Contents lists available at ScienceDirect

Forest Ecology and Management

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

Norway spruce productivity in southern Sweden is equally limited by nitrogen and phosphorous

Carl Svensson [a],[*],[1], Martin Karl-Friedrich Bader [a],[2], Ann-Mari Fransson [a],[3], Claes-Göran Alriksson [b], Martin Goude [c],[4], Johan Bergh [a],[5]

[a] *Linnaeus University, Faculty of Technology, Department of Forestry and Wood Technology, Växjö SE-35195, Sweden*
[b] *Linnaeus University, Faculty of Health and Life Sciences, Department of Biology and Environmental Science, SE-Kalmar 39182, Sweden*
[c] *Swedish University of Agricultural Sciences, SLU, Faculty of Forest Sciences, Unite of Field-based Forest Research, Åbacken 104, Simlångsdalen SE-31396, Sweden*

ABSTRACT

Nutrient limitation of forest growth, especially nitrogen (N) deficiency, is widespread in the boreal region. N fertilisation has thus become a common silvicultural practice in Fennoscandian Norway spruce stands, but to what extent phosphorus (P) is co-limiting productivity and how initial basal area affects the growth response to N addition remains unresolved. To address these questions, two experiments were established in mid-rotation Norway spruce stands in southern Sweden where decades of high atmospheric N deposition have reduced the severity of N-limitation. In a P experiment initiated in 2011, we tested P addition alone (two applications of 200 kg P ha^{-1}) and in a second study also starting in 2011 (NP experiment), a single dose of N was administered alone (200 kg ha^{-1} in thinned and unthinned stands, hereafter called N and N-unthinned treatments) and in combination with P (N+P = one-time 200 kg N ha^{-1}, two applications of 200 kg P ha^{-1} in thinned stands). P addition alone increased PAI (periodic annual increment) significantly by 21 % during the first, moister assessment period up to 2014 and by 18 % in the drier 2015–2019 period, resulting in a 10 % increase in final stem volume yield. In the NP experiment, significant PAI increases under favourable meteorological conditions up to 2014 occurred in all fertilisation treatments. The strongest effects were seen in the N-unthinned treatment while no significant additive effect resulted from the joint addition of N and P (N: +20 %, N-unthinned: +38 %, N+P: +23 %). In the drier 2015–2019 period, only the N+P treatment caused significantly greater PAI (+29 %). Final stem volume yield in the NP experiment significantly increased by 10 %, 39 % and 16 % in the N, N-unthinned and N+P plots, respectively. In both experiments, foliar P and thus P/N rose drastically in response to P addition alone or in combination with N. Minor increases in leaf area index (LAI) only occurred in P-containing treatments. Our findings indicate that Norway spruce productivity in southern Sweden is constrained to a similar extent by both N and P. Sustainable nutrient management in Norway spruce growing regions with high N loading (like southern Sweden) should prioritise P over N supply.

1. Introduction

The growth of boreal cold-temperate forests is often limited by low soil nutrient availability, especially nitrogen (N) (Tamm, 1991). Therefore, nutrient addition commonly results in a marked growth stimulation in northern forests (Bergh et al., 1999; Saarsalmi and Mälkönen, 2001; Tamm, 1991). Trees growing in nutrient-poor conditions usually respond quite strongly to fertilisation as an improved supply of nutrients gives rise to a greatly expanded needle mass and thus increased photosynthetic carbon (C) assimilation and productivity (Cannell, 1989). Without other strong limitations, increased photosynthesis is directly proportional to tree growth and biomass accumulation.

The nutrient-driven stimulation of photosynthesis is not only due to an enlargement of the leaf area but also to enhanced photosynthetic efficiency through increases in chlorophyll and Rubisco concentration and activity (Manter et al., 2005). This means that the photosynthetic efficiency typically increases under elevated N supply compared to an unfertilised stand of average nutritional status and production capacity (Roberntz and Stockfors, 1998). The greater stemwood production is also partly explained by changes in resource allocation between below- and aboveground biomass (Axelsson and Axelsson, 1986). Improved soil nutrient availability tends to reduce a tree's investment belowground (root growth, rhizosphere symbionts, exudation) while allocating more resources to aboveground organs (needles, branches, trunk). Fertilisation of Norway spruce and Scots pine with 150 kg N ha^{-1} in mid-to late-rotation stands stimulates growth usually by 10–20 m^3 ha^{-1} in Sweden and Finland (Ingerslev et al., 2001; Jacobson and Pettersson, 2001; Saarsalmi and Mälkönen, 2001). In Sweden, the fertiliser-induced growth stimulation is greater in the northern part of the country compared to the South (Bergh et al., 1999) and lasts for 6–10 years with a slightly longer fertiliser effect for Norway spruce than for Scots pine (Pettersson and Högbom, 2004).

The anthropogenic deposition of N has been high for many decades in Sweden but has decreased somewhat in the last 10 years and is commonly lower than in many European countries (Bertills and Näsholm, 2000; Karlsson et al., 2022). However, atmospheric N deposition varies greatly across Sweden, with the highest rates around 15 kg ha^{-1} y^{-1} occurring in the southwest but significantly lower loads in the central and northern parts of the country (Karlsson et al., 2022). The long-term N deposition has certainly reduced the degree and severity of N limitation in soils, especially in southern Sweden, but it remains uncertain to what extent this has alleviated N constraints to growth, not least because of the strong influence of humus type on N availability (Ericsson, 1995). In reforested areas situated on former agricultural land where chronic N enrichment has led to the accumulation of large soil nutrient legacies (Svensson et al., 2023b), high atmospheric N deposition may even result in N saturation and/or N leaching when N inputs exceed the retention capacity of the system. A set of thinning and fertilisation experiments starting in the 1960s in Scots pine and Norway spruce plantations across Sweden, covering a range of climate and site conditions, showed no growth response to N fertilisation in Norway spruce stands in southern Sweden (Bergh et al., 2014). At sites where water limitation can be ruled out, this indicates either N saturation or that nutrients other than N are limiting growth, *e.g.* phosphorous (P). Additional growth effects have sometimes been achieved when N was applied frequently at rather high doses, either separately or in combination with P and potassium (K) (Albrektson et al., 1977; Dralle and Larsen, 1995; Harrington and Wierman, 1990; Tamm et al., 1999). However, numerous studies in the boreal region have been unable to demonstrate additional growth stimulation linked to P and K supplementation suggesting no current shortage of these elements (Harrington and Devine, 2011; Newton and Amponsah, 2006; Nilsen and Abrahamsen, 2003). But nutrient deficiencies may develop over time, for example Akselsson et al. (2008) demonstrated progressive P-limitation in Norway spruce stands in south-central Sweden exposed to high N loading, which could be reversed by P addition. Nilsen (2001) proposed that the effects of additional nutrients in combination with N on growth and biomass production may be more significant in younger forests. For Norway spruce this has recently been demonstrated across large parts of Sweden (Blaško et al., 2022; Svensson et al., 2023a).

To shed light on the role of P in Norway spruce growth, alone and in combination with N, a set of experiments was established in 2011 in mid-rotation stands (30 – 38 years old) in southwest Sweden, where the highest atmospheric N deposition in the country occurs, which mitigates the widespread N limitation to some extent (Bahr et al., 2015; Karlsson et al., 2022). In a nested sub-experiment, we also tested the interaction between thinning and N addition in relation to growth, but for logistical reasons we restricted this to N fertilisation as this is used operationally in Fennoscandian forest management.

The objectives of this study were to (i) determine the growth response to P addition in mid-rotation Norway spruce stands in southwest Sweden, (ii) evaluate the growth response to N alone and in combination with P, (iii) examine the interactive effect of thinning and N fertilisation on spruce growth and (iv) provide forest practitioners with guidelines for N and P application.

2. Material and methods

2.1. Field site

This study was done in mid-rotation stands of Norway spruce (*Picea abies* (L.) Karst.) planted between 1974 and 1983 at the Tönnersjöheden Forest Research Park in the boreo-nemoral zone in southwest Sweden (56° 41' – 42' N, 13° 6' – 7' E; Fig. 1, Table 1). This area has a relatively high atmospheric N deposition of 14.5 kg N ha^{-1} yr^{-1} (Karlsson et al., 2022). Situated at an elevation between 70 and 120 m above sea level, the sites are characterised by various types of podzol (IUSS Working Group WRB, 2015) overlying glaciofluvial parent material with a C/N of 25 in the organic horizon (Almeida et al., 2019). O-horizon thickness varied between 5 and 20 cm. The A-horizon was between 5 and 10 cm in depth, followed by a ca. 3 cm wide E-horizon (eluvial horizon). The B-horizon varied in depth between approximately 15–25 cm followed by the undisturbed C-horizon. The pH (H$_2$O) at the experimental sites varied between 4.4 and 4.7.

