher SOC sequestration under N-fixing trees compared to a non-N fixer due to a greater accumulation of labile SOC and the retention of old SOC. The mechanisms behind the retention of old SOC by N fixers are poorly understood. Like other forms of N addition (e.g. N deposition), however, one explanation is that the increased N availability from N fixers suppresses ligninolytic enzyme activity, inhibiting the decomposition of high-lignin litter (Carreiro et al., 2000; Resh et al., 2002). Broad-leaved tree species, including grey alder, may also accumulate more C in stable form in the mineral soil compared to spruce, but spruce stands often have thicker forest floors with larger C stocks (Frouz et al., 2009; Vesterdal et al., 2013).

The estimation of N availability has traditionally been challenging, as the common extraction methods probably alter soil natural N status during soil sampling, sieving, and extraction itself (Inselsbacher, 2014). These soil preparation steps may stimulate microbial processes such as mineralisation and nitrification, thus changing the proportions of different N compounds. Microdialysis is a relatively new method in soil science. It was first applied to the measurements of soil N dynamics by Inselsbacher et al. (2011). In this method, a small probe is inserted into the soil, and sampling is based on diffusion of soil solutes across a semipermeable membrane of the probe. The target compounds are measured from the collected dialysates in the laboratory. This micro-scale method enables the detection of the supply of compounds that are readily available for uptake by plant roots from the soil solution including inorganic N compounds, ammonium (NH_4^+) and nitrate (NO_3^-), and low-molecular weight organic N compounds such as amino acids.

Tree species affect several important ecosystem functions, and introducing broad-leaved tree species to coniferous stands has positive effects on biodiversity, resistance to damage, and forest productivity (Huuskonen et al., 2021). In particular, N-fixing vegetation may improve soil fertility by increasing the content of soil organic matter and total N (Vidal et al., 2019). The long-term effects of alder on both soil fertility and the stability of soil C are not well known. This study aimed to increase knowledge about the long-term effects of grey alder on soil properties and tree growth in Norway spruce stands, focusing on plant-available N fluxes and soil C and N cycling and stocks. We conducted this study at two fertile 40-year-old Norway spruce stands in Southern Finland, where alder had been present at the early stage of stand development and cut 25–30 years ago. We hypothesised that the past presence of alder increased (i) the plant-available N fluxes and N stocks, and subsequently (ii) soil C stocks and (iii) spruce growth.

2. Material and methods

2.1. Study sites

The study sites, Luhdansuo (61°18′, 25°3′) and Porkkola (61°24′, 24°55′), were 40-year-old (age at diameter at breast height [DBH, 1.3 m]) Norway spruce (*Picea abies* (L.) Karst) stands in Padasjoki in Southern Finland. Both sites represent a relatively fertile *Oxalis acetosella - Vaccinium myrtillus* (OMT) site type, applying the Finnish forest site type classification (Cajander, 1949). The humus type is mor, and the soil is classified as Cambisol on both study sites (IUSS Working Group WRB, 2015). Stands were established in approximately 1980 by planting spruce seedlings on clear-cuts, after which grey alders (*Alnus incana* (L.) Moench.) regenerated naturally in one half of the spruce stands (alder treatment). In the other half, no alders had been present (control treatment). To our knowledge, there was no other previous land use except forestry at Luhdansuo, but at Porkkola, the area had previously been affected by grazing (both treatments) and slash-and-burn cultivation a long time ago, after which alder appeared (alder treatment). The exact density of alders is unknown, but in both sites the number of stems per hectare was high. Alders and spruces were about the same age, but as young grey alders grew faster than spruce, spruce saplings grew as undergrowth until the alders were cut in the early 1990 s (Porkkola) or in 1995 (Luhdansuo) from the alder treatment. At Luhdansuo, the control treatment was thinned in 2003, and both treatments were thinned in 2017. At Porkkola, the alder treatment was B-fertilised after the mid-1990 s, and both treatments were thinned in 2007–2008, after which alder treatment was fertilised with wood ash. The exact amount of ash is not known, but it is probably close to the amount recommended for mineral soils in Finland, 3000 kg ha^{-1}. The alder treatment of Porkkola is therefore referred to later as 'alder + ash treatment'. Two (Luhdansuo) or three (Porkkola) circular plots (r = 5.64 m) were established close to each other in each treatment (Fig. 1). We took microdialysis and soil samples from the organic (O) horizon and measured the trees in June 2021, taking the mineral soil samples in November 2021. Applying the classification by Food and Agriculture Organization of the United Nations (IUSS Working Group WRB, 2015), the soil type was silt loam throughout the 0–30 cm mineral soil profile at Luhdansuo and sandy loam–loam at Porkkola (Table S1). The clay content was slightly higher in the alder + ash versus the control treatment at Porkkola.

2.2. Determination of plant-available N fluxes in soil

We used microdialysis, a diffusion-based sampling method (Inselsbacher et al., 2011), to determine the plant-available N fluxes in early June. The microdialysis system setup and sampling protocol were the same as described by Smolander et al. (2022). Briefly, microdialysis sampling spots (20 cm × 20 cm) were located close (< 1 m) to the centre of the established plots. Four CMA 20 microdialysis probes (length 30 mm, outer diameter 0.5 mm; CMA Microdialysis AB, Kista, Sweden) were inserted vertically at a depth of 1.5 cm into the O horizon. The flow rate was 5 µl min^{-1}, and the sampling time was 52 min to collect 260 µl of dialysate for the analyses. Before and after the field sampling, blanks for each probe were determined by sampling from Milli-Q water and relative recoveries from standard N solution. The dialysates were stored at − 18 °C until the analyses of N compounds using a CLARIOstar microplate reader (BMG LABTECH). Ammonium-N was measured using a modified indophenol method (Hood-Nowotny et al., 2010), NO_3-N using vanadium (III) chloride and the Griess method (Miranda et al., 2001; Hood-Nowotny et al., 2010), with the modifications by Inselsbacher et al. (2011), and total free amino acid N using the fluorometric method (Jones et al., 2002), with the modifications by Darrouzet-Nardi et al. (2013). The *diffusive flux* (D) of the N compounds is expressed as nmol m^{-2} s^{-1} of N and is calculated as $D = c \times V / (A \times t)$, where c is the *concentration* of N compound in the dialysate (nmol l^{-1}), V is the *volume* of dialysate (l), A is the surface *area* of the membrane (m^2), and t is the sampling *time* (s). The mean blank values (flux from Milli-Q water before and after field sampling) of each probe were subtracted from the corresponding fluxes. The mean diffusive flux of the four dialysates collected from each plot was calculated, and the statistical tests were run on the plot-level means.