2.2. Experimental design and treatments

This study consisted of two separate experiments, a P experiment, where P alone was added to the plots and an NP experiment, where N alone and in combination with P was added. The P experiment was made up of 12 plots, arranged into six blocks, each consisting of a control (C) and a phosphorus-treated (P) plot, all of which were thinned in October-November 2010 (Table 1). P was applied twice as superphosphate in September 2011 and July 2012 at a dose of 200 kg P ha^{-1} (Table 2).

The NP site contained an additional treatment as a sub-experiment where N was added to unthinned stands to test the interaction between thinning and N fertilisation. For logistic reasons, we confined this to the addition of N as this is a commonly used practice in forestry. Prior to the start of the experiment in October-November 2010, all NP plots were thinned, except the N-unthinned plots (Table 1). The NP experiment consisted of 24 plots arranged in six blocks comprising the following 4 treatments: thinned control stands (C), N-fertilised thinned stands (N) using one application of 200 kg N ha^{-1}, N-fertilised unthinned stands (N-unthinned) using one application of 200 kg N ha^{-1}, N and P fertilisation in thinned stands (N+P) using 200 kg N ha^{-1} once plus 200 kg P ha^{-1} applied twice (Table 2). N was applied as ammonium nitrate in July 2011 and P as superphosphate in July 2011 and July 2012. The area of the plots ranged between 0.065 and 0.1 hectare, which was accounted for when estimating the area-based growth.

2.3. Tree measurements and growth

Tree height and diameter at breast height (DBH, 1.3 m above ground) were measured three times starting in 2009 in the NP experiment and in 2011 in the P experiment, followed by assessments at the end of the 2014 and 2019 growing seasons to calculate the standing volume and periodic annual increment (PAI). The DBH of each tree was measured crosswise using callipers and height was determined in a subsample of trees in the plots. Brandel's volume function (Brandel, 1990) was used to calculate the volume per tree in order to derive a mean stem volume per hectare for each plot. Growth was assessed as periodic annual increment (PAI) per stem, by calculating the difference in volume over the period between measurement dates. The first period comprised the start of the respective trial to 2014 and the second from 2015 to 2019.
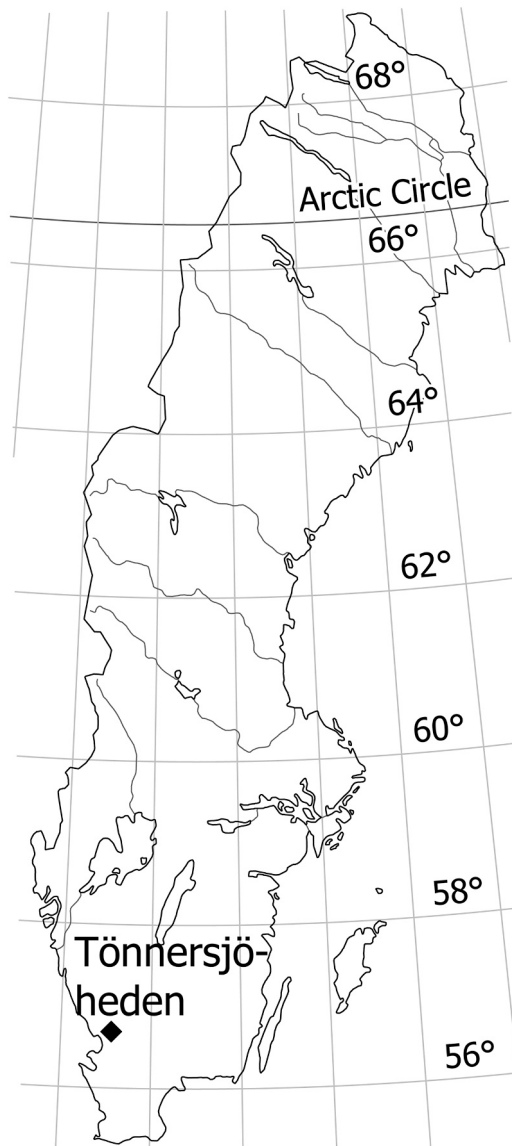
Fig. 1. Map of Sweden (GSD-Maps of Sweden © Lantmäteriet) showing the location of the P and NP experiments at the Tönnersjöheden forest research park.

2.4. Needle nutrient sampling and analysis

One-year-old needles were collected from the upper part of the green crown of 5 dominant or subdominant trees within a treatment at the end of the 2012, 2013 and 2016 growing seasons. Needle samples were merged (ca. 100 g dry weight) and their N concentration was determined using an elemental analyser (CNS-2000, LECO Corp., St. Joseph, MI, USA) and inductively coupled plasma (ICP) mass spectroscopy (Optima 7300 DV ICP-OES, PerkinElmer Inc., Waltham, MA, USA) was used to measure P concentration. The foliar P/N ratio was expressed as a percentage of P to N on a mass basis.

2.5. Soil sampling and analysis

Soil was sampled from all 12 P plots (6 controls and 6 P-fertilised) and in the control plots of the NP experiment on February 13 and 14 in 2023. The N and NP plots had been fertilised recently as part of a subsequent study and were therefore excluded. Soil was sampled along two parallel transects along the length of the plots. Ten subsamples were collected and merged into one composite sample per plot. Approximately 100 g mineral soil from 0 to 20 cm depth was collected after removing the humic layer in each subsample. The soil was sieved on site (8 mm mesh size).

The soil samples were kept in the refrigerator until the following day and then analysed for phosphate, nitrate and ammonium. The soils were extracted with 0.2 M KCl and centrifuged at 5000 rpm. The $H_2PO_4^-$, NO_3^- and NH_4^+ in the supernatant was analysed using colorimetric Hach-Lange kits (LCK 349, LCK 339, LCK 309, respectively) and a spectrophotometer (DR 3900, Hach Lange, Düsseldorf, Germany). Soil pH (H_2O) was analysed in the extract (soil/solution 1:5). Soil P was barely detectable in the control plots, whereas the soil P concentration was on average 1.6 µg g^{-1} P in the P-fertilised plots (Table 3). Total soil N availability was similar in all sampled plots with a somewhat larger share of NO_3^- relative to NH_4^+ in the P plots, while these two inorganic N compounds occurred in similar proportions in the control soil of the NP experiment (Table 3).

Soil water content and water-holding capacity (WHC) were determined by water saturation for approximately 36 hours and drying at 105 °C for 12 hours. Gravimetric soil moisture was above 20 % in all plots and mass based WHC was greater than 50 % in all plots (Table 3).

To examine the texture, soil was taken from the 12 plots (6 C and 6 P plots) in the P experiment and the control plots of the NP experiment and dried at 105 °C for 24 hours. Approximately 200 g mineral soil of each sample was sieved to four fractions (> 4 mm, 4 – 2 mm, 2 – 0.25 mm, < 0.25 mm) for 10 minutes and then the different fractions were weighed. The soil at the P site is derived from glacial sediments with silty-sandy texture and less than 10 % gravel. The soil of the NP site had a similar silty-sandy texture but was more strongly influenced by moraine material which was reflected in a larger proportion of gravel (> 10 %).

2.6. LAI

Leaf area index (LAI) was determined by indirect leaf area measurement as auxiliary data at 60 points per plot in April 2023. These points were systematically distributed along two diagonal transects (30 points per transect). This optical method comprised recordings of diffuse sky radiation using a plant canopy analyser (LAI-2200 C, LI-COR, Lincoln, NE, USA). The LAI measurements were corrected to better represent the true LAI of the stand, using correction functions developed by Goude et al. (2019).

2.7. Climate and metrological data

Climate and soil temperature data was obtained from the weather station near the Tönnersjöheden Forest Research Park in Simlångsdalen, as part of a climate monitoring program within the Swedish University of Agricultural Sciences Unit of Field-based Forest Research. Data acquisition and management follows the standard World Meteorological Organisation (WMO) protocols. Mean annual precipitation in the area is 1064 mm and the mean annual temperature is 6.4 °C (Hedwall et al., 2017). The 3-month standardized precipitation-evapotranspiration index (SPEI) was calculated to characterise dry and wet conditions during the study period (Fig. 2, R package *SPEI*, Vicente-Serrano et al., 2010).

2.8. Statistical analysis

All statistical analyses were performed in the R software environment (R Core Team, 2023). PAI and foliar N, P and P/N ratios were analysed as a function of the assessment period, fertiliser treatment, and their interaction using linear mixed effects (LME) models with 'block' as random term (R package *nlme*, Pinheiro et al., 2023). Stem volume and LAI were analysed in the same manner with fertiliser treatment as the sole explanatory variable because these response variables were only assessed once at the end of the study. Graphical model validation tools (residuals plots) were used to assess the underlying assumptions of

Table 1
Stand age, site index (SI), quadratic mean diameter (QMD), Lorey's mean height (H$_L$), basal area (BA) and standing volume (V) prior to the start of the nutrient treatments. The two right-most, grey-shaded columns give the basal area and standing volume removed by the pre-treatment thinning. Means ± standard error. C = unfertilised control, N = N fertilisation, N+P = joint N and P addition, N-unt = N fertilisation in unthinned stands, P = P fertilisation.