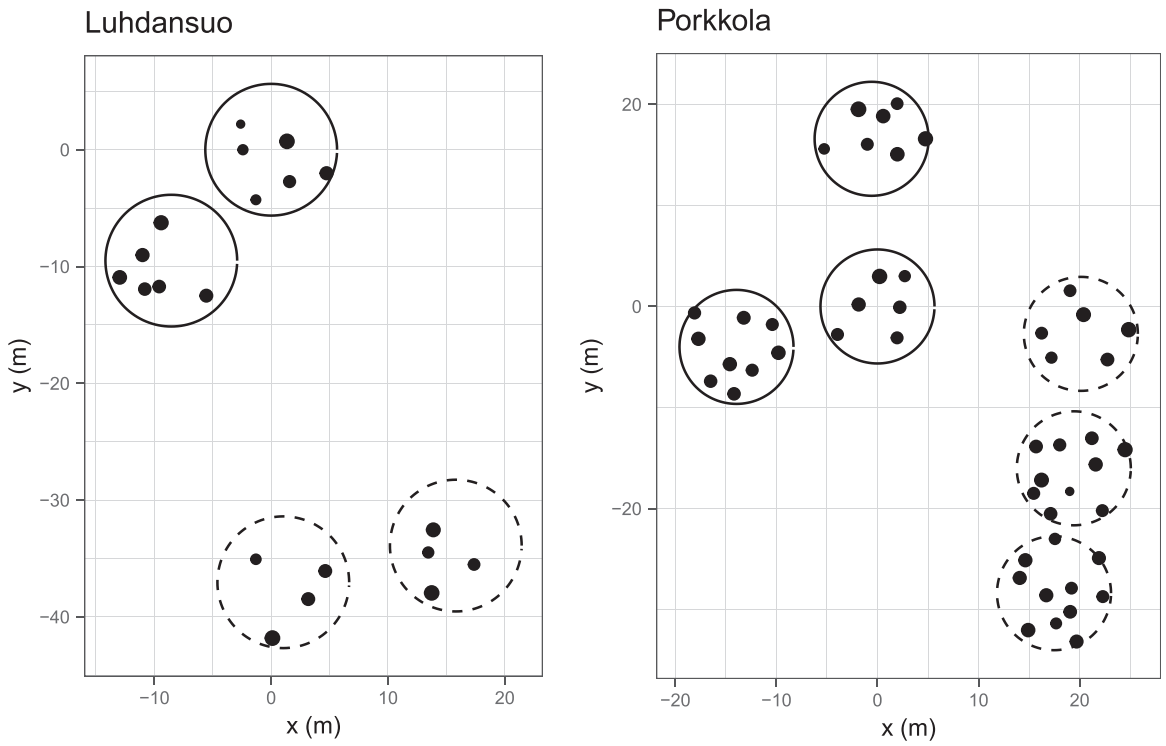

Fig. 1. Tree locations and their diameters at breast height (DBH) on the established circular plots (r = 5.64 m); circles with solid lines represent alder (+ ash, Porkkola) plots; those with dashed lines represent control plots. The area between the plots is a similar type of forest on both study sites, but at Porkkola, there is a small forest road between the alder and control treatments.

2.3. Soil sampling

We took samples of the O horizon with a corer (d = 58 mm) systematically from two circle diameters perpendicular to each other on each plot. The organic horizon thickness was measured from each core, and the resulting ten cores were combined into a composite sample per plot. O horizon samples were kept at 4 °C and sieved through a 6 mm mesh sieve two to four days after sampling; part of the sample was air-dried at 40 °C and ground (< 0.5 mm) to determine the SOC and N stocks. Due to stoniness, we dug a pit on each plot and sampled the pit wall from the mineral soil at depths of 0–10, 10–20, and 20–30 cm. To analyse the SOC and N stocks and particle size distribution with the method by sieving and sedimentation (ISO 11277:2009), the mineral soil samples were air-dried (40 °C) and sieved (< 2 mm).

2.4. Determinations of SOC and N stocks

The total C and N content of the air-dried O horizon and mineral soil samples was measured by dry combustion with a CHN analyser (Leco CHN-600). We assumed total C to consist fully of organic carbon, as inorganic C as carbonates is almost absent from Finnish forest soils. The *stoniness index* (Si) of the plots was determined using Viro's rod method (Viro, 1952), and the *stone and boulder content* (SB) was calculated as per Stendahl et al. (2009): SB (% volume) = 76.4 - 2.19 × Si.

The *bulk density* (BD, kg m^{-3}) of the O horizon samples was calculated by dividing the dry mass of the sample by its volume. The bulk density of the mineral soil samples was estimated by calculating the average of the outcomes of these two equations:

$BD = 1.7262 \times \exp(-0.3632 \times SOC^{0.5})$ (Nilsson and Lundin, 2006) and.

$BD = 0.111 \times 1.450 / (1.450 \times OM + (1 - OM) \times 0.111)$ (Federer et al., 1993), where SOC is *soil organic carbon* (% dry matter) measured with Leco, and OM is the *organic matter content* (g g^{-1} dry matter) obtained from the loss-on-ignition analysis.

Finally, the SOC and N stocks were calculated as per Blaško et al. (2020):

$$\text{SOC or N stock [Mg ha}^{-1}] = (\text{SOC or N \%} / 100 \times ((V_{soil} \times BD) \times (1 - CF))) \times 10,$$

where V_{soil} is the potential soil *volume* (l) in 1 m^2 of a 10-cm-thick mineral soil layer corrected for the SB %, and CF is the *fraction* of the coarse material (> 2 mm) in the soil sample (kg kg^{-1} dry matter).

2.5. Other characterisations of the organic horizon

We measured the pH of the O horizon from a soil-water suspension (15 ml of fresh soil: 25 ml of Milli-Q water). The soil dry matter content was determined by drying the soil overnight at 105 °C, after which the organic matter content was determined using loss-on-ignition (550 °C, 4 h).

C and N transformations and microbial biomass C and N content were determined from the fresh O horizon samples as described by Törmänen et al. (2018), with some modifications. Briefly, the rates of net N mineralisation and net nitrification were measured in a four-week aerobic incubation at constant moisture (60% water-holding capacity) and temperature (14 °C). Net N mineralisation was determined after 1 M potassium chloride (KCl) extraction as accumulation of NH_4- and NO_3-N during the incubation, and net nitrification was determined as accumulation of NO_3-N. The aerobic mineralisation of C was estimated by measuring the CO_2-C production rate three times during the four-week incubation (at 2, 13, and 20 days after the incubation started); the bottles were closed with gas-tight septa 21–23 h before the measurement using an Agilent 8890 gas chromatograph system with a thermal conductivity detector. The microbial biomass was measured using the fumigation-extraction method (Vance et al., 1987) with the conversion formulas by Martikainen and Palojärvi (1990) to calculate the amounts of C and N in the microbial biomass.

2.6. Tree measurements

On each plot, we measured the DBH and height (h) of each tree. The increment cores were taken from sample trees (4–5 trees per plot) at a height of 1.3 m. The ring widths of the tree were measured to an accuracy of 0.01 mm using a microscope, and the radial increments were cross-dated visually. The stem volumes (v [dm^3]) of spruces were calculated using the volume model by Laasasenaho (1982):

$v = \exp(-3.77543 + 1.91505 \times \ln(DBH) + 2.82541 \times \ln(h) - 1.53547 \times \ln(h - 1.3) - 0.0085726 \times DBH)$, where DBH is in cm, and h is in m.

2.7. Statistical analyses

A two-sample t-test was applied for the plot-level means of each soil or tree property to detect significant differences between the alder (or alder + ash) and control treatments. P-value < 0.10 was considered significant due to the long time that had elapsed since the alder removal, which had probably diluted the effect of alder. Statistical analyses were performed with R version 4.2.2 (R Core Team, 2022).

3. Results

3.1. Soil description

The organic horizon was statistically significantly thicker in the alder versus the control treatment at Luhdansuo, but no difference was observed at Porkkola (Table 1). The differences between the treatments in the moisture, organic matter content, and pH of O horizon were non-significant on both study sites.

Soils were relatively similar in their basic characteristics in the alder and control plots on both study sites (Table 1). Alder + ash plots had significantly lower volumetric content of stones and boulders than the control plots at Porkkola, whereas the alder plots at Luhdansuo tended to have higher stone and boulder content than the control.

3.2. Plant-available N fluxes

The differences in plant-available N fluxes between the treatments were non-significant on both study sites (Fig. 2, Table 2). Nevertheless, the mean NO_3-N and AA_{tot}-N fluxes tended to be lower in the alder + ash versus the control treatment at Porkkola. In the control treatment of Luhdansuo, there was a notably high NO_3-N flux value (> 20 nmol m^{-2} s^{-1}) from one microdialysis probe compared to the values from the other seven probes (< 1 nmol m^{-2} s^{-1}). The microdialysis sample volume was insufficient for the analysis of AA_{tot}-N in several cases, which led to 9 NAs (out of 16 samples) at Luhdansuo and 5 NAs (out of 24 samples) at Porkkola in the calculations of the plot-level mean AA_{tot}-N fluxes (there was at least one observation from each plot). Total N fluxes (sum of NH_4-N, NO_3-N, and AA_{tot}-N fluxes) did not differ significantly between treatments (Table S2).

Ammonium-N dominated the fluxes in all treatments except the control treatment at Porkkola, where AA_{tot}-N comprised half the total N flux, a significantly higher share than in the alder + ash treatment (Fig. 2, Table 2). Ammonium-N comprised a significantly higher share of the flux in the alder + ash treatment of Porkkola compared to the control. Nitrate-N comprised 10 ± 7% of the inorganic N flux (sum of NH_4-N and NO_3-N fluxes) in the alder treatment and 30 ± 20% in the control treatment at Luhdansuo ($p = 0.423$). At Porkkola, NO_3-N comprised a significantly lower share of the inorganic N flux in the alder + ash treatment (9 ± 5%) than in the control treatment (34 ± 9%, $p = 0.066$).

3.3. SOC and N stocks

The differences in SOC stocks and concentrations between the treatments were non-significant in each soil layer on both study sites (Fig. 3, Table 2 and Table S2). Nevertheless, the SOC stock tended to be larger in the O horizon of the alder versus the control treatment at Luhdansuo. The total SOC stock (the sum of SOC stocks in the O horizon and 0–30 cm mineral soil) was an average of 70.2 ± 2.6 Mg ha^{-1} of SOC in the alder treatment and 65.6 ± 1.2 Mg ha^{-1} of SOC in the control treatment at Luhdansuo ($p = 0.247$). At Porkkola, the total SOC stock was an average of 49.7 ± 7.4 Mg ha^{-1} of SOC in the alder + ash treatment and 53.9 ± 8.8 Mg ha^{-1} of SOC in the control treatment ($p = 0.732$).

The N stock of the O horizon was significantly higher in the alder versus the control treatment at Luhdansuo, whereas at Porkkola, there was no difference (Fig. 3, Table 2). At Luhdansuo, the N content of the mineral soil 0–10 cm layer was significantly higher in the alder versus the control treatment, whereas at Porkkola, the opposite trend was observed (Table S2). The total N stock (the sum of N stocks in the O horizon and 0–30 cm mineral soil) was an average of 4.1 ± 0.1 Mg ha^{-1} of N in the alder treatment of Luhdansuo, significantly higher than that of the control, 3.7 ± 0.0 Mg ha^{-1} of N ($p = 0.040$). At Porkkola, the total N stock was an average of 2.4 ± 0.3 Mg ha^{-1} of N in the alder + ash treatment and 2.6 ± 0.4 Mg ha^{-1} of N in the control treatment ($p = 0.703$).

The C:N ratios were lower throughout the soil profile at Luhdansuo than at Porkkola (Fig. 3). On both sites, the C:N of the O horizon tended to be lower in the alder versus the control treatment. The mineral soil C:N was significantly higher at a depth of 10–20 cm in the alder versus the control treatment at Luhdansuo.

3.4. Organic matter characteristics

At Luhdansuo, the C mineralisation rate was significantly lower in the alder versus the control treatment (Fig. 4, Table 2). Otherwise, the

Table 1
Soil basic characteristics at Luhdansuo and Porkkola. Bold p-values of t-tests are considered statistically significant ($p < 0.10$). FW = fresh weight, DW = dry weight.

	Luhdansuo (n = 2)					Porkkola (n = 3)				
	Alder		Control		P-value	Alder + ash		Control		P-value
	Mean	SE	Mean	SE		Mean	SE	Mean	SE	
Organic horizon										
Thickness (cm)	5.2	0.1	4.3	0.1	**0.029**	4.8	0.0	4.9	0.5	0.896
Moisture (% FW)	46	5	44	5	0.771	59	1	58	3	0.762
Organic matter content (% DW)	45	11	30	6	0.371	69	8	78	9	0.513
pH	4.5	0.2	4.8	0.1	0.342	4.6	0.4	4.3	0.2	0.479
Bulk density (kg m^{-3})	213	26	267	65	0.519	135	8	127	4	0.431
Mineral soil										
Stones and boulders, vol%	26	3.9	17	0.1	0.143	43	2.6	51	1.7	**0.065**
Bulk density, 0-10 cm (kg m^{-3})	633	21	719	58	0.299	810	45	691	86	0.288
Bulk density 10-20 cm (kg m^{-3})	993	29	1039	23	0.342	1000	55	966	27	0.614
Bulk density 20-30 cm (kg m^{-3})	1199	25	1197	12	0.945	1060	42	1033	49	0.698