Experiment	Treatment	Stand characteristics						Removal	
		Age (years)	SI (m)	QMD (cm)	H$_L$ (m)	BA (m² ha⁻¹)	V (m² ha⁻¹)	BA (m² ha⁻¹)	V (m² ha⁻¹)
NP	C	31.4 ± 0.6	33.4 ± 0.7	14.9 ± 0.6	13.5 ± 0.3	17.0 ± 0.1	116.9 ± 2.9	5.3 ± 0.9	35.1 ± 7.4
NP	N	30.6 ± 1.0	34.4 ± 0.7	15.5 ± 0.5	14.1 ± 0.5	17.0 ± 0.0	122.1 ± 4.0	6.5 ± 0.5	44.8 ± 4.1
NP	N+P	30.5 ± 0.8	34.3 ± 0.7	15.5 ± 0.4	13.8 ± 0.3	16.9 ± 0.1	118.7 ± 2.3	6.8 ± 0.6	45.8 ± 4.8
NP	N-unt	31.7 ± 0.5	34.6 ± 0.6	15.3 ± 0.2	14.4 ± 0.2	25.3 ± 0.4	186.5 ± 4.9	0.1 ± 0.1	0.4 ± 0.4
P	C	38.0 ± 0.0	31.5 ± 0.4	15.8 ± 0.3	15.0 ± 0.3	22.1 ± 0.8	171.0 ± 9.4	0.0 ± 0.0	0.4 ± 0.3
P	P	38.0 ± 0.0	31.5 ± 0.6	15.8 ± 0.4	15.0 ± 0.3	23.1 ± 0.7	178.1 ± 8.3	0.1 ± 0.0	0.7 ± 0.4

Table 2
Summary of the added nutrients and their quantities (kg ha⁻¹), the commercial products used and their timing of application to the respective treatments. N* = Nitrogen thinned and Nitrogen unthinned.

Year	Plot	Product 1	Product 2	N	P	Ca	Mg	S	B
2011	N*	Yara Skog-CAN		200	0	37	18	0	1.5
2012	N*			0	0	0	0	0	0
Total	**N***			**200**	**0**	**37**	**18**	**0**	**1.5**
2011	NP	Yara Skog-CAN	Yara Superfosfat P20	200	200	37	18	12	1.5
2012	NP		Yara Superfosfat P20	0	200	0	0	12	0
Total	**NP**			**200**	**400**	**37**	**18**	**24**	**1.5**
2011	P	Yara Forforiravinne 1–9–0 Ca		22	200	140	0	222	0
2012	P	Yara Superfosfat P20		0	200	0	0	12	0
Total	**P**			**22**	**400**	**140**	**0**	**234**	**0**

normally distributed errors and variance homoscedasticity. The LMEs for PAI showed no gross violations of the model assumptions. Heteroscedasticity occurred in the LME for stem volume yield in the P experiment and was modelled using an exponential variance function (*varExp*) with fertilisation treatment as grouping variable (stratified variance modelling by treatment group; R packge *nlme*, Pinheiro et al., 2023). In the P experiment, heteroscedastic error patterns in the LMEs associated with the foliar N concentration were modelled using an exponential variance function (*varExp*). In case of the foliar P concentration, a combination of a power variance function (*varPower*) and a constant variance function (*varIdent*) allowing different variances across treatment groups, were used. In the LME related to the P/N ratio, heteroscedasticity was modelled using an exponential variance function (*varExp*) with 'year' as grouping variable. In the NP experiment, the LME associated with leaf N showed homogeneous errors. Heteroscedasticity in the LME for leaf P was dealt with using a constant variance function permitting differing variance among treatment groups (*varIdent*), while a power variance function (*varPower*) was used in the P/N analysis. In the LME for the LAI related to the P experiment, heteroscedasticity was modelled using an exponential variance function (*varExp*) with fertilisation treatment as grouping variable.

The significance of the fixed effects was determined using a backwards selection approach based on likelihood ratio tests. To minimise disruption of the reading flow, we report the degrees of freedom of the *L*-statistic as subscript. *Post hoc* testing was performed using Tukey contrasts to determine significant differences at $\alpha = 0.05$ between the different fertilisation treatments (R package *emmeans*, Lenth, 2023).

3. Results

3.1. Meteorological conditions

The SPEI values indicated rather moist conditions until the end of 2014, followed by an intermediate year, and a relatively dry period from 2016 – 2019 (Fig. 2). The lowest SPEI values, around −1.5, occurred in 2018 and in the beginning of 2019 in the wake of the severe pan-European 2018 summer drought.

Throughout the study, mean monthly air temperature during the May–September growing season ranged between 8.9 °C (May 2015) and 19.3 °C (July 2018). Soil temperature at 20 cm depth never dropped below the freezing point with a winter minimum of 0.2 °C and summer maximum of 18 °C (Fig. 2). Monthly precipitation varied between 8.5 mm (July 2018) and 214 mm (September 2012) during the study period (Fig. 2).

Table 3
Soil phosphorous, nitrate and ammonium concentration as well as gravimetric water content (GWC) and water holding capacity (WHC) in 2023 in control and P-treated plots of the P trial and the control plots of the NP trial. Means ± standard deviation (*n* = 6).

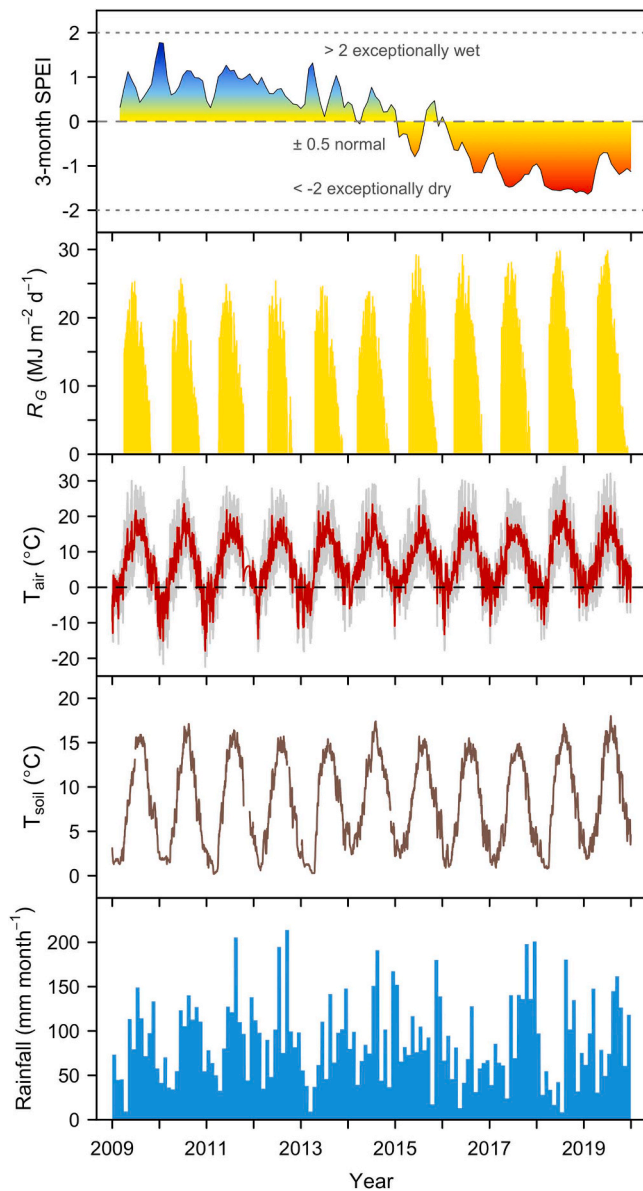| Experiment	Treatment	P (µg g⁻¹)	NO$_3^-$ (µg g⁻¹)	NH$_4^+$ (µg g⁻¹)	GWC (%)	WHC (%)	Share of particles (< 0.2 mm)
P	C	0.1 ± 0.02	1.2 ± 0.1	0.8 ± 0.1	22.8 ± 2.0	57.8 ± 3.2	38.4 ± 5.3
P	P	1.6 ± 1.1	1.2 ± 0.1	0.5 ± 0.1	21.4 ± 2.3	52.2 ± 1.7	38.1 ± 3.4
NP	C	0.03 ± 0.01	0.8 ± 0.2	0.9 ± 0.3	27.7 ± 3.9	56.7 ± 3.9	33.5 ± 6.3

Fig. 2. 3-month Standardized Precipitation-Evaporation Index (SPEI), daily global radiation (R_G) during the growing season, air temperature at 1.7 m height (T_{air}), soil temperature at 20 cm depth (T_{soil}), and monthly precipitation near the study site. The red line in the T_{air} plot indicates daily means and the surrounding grey area gives the daily minima and maxima.