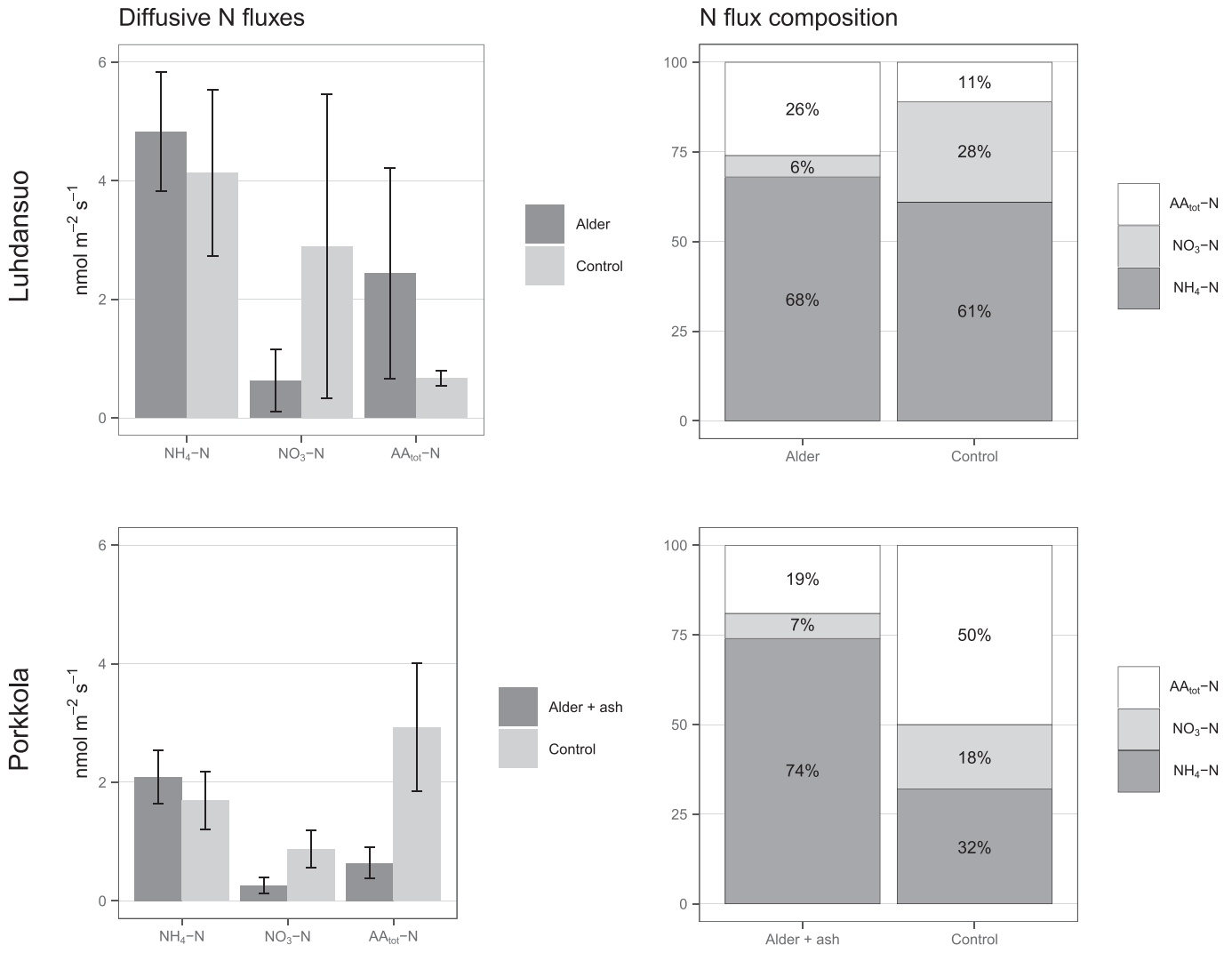

Fig. 2. Diffusive fluxes of different N forms (left; mean ± SE) and their percentages of the total flux (right; sum of the fluxes of NH_4-N, NO_3-N and AA_{tot}-N) at Luhdansuo (top; n = 2) and Porkkola (bottom; n = 3). AA_{tot} = total amino acids. See Table 2 for p-values.

differences in the C and N cycling processes and KCl-extractable NH_4- and NO_3-N concentrations were non-significant on both sites.

Microbial biomass C:N was significantly smaller in the alder versus the control treatment at Luhdansuo, but the differences in the content of microbial biomass C and N were non-significant on both sites (Fig. 5, Table 2). The concentration of dissolved N tended to be smaller in the alder versus the control treatment at Luhdansuo. When net N mineralisation rate was calculated as per microbial N, it was significantly lower in the alder treatment compared with the control at Luhdansuo. The concentration of dissolved organic C did not differ between the treatments at either of the study sites (Table S2).

3.5. Tree and stand characteristics

The annual ring widths of spruces already showed slightly increased growth during the presence of alder at Luhdansuo and after alder removal on both study sites, the effect lasting a total of up to six years on both sites (Fig. 6, Table 3 and Table S3). However, the differences in current diameters and other tree and stand characteristics were non-significant on both study sites (Table 4). Crown base height tended to be higher in the alder + ash versus the control treatment at Porkkola.

4. Discussion

We aimed to discover whether the presence of grey alder at the regeneration stage had any long-term effects on soil C and N cycling and stocks and tree growth in Norway spruce stands. Unfortunately, no field experiments have been established for this purpose, and to study the effects of alder, neither of our study sites represented a truly replicated experiment. However, the stands had been established on the same geological formation and probably on soil that had originally been similar, and the history of the stands was well documented. Moreover, soil texture revealed no major differences between the treatments. It is therefore justified to attribute the observed differences in soil properties to the past presence of grey alder at Luhdansuo and the combination of grey alder and ash fertilisation at Porkkola. We used p-value of 0.10 as the threshold of statistical significance to consider the possible dilution in the soil properties over the years, diminishing the effect of the past presence of alder.

The total N stock and O horizon thickness were larger, and the microbial biomass C:N and C mineralisation rate were lower in the alder versus the control treatment on one study site, Luhdansuo, 25 years after alder removal. However, the results did not indicate higher N availability or SOC stocks due to the past presence of alder. On both sites, the annual ring widths of spruces were larger in the alder versus the control treatment for up to six years due to the presence of alders, but the

Table 2
Probabilities of significant differences ($p < 0.10$, bold) in soil properties between alder (+ash, Porkkola) and the control treatments. The results are presented in Figs. 2–5. O = organic; AA_{tot} = total amino acids; NA = not applicable.

Variable	Luhdansuo (n = 2)	Porkkola (n = 3)
NH_4-N flux	0.726	0.579
NO_3-N flux	0.478	0.152
AA_{tot} -N flux	0.425	0.109
NH_4-N, % of total flux	0.794	**0.007**
NO_3-N, % of total flux	0.377	0.222
AA_{tot} -N, % of total flux	0.345	**0.030**
C stock, O horizon	0.158	0.814
C stock, 0-10 cm	0.544	0.456
C stock, 10-20 cm	0.771	0.892
C stock, 20-30 cm	0.568	0.955
N stock, O horizon	**0.066**	0.948
N stock, 0-10 cm	0.629	0.218
N stock, 10-20 cm	0.772	0.722
N stock, 20-30 cm	NA	0.328
C:N, O horizon	0.190	0.135
C:N, 0-10 cm	0.609	0.230
C:N, 10-20 cm	**0.071**	0.770
C:N, 20-30 cm	NA	0.715
Net N mineralisation	0.202	0.453
Nitrification	0.483	0.536
C mineralisation	**0.052**	0.262
NH_4-N concentration	0.650	0.815
NO_3-N concentration	0.460	0.374
Microbial biomass C	0.227	0.351
Microbial biomass N	0.941	0.370
Microbial biomass C:N	**0.089**	0.855
Dissolved N	0.115	0.232
Net N mineralisation / Microbial N	**0.039**	0.598

differences in the current tree diameters or diameter increments were non-significant.

The plant-available N fluxes were at the same level as previously observed in situ in boreal Scots pine forests using a similar microdialysis system setup (Buckley et al., 2017; Smolander et al., 2022). The microdialysis technique enables the measurement of N supply available for uptake by plant roots from the soil solution. The measured N flux is affected by the physical constraints to the movement of soil solutes and the ongoing soil biological and chemical processes, including N uptake by plant roots, the microbial processes of N cycling, and cation exchange.

At Luhdansuo, the low C:N ratio and high rate of net nitrification and the concentrations of total N and NO_3-N pointed to high fertility of the site, even without the presence of alder (Tamminen, 1991; Smolander and Kitunen, 2011). Although the KCl-extractable NO_3-N concentration was almost 150 times higher at Luhdansuo than at Porkkola, the NO_3-N flux was only three times higher. One explanation is that soil sampling and sieving related to the extraction method may stimulate N cycling processes (Inselsbacher, 2014), whereas the fluxes may reflect almost undisturbed soil N status (Inselsbacher et al., 2011). The high NO_3-N concentration at Luhdansuo may thus be due to stimulated nitrification during sample processing, as net nitrification rates pointed to an abundance of nitrifying bacteria. Another possible explanation of this discrepancy is the different spatial scale of the soil and microdialysis sampling. Microdialysis has the potential to measure soil N dynamics with a high spatial and temporal resolution (Inselsbacher et al., 2011; Leitner et al., 2017), but the method is laborious in the field. Due to the fine-scale nature of the technique and the heterogeneity of forest soils, the results of microdialysis sampling (four probes per plot in our study) may not represent the whole plot as well as representative soil sampling (ten soil cores with a diameter of 58 mm per plot, which were pooled). The spatial and temporal resolution of microdialysis sampling is also

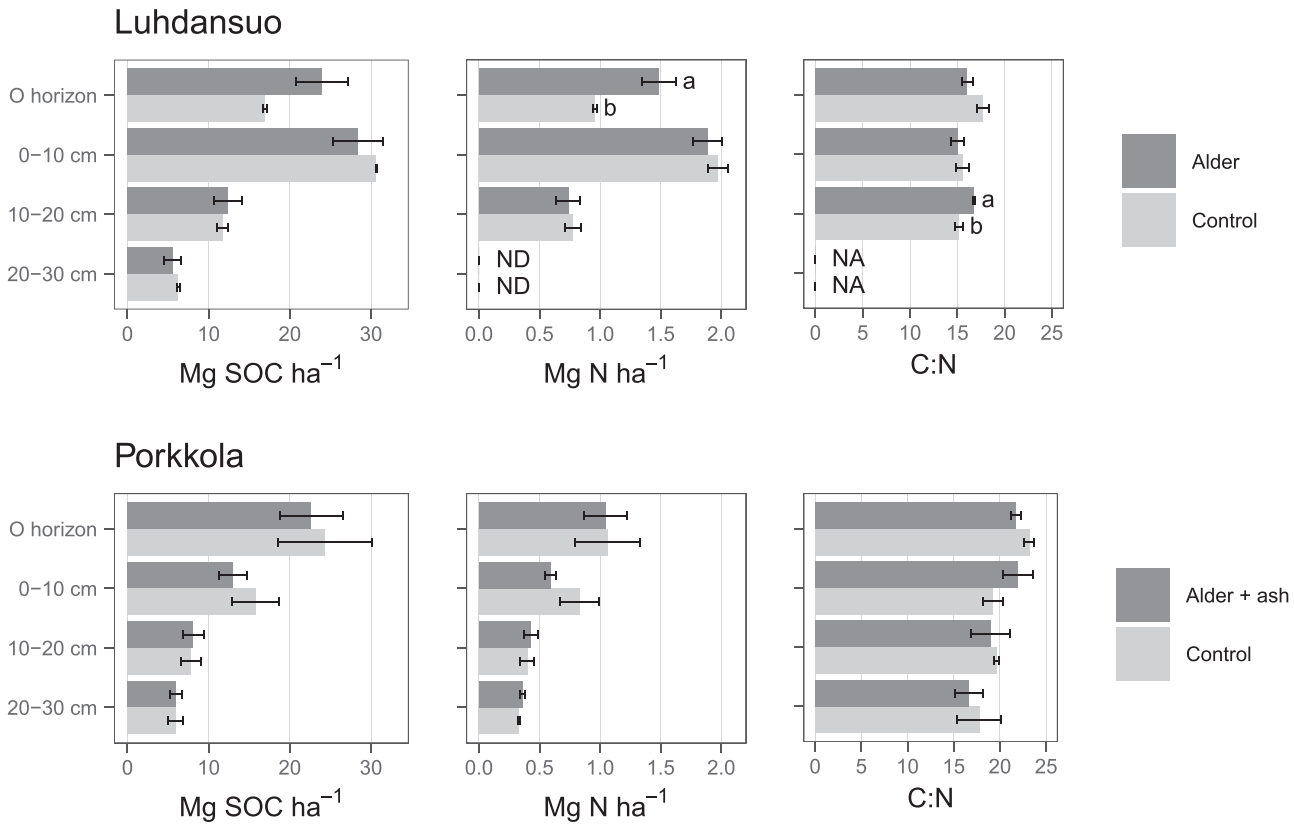

Fig. 3. Soil C and N stocks and C:N in different layers at Luhdansuo (top; n = 2) and Porkkola (bottom; n = 3). The bar represents mean ± SE. Statistically significant differences between the treatments ($p < 0.10$) are marked with different letters. SOC = soil organic carbon; ND = not detected; NA = not applicable. See Table 2 for p-values.