3.2. Tree growth

In the P experiment, there was no significant treatment × year interaction on PAI ($L_1 = 1.55$, $P = 0.21$) but both main effects were statistically significant. Adding 200 kg P ha^{-1} to the strongly P-deficient soil (Table 3) increased PAI by 21 % (+ 3.74 m^3 ha^{-1} yr^{-1}) relative to the control from 2011 to 2014 and by 18 % (+ 2.63 m^3 ha^{-1} yr^{-1}) in the 2015–2019 period ($L_1 = 23.52$, $P < 0.001$; Fig. 3A). Irrespective of treatment, PAI was 24 % higher in the moister first period than in the following markedly drier period (Figs. 2 and 3 A; $L_1 = 28.79$, $P < 0.001$; Fig. 3A). The P-driven stimulation of PAI resulted in a significantly larger stem volume compared to the control (+ 10 %, $L_1 = 3.86$, $P = 0.049$; Fig. 3B).

In the NP experiment, conducted on severely P-depauperate soil (Table 3), we found a significant treatment × year interaction on PAI ($L_3 = 16.01$, $P = 0.001$). In the 2009–2014 period, a *post hoc* analysis revealed that all fertiliser treatments increased PAI significantly relative

to the control (Fig. 3C). The peak increase of 38 % occurred in the N-unthinned treatment (+ 6.8 m^3 ha^{-1} yr^{-1}), which was significantly higher than the 20 % increase in PAI observed in the N treatment (+ 3.6 m^3 ha^{-1} yr^{-1}) but did not differ significantly from the 23 % PAI increase following N+P addition (+ 4.0 m^3 ha^{-1} yr^{-1}).

In the second, notably drier period between 2015 and 2019, the N and N-unthinned treatments produced virtually no extra growth compared to the unfertilised control while N+P addition caused a significant increase in PAI of 29 % (+ 5.3 m^3 ha^{-1} yr^{-1}; Fig. 3C). At the final assessment in 2019, the stem volume of standing trees was significantly greater in all treatments compared to the control ($L_3 = 53.8$, $P < 0.001$). N-addition alone increased stem volume by 10 % in thinned plots and by ca. 39 % in unthinned stands, while the joint application of N+P resulted in a 16 % increase in stem volume in thinned plots (Fig. 3D).

3.3. Needle N, P and P/N

In the P experiment, P addition caused a small increase in foliar N compared to the control in 2012 (+11 %) and 2013 (+8 %) but not in 2016, and on a whole this trend did not result in a significant treatment × year interaction at an alpha level of 0.05 ($L_2 = 4.99$, $P = 0.082$). In a simplified model without interaction term, the main effect of P addition on foliar N was also not significant ($L_1 = 2.71$, $P = 0.099$). Overall, foliar N showed a significant decrease over time from around 1.5 to 1.2 % (main effect of assessment year: $L_2 = 30.54$, $P < 0.001$; Fig. 4A). As anticipated, P fertilisation strongly increased foliar P concentration relative to the control, but the effect size varied across years from 2.5 to 3.4-fold (smallest increase in 2016) resulting in a significant treatment × year interaction ($L_2 = 20.97$, $P < 0.001$; Fig. 4 B). P addition strongly increased foliar P/N ratios and this effect varied with time resulting in a significant treatment × year interaction ($L_2 = 11.87$, $P = 0.003$; Fig. 4C). In the control trees, foliar P/N ranged between 7.3 and 7.5 while needles from P-treated trees showed values between 18.4 and 23 (Fig. 4C). In the NP experiment, we detected a significant treatment × year interaction on foliar N concentration ($L_6 = 31.83$, $P < 0.001$; Fig. 4D). The largest treatment effect occurred in 2012, when N-fertilised trees showed the highest foliar N, significantly exceeding control values by 31 % (Fig. 4D). Trees in the N-unthinned treatment also showed significantly higher foliar N compared to the control (+16 %) while the N+P treatment did not result in statistically significant differences (Fig. 4D). In 2013, the strongly elevated foliar N in the N-treatment had vanished and only the trees in the N-unthinned treatment showed significantly higher needle N relative to the control (+14 %, Fig. 4D). In 2016, all treatments showed similar foliar N values around 1.3 % (Fig. 4D). Foliar P concentrations did not differ significantly among the control, N and N-unthinned treatments (ca. 840 – 1040 mg kg^{-1}) but were between 2.3 and almost three times greater in needles of trees receiving N+P (Fig. 4E). As this pattern was consistent across assessments, there was no treatment × year interaction ($L_6 = 5.72$, $P = 0.455$) but both main effects were statistically significant (fertiliser treatment: $L_3 = 34.13$, $P < 0.001$; year: $L_2 = 19.95$, $P < 0.001$). Foliar P/N also exhibited a significant treatment × year interaction ($L_6 = 12.85$, $P = 0.045$). The N+P treatment invariably resulted in greatly elevated P/N ratios between 13.6 and 16.4 across years, while the values in the other treatments remained consistently below the critical P/N ratio of 10 (indicating a shift towards P-limitation), albeit with some statistically significant differences in the first year of assessment (Fig. 4F).

3.4. LAI

In the P experiment, P addition resulted in a small but statistically significant increase in LAI of 5 % roughly 10 years after application ($L_1 = 3.96$, $P = 0.047$, Fig. 5 A). In the NP experiment, we also found a significant overall treatment effect ($L_3 = 51.03$, $P < 0.001$, Fig. 5 B). The greatest LAI of 12.3 occurred in the N-unthinned treatment and a *post hoc* comparison
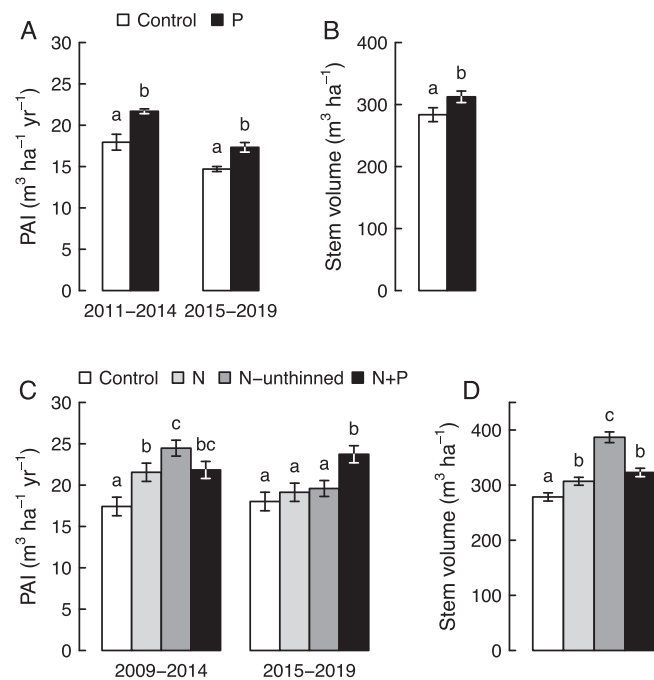
Fig. 3. Periodic annual increment (PAI) of Norway spruce during the two periods 2011–2014 and 2015–2019 in the P experiment (A) and stem volume of standing trees at the time of the final assessment in 2019 (B). PAI in the NP experiment for the time spans 2009–2014 and 2015–2019 (C) and stem volume of standing trees in 2019 (D). Means ± standard errors, $n = 6$ blocks. Different lower-case letters indicate statistically significant differences $\alpha = 0.05$ (*post hoc* analysis based on Tukey contrasts).

showed that it was significantly higher than LAI values in the remaining treatments, corresponding to a 27 % increase over the control, 22 % over the N treatment and 15 % over the N+P treatment. The second highest LAI of 10.7 was seen in the N+P treatment, which was significantly larger than the LAI in the control and the N treatment (Fig. 5. B).