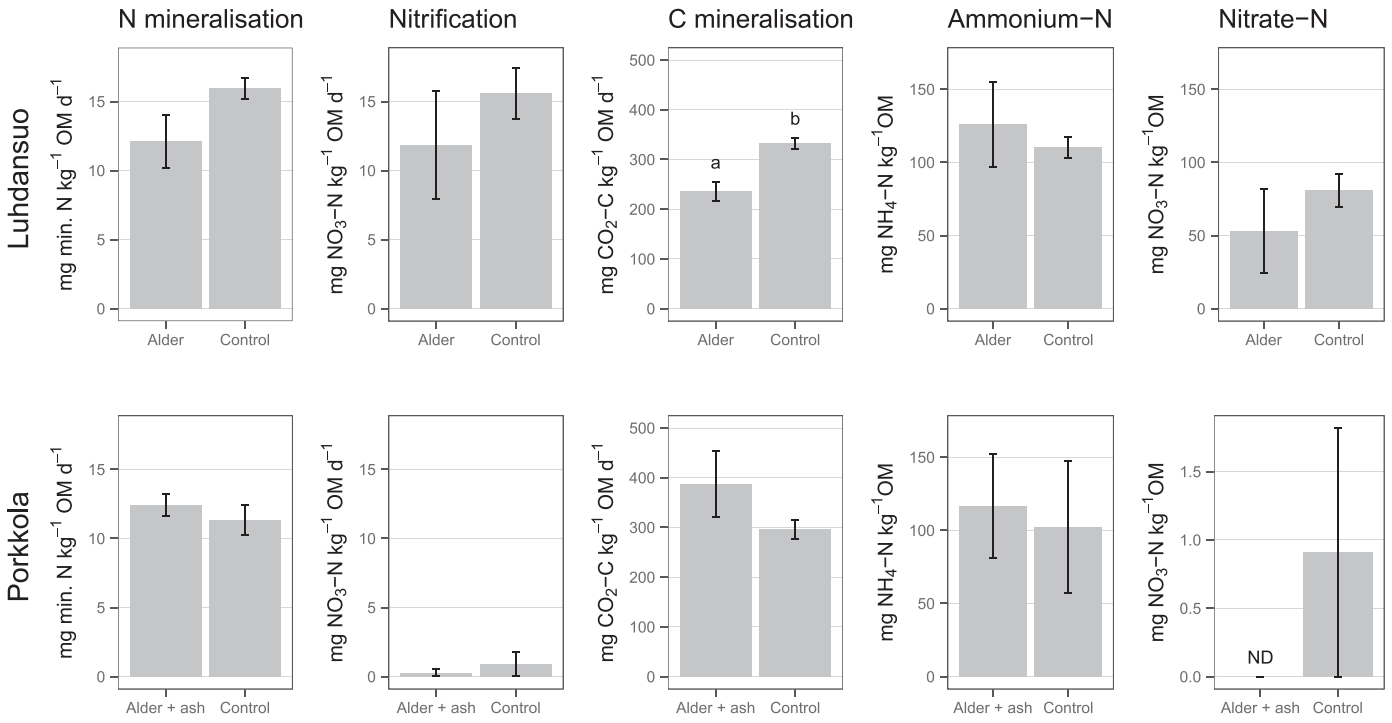

Fig. 4. N and C cycling processes and inorganic N concentrations in the samples taken from the organic horizon at Luhdansuo (top; n = 2) and Porkkola (bottom; n = 3). The bar represents mean ± SE. Note the different scale for nitrate-N concentration on the different study sites. Statistically significant differences between treatments ($p < 0.10$) are marked with different letters. OM = organic matter, ND = not detected. See Table 2 for p-values.

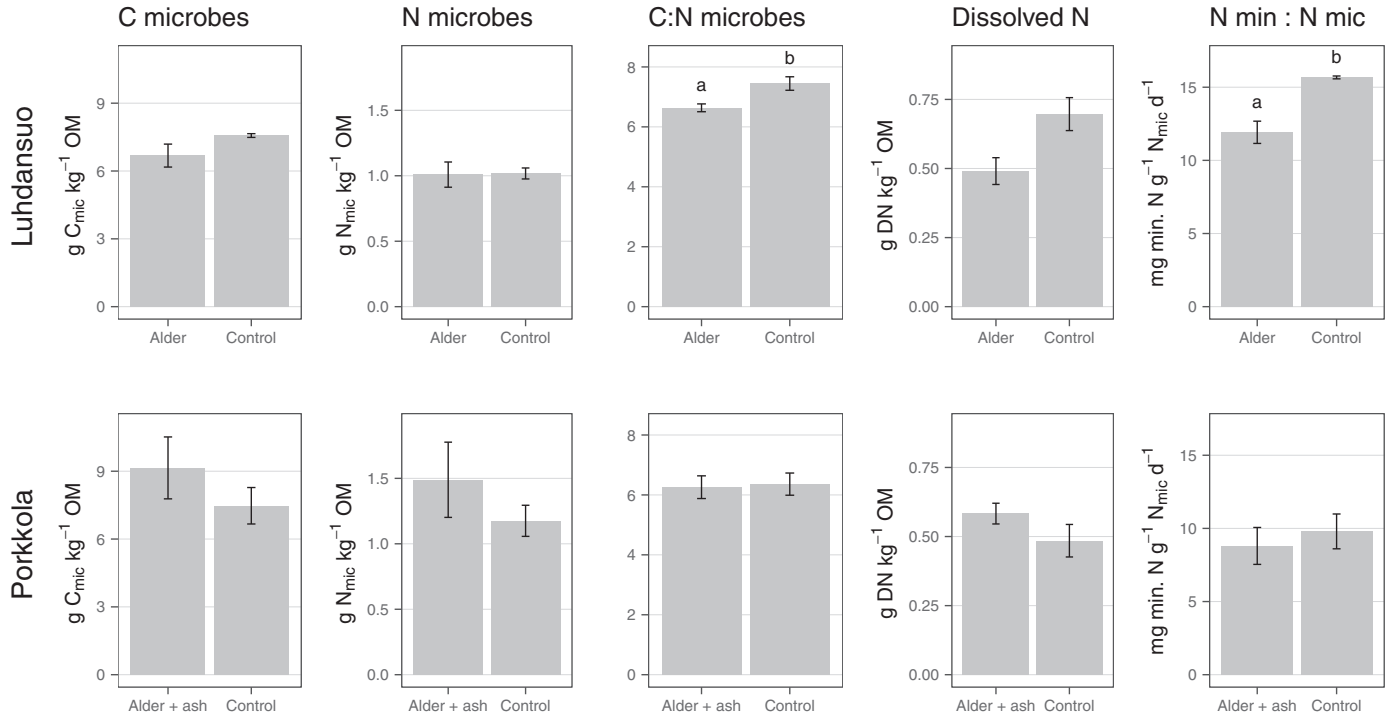

Fig. 5. Microbial biomass C, N, and C:N, and the concentration of dissolved N and net N mineralisation (N min) calculated as per microbial N (N mic) at Luhdansuo (top; n = 2) and Porkkola (bottom; n = 3). The bar represents mean ± SE. Statistically significant differences between treatments ($p < 0.10$) are marked with different letters. OM = organic matter. See Table 2 for p-values.

very different from that of taking increment cores from trees. Measuring tree ring widths allows us to look in the past decades at stand-level scale, being a more suitable approach for assessing the effects of past presence of alder than the spatially (cm) and temporally (hour) highly variable fluxes.