4. Discussion

4.1. Tree growth

When it comes to nutrient amendments in boreal forests, the focus has traditionally been on N, while P has received far less attention so far despite meta-analytic evidence that P limitation is equally pronounced as N limitation (Elser et al., 2007) and models suggesting that this would occur in south-western Sweden (Akselsson et al., 2008). In this study, we set out to assess whether P availability constrains Norway spruce productivity in southern Sweden and to examine the extent of co-limitation with regard to N. During the first assessment period until 2014, individually added P and N produced similar growth increases of around 20 % in our two experiments (Fig. 3), while the combined application of N and P in the NP experiment failed to stimulate productivity further. This hints at sub-additive independent co-limitation according to the widely accepted framework of nutrient co-limitation by Harpole et al. (2011), *i.e.* both N and P applied individually stimulate growth, but the effect of the joint addition of N and P is smaller than the sum of the individual responses. However, since our NP experiment lacks a pure P treatment, we cannot provide conclusive evidence of sub-additive independent co-limitation, as this requires a full factorial experiment to avoid confounding. The level of the N-driven growth stimulation in thinned stands in our study is about a third lower than the *ca.* 30 % (10–20 m³ ha⁻¹) commonly achieved with the traditional one-time fertilisation late in the rotation (Hedwall et al., 2014; Ingerslev et al., 2001). Stand developmental stage certainly plays a role in this context, with younger Norway spruce stands (∼ 20 years) responding more vigorously to elevated N supply (Blaško et al., 2022; Svensson et al., 2023a) and therefore one might anticipate stronger fertilisation effects

in our study. Blaško et al. (2022) showed that long-term N-addition in young Norway spruce stands in central and southern Sweden increased aboveground biomass C accumulation 1.5 times more than belowground (predominantly stumps and coarse roots > 2 mm), while fine root biomass surprisingly remained unchanged. Soil N enrichment resulting from long-term elevated atmospheric N deposition (Bertills and Näsholm, 2000; Karlsson et al., 2022) has partly eliminated the widespread N deficiency in the wider study region (as suggested by the relatively high initial site indices), which may largely explain the lower-than-expected growth stimulation. This notion agrees with the study by Bergh et al. (2014) that found no overall N-related growth stimulation in response to long-term fertilisation in Norway spruce stands predominantly located in southern Sweden. The authors ascribed the lacking N growth response to high initial site fertility either resulting from anthropogenic N loading or due to natural causes such as edaphic conditions. This area of Sweden typically features soils with a strong accumulation of organic matter, which can accumulate N over time. In a re-fertilisation study using long-term N-addition trials in mature Scots pine and Norway spruce stands across Sweden, N supply alone (2–14 years after the previous application) increased growth on average by 57 %, while its combination with P, K and magnesium produced only insignificant growth gains (Jacobson and Pettersson, 2001). This lack of an increase in effect size with joint N and P application relative to pure N application reported by Jacobson and Pettersson (2001) is in line with our findings after the first assessment under favourable weather conditions (but see discussion below related to the drier period during the second assessment). However, similar to our NP experiment, Jacobson and Petterson's (2001) study did not include the addition of P alone and therefore independent co-limitation by N and P could not be reliably established.

Nitrogen addition to soils may increase P availability and uptake through an upregulation of phosphatase activity and thus delay or alleviate P limitation (Arenberg and Arai, 2021; Marklein and Houlton, 2012). Reductions in soil pH resulting from long-term N fertilisation (Högberg et al., 2006) can have the opposite effect on the availability of P, as it becomes increasingly immobilised by aluminium (Al^{3+}) and iron
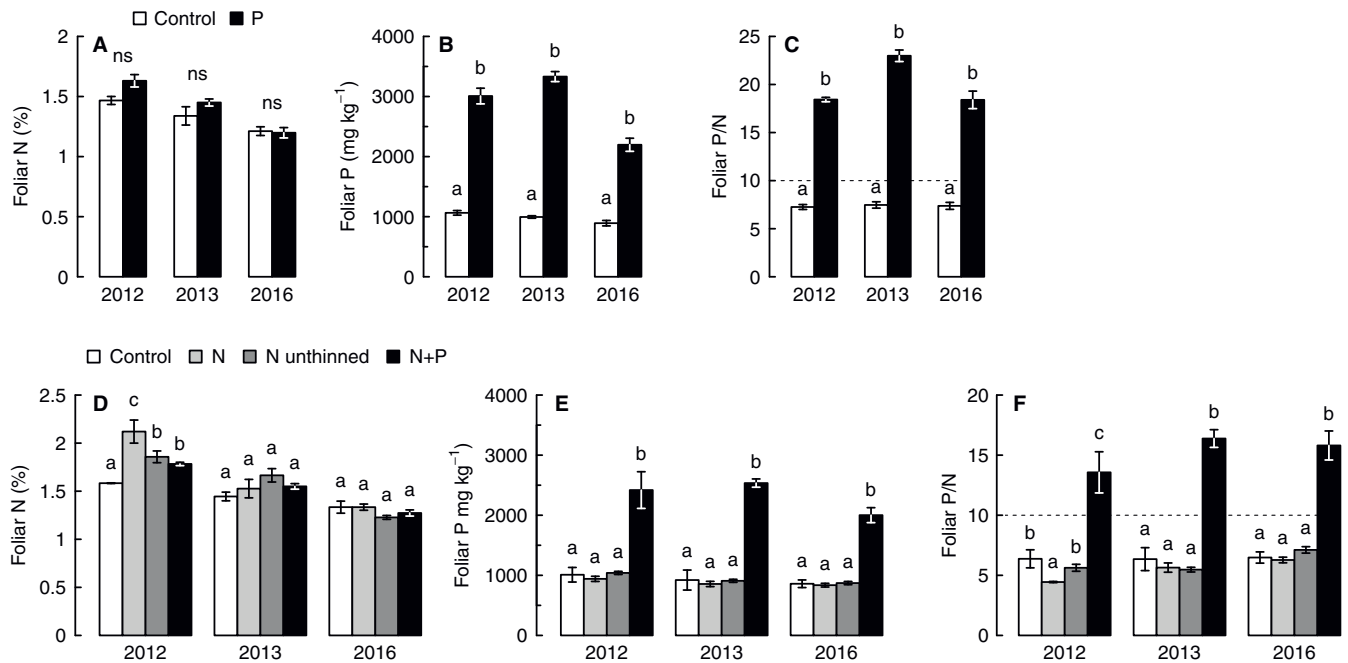
Fig. 4. (A) Foliar N (%), (B) foliar P (mg kg^{-1}) and (C) foliar P/N of Norway spruce in the pure P experiment in 2012, 2013 and 2016. (D) Foliar N (%) and (E) foliar P (mg kg^{-1}) and (F) foliar P/N of Norway spruce in the NP experiment in the same sampling years. Means ± standard errors ($n = 3$ blocks in the P trial and $n = 3–6$ plots in the N+P trial). ns = not significant. Different lower-case letters indicate statistically significant differences at $\alpha = 0.05$ (*post hoc* analysis based on Tukey contrasts). The foliar P/N ratio was expressed as a percentage of P to N on a mass basis. The dashed lines in C and F indicate P/N target ratios for Norway spruce according to Linder (1995).
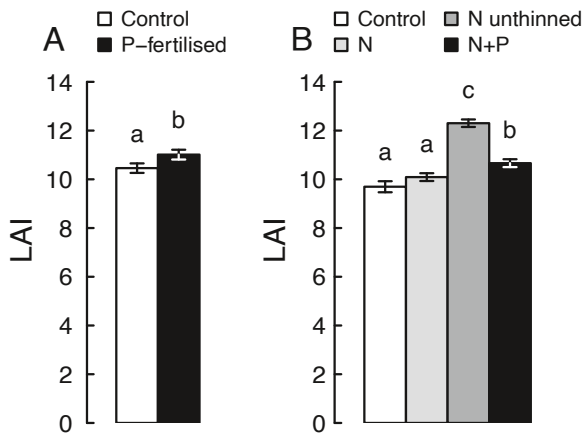

Fig. 5. Leaf area index (LAI) in the P experiment (A) and the NP experiment (B) in spring 2023. Means ± standard error, $n = 6$ blocks. Different lower-case letters indicate statistically significant differences at $\alpha = 0.05$ (*post hoc* analysis using Tukey contrasts).

(Fe^{3+}) ions. The unchanged foliar P levels in the N treatments relative to the control seen in our NP experiment support neither of the above scenarios (Fig. 4 E). Given the low soil pH at our sites (4.4 – 4.7) together with the strong P deficiency, one would expect P immobilisation to prevail and thus the steady foliar P values could be indicative of a dynamic equilibrium between P mobilisation and immobilisation. However, suboptimal foliar P/N ratios in the N treatments of our NP experiment clearly indicate imbalances in P:N stoichiometry, which could only be eliminated when P was included (see Fig. 4F and Section 4.2 below).

The N-induced stimulation of PAI observed in our NP experiment during the first assessment period until 2014, disappeared completely during the second assessment period (2015–2019), while the N+P treatment continued to generate greater growth (Fig. 3). This finding probably largely reflects differences in soil nutrient retention. Phosphorous mobility in soils is quite low, resulting in small leaching losses, which means that P additions can cause a sustained increase in soil P availability as evidenced by elevated soil P supply 30 years after fertilisation at a similar site in southern Sweden (Fransson and Bergkvist, 2000). The retention of N in the soil after fertilisation is generally lower due to its greater solubility and mobility compared to P. The prevailing coarse-textured glacial till soils in the study area are prone to N-leaching, which may further reduce N availability. We can therefore not rule out that the waning N-fertilisation effect on PAI seen in the second assessment period may at least partly be due to microbial immobilisation, plant uptake (Houle et al., 2024) and/or soil N losses. The stronger P retention in the soil may also promote sustained stimulation of microbial activity, which can improve overall soil nutrient availability (Thirukkumaran and Parkinson, 2002).

Remarkably, the P-induced growth stimulation in the P trial remained almost unchanged during the drier second assessment period (2015–2019). Whether this is related to a P-driven increase in Norway spruce tolerance to water deficit cannot be answered here but warrants further investigation through controlled experiments, as P-mediated stimulation of drought tolerance has been previously reported. For example, in a study on the drought-sensitive, N-fixing *Alnus cremastogyne*, P addition enhanced drought tolerance through an upregulation of the antioxidant defence linked to enhanced enzyme activity and by improving osmotic adjustment (Tariq et al., 2018). The recent finding of a P-ring (P-enriched cells encircling the vascular tissue) in the roots of multiple distantly related plant species, including Stone pine (*Pinus pinea*), also suggests that P plays an important role in solute transport and thus drought adaptation (Acharya and Pesacreta, 2023). Any P-mediated increase in drought resilience will likely be complemented by greater water-use-efficiency of Norway spruce in the future given the strong response of shoot photosynthesis to rising atmospheric CO_2 (Bader et al., 2016). CO_2-driven increases in the WUE of Norway spruce are more closely related to photosynthesis than to water savings

(Leuzinger and Bader, 2012) and it has been shown that WUE improvement requires adequate N supply (Ofori-Amanfo et al., 2023).

In addition to the two potential explanations for the prolonged effect of P fertilization (soil retention, potential role in drought tolerance), there may also be physiological benefits associated with a favorable P supply, promoting longer-lasting growth stimulation compared to N. Ample P availability is vital for membrane integrity and ensures that the energy requirements for nutrient uptake and transport in plants (specifically adenosine triphosphate-fueled transporters) are met (Malhotra et al., 2018), which is an essential prerequisite for supporting high growth rates. In addition, P supports root development and is heavily involved in photosynthetic C assimilation mainly via energy transfer and enzyme regulation (e.g. Rubisco activation), therefore P shortage may rapidly trigger cascading effects that directly and indirectly limit key photosynthetic processes such as photophosphorylation or the regeneration of ribulose-1,5-bisphosphate (RuBP, the principal CO_2 acceptor) (Malhotra et al., 2018) resulting in reduced C fixation and hence potential growth losses, despite adequate N supply.

In our study, the N-driven stimulation of PAI was stronger in unthinned than in thinned plots and this is consistent with findings for Scots pine which maintained stronger fertiliser responses in un-thinned vs. thinned plots over a 30-year period across Sweden (Bergh et al., 2014). We come to the same conclusion as Bergh et al. (2014), that thinning operations must have reduced LAI below the level required to achieve maximum productivity. With regard to forest management, this suggests that thinning guidelines should be reconsidered if forest planning includes fertilisation (Persson et al., 2024). One should also bear in mind that the strong stimulation of productivity in unthinned stands may be offset over time by higher competition-based mortality (Pretzsch and Grote, 2024), whereas timber quality may be even better in unthinned stands (Krajnc et al., 2019).

Finally, it should be noted that Brandel's (1990) empirical volume function assumes a strict allometric DBH-height relationship and does therefore not take into account potential fertiliser-induced increases in biomass allocation to branches and foliage. While the leaf/stem biomass ratio in closed-canopy Norway spruce stands has been reported to remain largely unaffected by fertiliser addition (Axelsson and Axelsson, 1986; Blaško et al., 2022), the biomass allocation to adventitious branches increased by 30 % in response to nutrient enrichment (Axelsson and Axelsson, 1986). This implies that our nutrient-driven gains in stem volume should be regarded as slightly conservative estimates.

4.2. Foliar N, P and P/N

In 2012 and 2013, P-treated trees in the P trial showed slightly higher foliar N than the control but these differences had entirely vanished by 2016 (Fig. 4). Although this trend was not statistically significant (at the given alpha level and sample size), it may imply a P-induced stimulation of N uptake or reallocation to maintain foliar nutrient stoichiometry as has previously been shown for P-fertilised *Eucalyptus grandis* (Graciano et al., 2006) and thus deserves closer examination in future studies. In the NP experiment, fertiliser-induced increases in needle N seen in N or N-unthinned treatments in 2012–2013 seem to have been reallocated to stem growth as indicated by similar values across treatments in 2016. The generally lower foliar N values in 2016 may reflect reduced N availability due to immobilisation, accrual in plant biomass and soil losses but could also be partly related to the onset of drier conditions hampering N uptake. Foliar N concentrations in Norway spruce growing in the Fennoscandian region have been reported to range between 1 % and 1.8 % (Linder, 1995; Sikström et al., 1998), which puts our values from 2012 and 2013 in the upper range (Fig. 4). The relatively high foliar N values seen in the control trees of both experiments, imply that continuously high atmospheric N deposition in this area has largely eliminated needle N deficiency (Karlsson et al., 2022) and to some extent, this could even be due to foliar N uptake (Rennenberg and Gessler, 1999; Wilson and Tiley, 1998). The addition

of P alone (P experiment) or in combination with N (NP experiment) increased needle P and thus P/N well beyond the empirically established target ratio of 10 % (percent of N on a mass basis, Linder, 1995), while all other treatments including the control showed P/N ratios < 10 indicating suboptimal P supply relative to N availability (Ericsson et al., 1993; Linder, 1995). Trees can stimulate P mobilisation through enhanced phosphatase activity under various soil stress conditions including P deficiency (Clarholm and Rosengren-Brinck, 1995; Haroni et al., 2020) and the same effect and underlying mechanism have been reported for N addition (Marklein and Houlton, 2012). However, given the low baseline level of soil P in the control plots of both experiments (Table 3), it is highly unlikely that greater phosphatase activity could make sufficient P available to eliminate the prevailing deficiency, which is corroborated by our foliar P and P/N data from the NP experiment (Fig. 4). However, since foliar P levels did not decrease in response to N addition, this may indicate a sufficiently large phosphatase effect to counteract the probable increase in P immobilisation related to a decline in pH usually caused by N addition (Högberg et al., 2006).

Although the addition of N and P generally leads to greater biomass accumulation above- and belowground, the allocation of resources typically shifts in favour of aboveground organs (Blaško et al., 2022; Feng et al., 2023). If fewer fine roots result from of such a change in resource allocation, this could affect nutrient uptake. However, our results show no sign of impaired nutrient uptake regarding N and P, which is consistent with the unchanged fine root biomass in response to nutrient addition across five long-term fertilisation experiments in Norway spruce stands in central and southern Sweden (Blaško et al., 2022).

4.3. LAI

The potential for nutrient-driven increases in LAI is greatest in aggrading conifer stands where canopies have not closed yet (Albrektson et al., 1977; Brockley, 2010; Colbert et al., 1990). At the time of fertilisation, our stands were at mid-rotation and had already reached canopy closure, leaving little scope for further increases in leaf area, although peak LAI values > 20 have been documented for conifer stands (Asner et al., 2003; Iio et al., 2014). Indeed, our findings from the P experiment indicate that stand-level leaf area in these southern Swedish spruce stands is P-limited, albeit only to a small extent. This is corroborated by the results of the NP experiment, where among the thinned treatments only the N+P treatment stimulated greater LAI. Unsurprisingly, in the absence of thinning substantially higher LAI values close to 13 can be attained (see N-unthinned in Fig. 5 B). We have not measured foliage mass but Blaško et al. (2022) reported that needle biomass remained unresponsive to NPK-fertilisation across five long-term studies in young Norway spruce plantations in central and southern Sweden. If this holds true for our experiments, then the observed increase in LAI would be a result of an increase in SLA (specific leaf area), which has indeed been reported to be more responsive to P rather than N in Mongolian pine (Zheng et al., 2017).

5. Conclusions

Our findings demonstrate that on (relatively) nutrient-poor soils it is possible to achieve a similarly strong stem growth stimulation in Norway spruce with the addition of P instead of N. The lower-than-expected growth response to N fertilisation and the relatively high initial site indices indicate a partial elimination of soil N deficiency through chronic N deposition in southern Sweden. Our study provides fundamental and practical information for the development of sustainable nutrient management strategies in Norway spruce stands. Most importantly, in Norway spruce growing regions with high N loading originating from atmospheric deposition or other sources, we strongly recommend prioritising the supply of P over N.