Grey alder has the potential to accumulate large amounts of N in the soil, mainly through its leaf litter. The estimated amount of soil N input varies from 40 to 150 kg ha^{-1} $year^{-1}$, depending on the alder species,

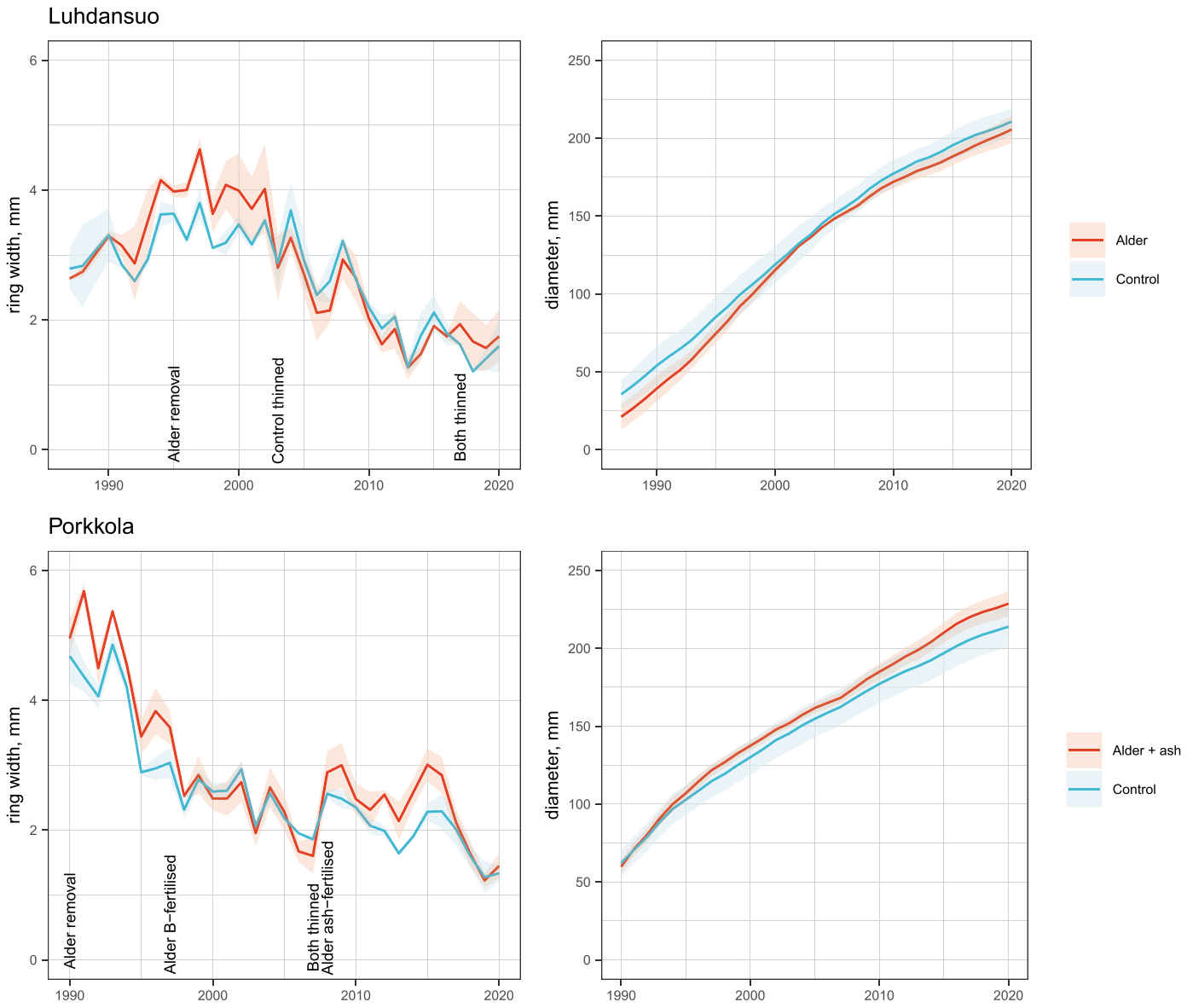

Fig. 6. Tree ring widths (left) and accumulated diameter (right) at Luhdansuo (top; n = 2) and Porkkola (bottom; n = 3); the line represents mean ± SE. See Table 3 for p-values.

the density of the stand, and the growth conditions (Mikola, 1966; Binkley et al., 1992; Aosaar, 2012). Alder was abundant at Porkkola for about 10 years and at Luhdansuo for 15 years, suggesting a considerable N input to the soil. N accumulation was evident at Luhdansuo, where the N stock was still higher in the alder than the control treatment 25 years after alder removal.

Against our hypothesis, the past presence of alder did not increase SOC stocks significantly. At Luhdansuo, alder plots tended to have larger mean SOC stock in the O horizon than the control plots and no differences in the mineral soil, which was also contrary to our expectations. Spruce produces recalcitrant litter, creating a large SOC stock in the O horizon, whereas N-fixing vegetation often enhances SOC accumulation in the mineral soil (Frouz et al., 2009; Nave et al., 2009). The thicker O horizon in the alder treatment of Luhdansuo could be due to increased N availability in the past, which led to a higher litter yield and may simultaneously have reduced organic matter decomposition and C mineralisation rates. SOC sequestration by N fixers has previously been attributed to the increased accumulation of labile SOC through the production of N-rich leaf litter, as well as increased retention of old SOC (Resh et al., 2002; Aosaar et al., 2013). In mineral soil, SOC is mainly stabilised through interactions with clay minerals and occlusion inside the soil aggregates (von Lützow et al., 2006). Clay content was relatively high at Luhdansuo, providing a large surface area for the binding of SOC. We therefore expected to see higher SOC stocks in the mineral soil of the alder treatment, especially at Luhdansuo. It is possible that our fertile study sites initially had large SOC stocks, which could explain the lack of a long-lasting effect of alder on SOC stock.