CRediT authorship contribution statement

Carl Svensson: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Martin Karl-Friedrich Bader:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Data curation. **Ann-Mari Fransson:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Claes-Göran Alriksson:** Writing – review & editing, Data curation. **Martin Goude:** Writing – review & editing, Data curation, Conceptualization. **Johan Bergh:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of Competing Interest

We have no conflicts of competing interest to disclose.

Data availability

Data will be made available on request.

Acknowledgements

References

Acharya, A., Pesacreta, T.C., 2023. P-ring: the conserved nature of phosphorus enriched cells in seedling roots of distantly related species. Plant Signal Behav. 18, 2217389 https://doi.org/10.1080/15592324.2023.2217389.

Akselsson, C., Westling, O., Alveteg, M., Thelin, G., Fransson, A.M., Hellsten, S., 2008. The influence of N load and harvest intensity on the risk of P limitation in Swedish forest soils. Sci. Total Environ. 404, 284–289. https://doi.org/10.1016/j.scitotenv.2007.11.017.

Albrektson, A., Aronsson, A., Tamm, C.O., 1977. Effects of forest fertilization on primary production and nutrient cycling in the forest ecosystem. Silva Fenn. 11, 233–239.

Almeida, J.P., Rosenstock, N.P., Forsmark, B., Bergh, J., Wallander, H., 2019. Ectomycorrhizal community composition and function in a spruce forest transitioning between nitrogen and phosphorus limitation. Fungal Ecol. 40, 20–31. https://doi.org/10.1016/j.funeco.2018.05.008.

Arenberg, M.R., Arai, Y., 2021. Nitrogen species specific phosphorus mineralization in temperate floodplain soils. Sci. Rep. 11, 17430 https://doi.org/10.1038/s41598-021-96885-5.

Asner, G.P., Scurlock, J.M.O., Hicke, J.A., 2003. Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. Glob. Ecol. Biogeogr. 12, 191–205. https://doi.org/10.1046/j.1466-822X.2003.00026.x.

Axelsson, E., Axelsson, B., 1986. Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization. Tree Physiol. 2, 189–204. https://doi.org/10.1093/treephys/2.1-2-3.189.

Bader, M.K.-F., Mildner, M., Baumann, C., Leuzinger, S., Körner, C., 2016. Photosynthetic enhancement and diurnal stem and soil carbon fluxes in a mature Norway spruce stand under elevated CO₂. Environ. Exp. Bot. 124, 110–119. https://doi.org/10.1016/j.envexpbot.2015.12.005.

Bahr, A., Ellström, M., Bergh, J., Wallander, H., 2015. Nitrogen leaching and ectomycorrhizal nitrogen retention capacity in a Norway spruce forest fertilized with nitrogen and phosphorus. Plant Soil 390, 323–335. https://doi.org/10.1007/s11104-015-2408-6.

Bergh, J., Linder, S., Lundmark, T., Elfving, B., 1999. The effect of water and nutrient availability on the productivity of Norway spruce in northern and southern Sweden. Ecol. Manag. 119, 51–62. https://doi.org/10.1016/S0378-1127(98)00509-X.

Bergh, J., Nilsson, U., Allen, H.L., Johansson, U., Fahlvik, N., 2014. Long-term responses of Scots pine and Norway spruce stands in Sweden to repeated fertilization and thinning. Ecol. Manag. 320, 118–128. https://doi.org/10.1016/j.foreco.2014.02.016.

Bertills, U., Näsholm, T., 2000. Effects of Nitrogen Deposition on Forest Ecosystems, Swedish Environmental Protection Agency.

Blaško, 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, 156327. https://doi.org/10.1016/j.scitotenv.2022.156327.

Brandel, G., 1990. Volymfunktioner för enskilda träd. Tall, gran och björk. Garpenberg.

Brockley, R.P., 2010. Effects of repeated fertilization in a young spruce stand in central British Columbia. Can. J. Res 40, 1687–1697. https://doi.org/10.1139/X10-123.

Cannell, M.G.R., 1989. Physiological basis of wood production: a review. Scand. J. Res 4, 459–490. https://doi.org/10.1080/02827588909382582.

Clarholm, M., Rosengren-Brinck, U., 1995. Phosphorus and nitrogen fertilization of a Norway spruce forest-effects on needle concentrations and acid phosphatase activity in the humus layer. Plant Soil 175, 239–249. https://doi.org/10.1007/BF00011360.

Colbert, S.R., Jokela, E.J., Neary, D.G., 1990. Effects of annual fertilization and sustained weed control on dry matter partitioning, leaf area, and growth efficiency of juvenile loblolly and slash pine. Sci 36, 995–1014. https://doi.org/10.1093/forestscience/36.4.995.

R. Core Team, 2023. R: A Language and Environment for Statistical Computing.

Dralle, K., Larsen, J.B., 1995. Growth response to different types of NPK-fertilizer in Norway spruce plantations in Western Denmark. Plant Soil 168–169 501–504. https://doi.org/10.1007/BF00029362.

Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol. Lett. 10, 1135–1142. https://doi.org/10.1111/j.1461-0248.2007.01113.x.

Ericsson, T., 1995. Growth and shoot: root ratio of seedlings in relation to nutrient availability. Plant Soil 168–169 205–214. https://doi.org/10.1007/BF00029330.

Ericsson, A., Nordén, L.G., Näsholm, T., Walheim, M., 1993. Mineral nutrient imbalances and arginine concentrations in needles of *Picea abies* (L.) Karst. from two areas with different levels of airborne deposition. Trees 8, 67–74. https://doi.org/10.1007/BF00197683.

Feng, H., Guo, J., Peng, C., Kneeshaw, D., Roberge, G., Pan, C., Ma, X., Zhou, D., Wang, W., 2023. Nitrogen addition promotes terrestrial plants to allocate more biomass to aboveground organs: a global meta-analysis. Glob. Chang Biol. 29, 3970–3989. https://doi.org/10.1111/gcb.16731.

Fransson, A.M., Bergkvist, B., 2000. Phosphorus fertilisation causes durable enhancement of phosphorus concentrations in forest soil. Ecol. Manag. 130 https://doi.org/10.1016/S0378-1127(99)00184-X.

Goude, M., Nilsson, U., Holmström, E., 2019. Comparing direct and indirect leaf area measurements for Scots pine and Norway spruce plantations in Sweden. Eur. J. Res 138, 1033–1047. https://doi.org/10.1007/s10342-019-01221-2.

Graciano, C., Goya, J.F., Frangi, J.L., Guiamet, J.J., 2006. Fertilization with phosphorus increases soil nitrogen absorption in young plants of *Eucalyptus grandis*. Ecol. Manag. 236, 202–210. https://doi.org/10.1016/j.foreco.2006.09.005.

Haroni, N.N., Zarafshar, M., Badehian, Z., Sharma, A., Bader, M.K.-F., 2020. Tree seedlings suffer oxidative stress but stimulate soil enzyme activity in oil sludge-contaminated soil in a species-specific manner. Trees 34, 1267–1279. https://doi.org/10.1007/s00468-020-01996-7.

Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E.S., Elser, J.J., Gruner, D.S., Hillebrand, H., Shurin, J.B., Smith, J.E., 2011. Nutrient co-limitation of primary producer communities. Ecol. Lett. 14, 852–862. https://doi.org/10.1111/j.1461-0248.2011.01651.x.

Harrington, C.A., Devine, W.D., 2011. Stand development following precommercial thinning and fertilization treatments in a western redcedar (*Thuja plicata*) dominated forest. Can. J. Res 41, 151–164. https://doi.org/10.1139/X10-193.

Harrington, C.A., Wierman, C.A., 1990. Growth and foliar nutrient response to fertilization and precommercial thinning in a coastal western red cedar stand. Can. J. Res. 20, 764–773. https://doi.org/10.1139/x90-101.

Hedwall, P.O., Bergh, J., Brunet, J., 2017. Phosphorus and nitrogen co-limitation of forest ground vegetation under elevated anthropogenic nitrogen deposition. Oecologia 185, 317–326. https://doi.org/10.1007/s00442-017-3945-x.

Hedwall, P.O., Gong, P., Ingerslev, M., Bergh, J., 2014. Fertilization in northern forests - biological, economic and environmental constraints and possibilities. Scand. J. Res 29, 301–311. https://doi.org/10.1080/02827581.2014.926096.

Högberg, P., Fan, H., Quist, M., Binkley, D., Tamm, C.O., 2006. Tree growth and soil acidification in response to 30 years of experimental nitrogen loading on boreal forest. Glob. Chang Biol. 12, 489–499. https://doi.org/10.1111/j.1365-2486.2006.01102.x.