Alder has the potential to decrease soil pH by stimulating soil processes such as nitrification (Hart et al., 1997). The pH effect strongly depends on the compared tree species; generally, broadleaved species increase soil pH compared to conifers. Mikola (1966) found an increase in the soil pH of a spruce stand by alder leaf litter, which was probably explained by the use of different tree species to those in the research by Hart et al. (1997). Wood ash often raises soil pH, and the effect is long-lasting (Saarsalmi et al., 2010). Both pH and organic matter characteristics often showed opposite trends on the two study sites, probably related to the effect of ash at Porkkola. Ash fertilisation had possibly stimulated microbial activity and thus led to increased organic matter decomposition rates at Porkkola, resulting in the current tendency of smaller C concentrations and stocks in the topsoil of alder + ash versus

Table 3
Summary of t-tests for the differences in ring widths (Fig. 6.) between alder (+ash, Porkkola) and the control treatments. Bold p-values are considered statistically significant ($p < 0.10$). NA = not available.

	Luhdansuo (n = 2)			*Porkkola (n = 3)*		
Year	Statistic	Degrees of freedom	p-value	Statistic	Degrees of freedom	p-value
1987	-0.49	2	0.671	NA	NA	NA
1988	-0.14	2	0.902	NA	NA	NA
1989	-0.11	2	0.925	NA	NA	NA
1990	-0.03	2	0.976	0.53	4	0.625
1991	1.72	2	0.228	5.00	4	**0.007**
1992	0.48	2	0.681	1.37	4	0.242
1993	1.16	2	0.365	2.46	4	**0.070**
1994	2.43	2	0.136	1.90	4	0.130
1995	2.18	2	0.161	1.99	4	0.117
1996	5.54	2	**0.031**	2.21	4	**0.092**
1997	2.81	2	0.107	1.59	4	0.187
1998	1.81	2	0.212	1.41	4	0.232
1999	2.15	2	0.164	0.21	4	0.845
2000	0.88	2	0.470	-0.47	4	0.661
2001	1.09	2	0.391	-0.42	4	0.699
2002	0.70	2	0.555	-0.59	4	0.585
2003	-0.12	2	0.918	-0.53	4	0.626
2004	-0.89	2	0.467	0.26	4	0.810
2005	-0.39	2	0.734	0.34	4	0.751
2006	-0.61	2	0.602	-1.72	4	0.160
2007	-1.18	2	0.360	-0.93	4	0.406
2008	-0.93	2	0.451	1.00	4	0.375
2009	0.07	2	0.953	1.38	4	0.239
2010	-0.84	2	0.488	0.52	4	0.629
2011	-0.95	2	0.442	0.78	4	0.479
2012	-0.61	2	0.604	5.34	4	**0.006**
2013	-0.04	2	0.970	1.67	4	0.170
2014	-0.76	2	0.526	3.17	4	**0.034**
2015	-0.76	2	0.526	2.57	4	**0.062**
2016	-0.24	2	0.833	1.45	4	0.220
2017	0.88	2	0.473	0.33	4	0.761
2018	1.05	2	0.406	0.14	4	0.899
2019	0.42	2	0.717	-0.19	4	0.855
2020	0.27	2	0.814	0.49	4	0.647

the control treatment.

Significant differences in soil properties between the treatments were observed more often at Luhdansuo, where alders were present 25 years ago. At Porkkola, the ash fertilisation on alder plots significantly increased the annual ring widths of spruces for more than five years. Saarsalmi et al. (2010) observed a long-lasting effect of combined ash and N fertilisation on the volume growth of Norway spruce. Thus, the current soil and tree properties of the Porkkola study site may reflect the combined effect of alder presence (30 years ago) and ash fertilisation (13 years ago).

Based on annual ring widths, alder removal boosted spruce growth on our study sites, but it was not reflected in the current tree diameters or current growing stock volume. Binkley et al. (1992) observed that alder increased conifer growth on N-poor sites but even decreased it on N-rich sites. Urli et al. (2020) found that American green alder facilitated the growth of Jack pine during six years after stand establishment, whereas the growth of black spruce remained unaffected. Competition for water and light between the major tree species and the intercropped N-fixing vegetation probably hampered the volume growth and survival of the major tree species, especially at the early stages of stand development, in a study conducted by Vidal et al. (2019). After crushing the N-fixing vegetation, its benefits for soil fertility compensated for the drawbacks in the same study. The net effect of alder on spruce growth was neutral even on our relatively fertile study sites. There is therefore potential to improve soil properties without hindering the growth of Norway spruce by allowing grey alders to grow on regeneration areas planted for spruce.

The conclusions of our study are limited because of a small sample size and the absence of less fertile sites where alder may have a higher potential for soil improvement. Leaving alders as an admixture in conifer forests may be a more sustainable alternative to N fertilisation, although these two methods for adding N to forest soils cannot be directly compared. However, the period of increased growth as affected by alder lasted for six years in our study, which is the same magnitude as the effect of N fertilisation, which lasts for seven to ten years (Pettersson and Högbom, 2004). We must note that the increased growth observed in our study cannot be entirely attributed to the soil-improving effect of alder, as the thinning caused by alder removal may also have affected spruce growth.

5. Conclusions

Overall, the soil results did not suggest higher N availability or SOC stocks due to the past presence of alder, but even after 25 years, we observed an increased soil N stock on one site. The tree ring widths were larger in the alder versus the control treatment for six years after alder removal on both sites, but no differences were observed in the current tree diameters or diameter increments. In conclusion, most of the soil or tree properties did not differ significantly between treatments, probably because the effect of alder had faded 25 to 30 years after its removal, and because the sites were initially fertile. More information is needed about the long-term effects of alder on less fertile sites and the duration of those effects.

CRediT authorship contribution statement

Soronen Päivi: Formal analysis, Funding acquisition, Investigation, Methodology, Writing – original draft. **Henttonen Helena M.:** Investigation, Methodology, Writing – review & editing. **Smolander Aino:** Funding acquisition, Investigation, Methodology, Supervision, Writing – review & editing.

Declaration of Competing Interest

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

Table 4
Tree and stand characteristics and the probabilities of significant t-test differences (unless otherwise mentioned) between treatments. DBH = diameter at breast height.

	Luhdansuo (n = 2)					Porkkola (n = 3)				
	Alder		Control		P-value	Alder + ash		Control		P-value
	Mean	SE	Mean	SE		Mean	SE	Mean	SE	
DBH (cm)	23	1.9	24	0.2	0.586	25	0.5	24	0.2	0.386
Height (m)	21	1.9	21	0.4	0.749	23	0.2	23	0.2	0.951
Crown base height (m)	10	0.8	10	0.7	0.789	10	5.4	9	1.7	0.106
Volume (dm^3)	434	96	491	12	0.615	551	32	531	12	0.594
N/ha	600	0.0	400	0.0	0.194*	734	88	901	153	0.398
Basal area ($m^2\ ha^{-1}$)	25	3.6	19	0.3	0.215	37	4.3	43	6.6	0.478
Volume ($m^3\ ha^{-1}$)	261	58	197	5	0.383	404	50	475	72	0.462

* Wilcoxon rank sum test with continuity correction

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2023.121686.

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