Houle, D., Moore, J.D., Renaudin, M., 2024. Eastern Canadian boreal forest soil and foliar chemistry show evidence of resilience to long-term nitrogen addition. Ecol. Appl. 34, e2958 https://doi.org/10.1002/eap.2958.

Iio, A., Hikosaka, K., Anten, N.P.R., Nakagawa, Y., Ito, A., 2014. Global dependence of field-observed leaf area index in woody species on climate: a systematic review. Glob. Ecol. Biogeogr. 23, 274–285. https://doi.org/10.1111/geb.12133.

Ingerslev, M., Mälkönen, E., Nilsen, P., Nohrstedt, H.Ö., Óskarsson, H., Raulund-Rasmussen, K., 2001. Main findings and future challenges in forest nutritional research and management in the Nordic countries. Scand. J. Res 16, 488–501. https://doi.org/10.1080/02827580152699330.

IUSS Working Group WRB, 2015. World Reference Base for Soil Resources 2014, update 2015 International soil classification system for naming soils and creating legends for soil maps., International soil classification system for naming soils and creating legends for soil maps. Rome.

Jacobson, S., Pettersson, F., 2001. Growth responses following nitrogen and N-P-K-Mg additions to previously N-fertilized Scots pine and Norway spruce stands on mineral soils in Sweden. Can. J. Res 31, 899–909. https://doi.org/10.1139/cjfr-31-5-899.

Karlsson, P.E., Akselsson, C., Hellsten, S., Pihl Karlsson, G., 2022. Twenty years of nitrogen deposition to Norway spruce forests in Sweden. Sci. Total Environ. 809, 152192 https://doi.org/10.1016/j.scitotenv.2021.152192.

Krajnc, L., Farrelly, N., Harte, A.M., 2019. The effect of thinning on mechanical properties of Douglas fir, Norway spruce, and Sitka spruce. Ann. Sci. 76, 3. https://doi.org/10.1007/s13595-018-0787-6.

Leuzinger, S., Bader, M.K.-F., 2012. Experimental vs. modeled water use in mature Norway spruce (*Picea abies*) exposed to elevated CO_2. Front Plant Sci. 3 (229) https://doi.org/10.3389/fpls.2012.00229.

Linder, S., 1995. Foliar analysis for detecting and correcting nutrient imbalances in Norway spruce. Ecol. Bull. 44, 178–190.

Malhotra, H., Vandana, Sharma, S., Pandey, R., 2018. Phosphorus nutrition: plant growth in response to deficiency and excess. in: Plant Nutr. Abiotic Stress Toler. https://doi.org/10.1007/978-981-10-9044-8_7.

Manter, D.K., Kavanagh, K.L., Rose, C.L., 2005. Growth response of Douglas-fir seedlings to nitrogen fertilization: importance of Rubisco activation state and respiration rates. Tree Physiol. 25, 1015–1021. https://doi.org/10.1093/treephys/25.8.1015.

Marklein, A.R., Houlton, B.Z., 2012. Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems. N. Phytol. 193, 696–704. https://doi.org/10.1111/j.1469-8137.2011.03967.x.

Newton, P.F., Amponsah, I.G., 2006. Systematic review of short-term growth responses of semi-mature black spruce and jack pine stands to nitrogen-based fertilization treatments. Ecol. Manag. 237, 1–14. https://doi.org/10.1016/j.foreco.2006.10.009.

Nilsen, P., 2001. Fertilization experiments on forest mineral soils: a review of the Norwegian results. Scand. J. Res 16, 541–554. https://doi.org/10.1080/02827580152699376.

Nilsen, P., Abrahamsen, G., 2003. Scots pine and Norway spruce stands responses to annual N, P and Mg fertilization. Ecol. Manag. 174, 221–232. https://doi.org/10.1016/S0378-1127(02)00024-5.

Ofori-Amanfo, K.K., Klem, K., Veselá, B., Holub, P., Agyei, T., Juráň, S., Grace, J., Marek, M.V., Urban, O., 2023. The effect of elevated CO_2 on photosynthesis is modulated by nitrogen supply and reduced water availability in *Picea abies*. Tree Physiol. 43, 925–937. https://doi.org/10.1093/treephys/tpad024.

Persson, M., Bader, M.K.-F., Holmström, E., 2024. Exploring the interplay between within-stand variation and thinning practices in southern Sweden. Ecol. Manag. 561, 121888 https://doi.org/10.1016/j.foreco.2024.121888.

Pettersson, F., Högbom, L., 2004. Long-term growth effects following forest nitrogen fertilization in *Pinus sylvestris* and *Picea abies* stands in Sweden. Scand. J. Res 19, 339–347. https://doi.org/10.1080/02827580410030136.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Core Team, R., 2023. nlme: linear and nonlinear mixed effects models. R. -Proj. v. 3., 1–164.

Pretzsch, H., Grote, R., 2024. Tree Mortality: Revisited Under Changed Climatic and Silvicultural Conditions, in: Lüttge, U., Cánovas, F.M., Risueño, M.-C., Leuschner, C., Pretzsch, Hans (Eds.), Progress in Botany Vol. 84. Springer Nature Switzerland, Cham, pp. 351–393. https://doi.org/10.1007/124_2023_69.

Rennenberg, H., Gessler, A., 1999. Consequences of N deposition to forest ecosystems - Recent results and future research needs. Water Air Soil Pollut. 116, 47–64. https://doi.org/10.1023/A:1005257500023.

Roberntz, P., Stockfors, J., 1998. Effects of elevated CO_2 concentration and nutrition on net photosynthesis, stomatal conductance and needle respiration of field-grown Norway spruce trees. Tree Physiol. 18, 233–241. https://doi.org/10.1093/treephys/18.4.233.

Saarsalmi, A., Mälkönen, E., 2001. Forest fertilization research in Finland: a literature review. Scand. J. Res 16, 514–535. https://doi.org/10.1080/02827580152699358.

Sikström, U., Nohrstedt, H.Ö., Pettersson, F., Jacobson, S., 1998. Stem-growth response of *Pinus sylvestris* and *Picea abies* to nitrogen fertilization as related to needle nitrogen concentration. Trees 12, 208–214. https://doi.org/10.1007/PL00009712.

Svensson, C., Bader, M.K.-F., Forsmark, B., Nilsson, U., Lundmark, T., Nordin, A., Bergh, J., 2023a. Early and repeated nutrient additions support far greater stemwood production in norway spruce than traditional late-rotation fertilisation. Ecol. Manag. 549, 121425 https://doi.org/10.1016/j.foreco.2023.121425.

Svensson, C., Bader, M.K.-F., Löf, M., Johansson, U., Bergh, J., 2023b. Fertilisation and irrigation have no effects on growth of oak (*Quercus robur*, *Q. petraea*) stands on abandoned farmland in southwest Sweden. Ecol. Manag. 529, 120700 https://doi.org/10.1016/j.foreco.2022.120700.

Tamm, O.C., 1991. Nitrogen in terrestrial ecosystems: questions of productivity, vegetational changes, and ecosystem stability. Ecol. Studies 8, 1–115. https://doi.org/10.1007/978-3-642-75168-4.

Tamm, C.O., Aronsson, A., Popovic, B., Flower-Ellis, J., 1999. Optimum nutrition and nitrogen saturation in Scots pine stands. Stud. Suec. 206.

Tariq, A., Pan, K., Olatunji, O.A., Graciano, C., Li, Z., Sun, F., Zhang, L., Wu, X., Chen, W., Song, D., Huang, D., Xue, T., Zhang, A., 2018. Phosphorous fertilization alleviates drought effects on Alnus cremastogyne by regulating its antioxidant and osmotic potential. Scientific Reports 8, 5644. https://doi.org/10.1038/s41598-018-24038-2.

Thirukkumaran, C.M., Parkinson, D., 2002. Microbial activity, nutrient dynamics and litter decomposition in a Canadian Rocky Mountain pine forest as affected by N and P fertilizers. Ecol. Manag. 159 https://doi.org/10.1016/S0378-1127(01)00432-7.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Clim. 23 https://doi.org/10.1175/2009JCLI2909.1.

Wilson, E.J., Tiley, C., 1998. Foliar uptake of wet-deposited nitrogen by Norway spruce: an experiment using [15]N. Atmos. Environ. 32, 513–518. https://doi.org/10.1016/S1352-2310(97)00042-3.

Zheng, L.L., Zhao, Q., Yu, Z.Y., Zhao, S.Y., Zeng, D.H., 2017. Altered leaf functional traits by nitrogen addition in a nutrient-poor pine plantation: a consequence of decreased phosphorus availability. Sci. Rep. 7, 7415. https://doi.org/10.1038/s41598-017-07170-3.