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Forest fertilization transiently increases soil CO_2 efflux in young Norway spruce stands in Sweden

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ABSTRACT

Late-rotation fertilization of Norway spruce stands is a frequently used management tool in Fennoscandia to increase timber yields. Meanwhile, the growing demand for renewable resources has sparked great interest in earlier and repeated fertilizer application but it remains unclear how this affects carbon dioxide (CO_2) fluxes in the understory, especially forest floor respiration (R_{ff}). This study investigated the effects of forest fertilization on R_{ff} and net forest floor exchange (NFFE) in young, nitrogen (N) limited Norway spruce stands in southern Sweden. In a short-term dose experiment, R_{ff} and NFFE were recorded during 2016 after varying doses of N (0, 150, 300, or 450 kg ha^{-1} of N, hereafter N0, N150, N300, N450) were added to circular, 3-m-diameter plots in April. In a second, long-term experiment, two stand-level fertilizer applications with 150 kg ha^{-1} of N on each occasion were performed in 2014 and 2016 and R_{ff} was measured at semi-regular intervals from mid-2013 to the end of 2017. In the dose experiment, fertilization increased R_{ff} by 23 %, 81 % and 55 % in the N150, N300 and N450 treatments, respectively. Under well-lit conditions, the N300 and N450 treatments significantly enhanced photosynthetic CO_2 uptake of the forest floor vegetation by 97 % and 66 %, respectively, while the N150 treatment had no significant effect. The results of the long-term experiment indicate an initial stimulation of R_{ff}, but this effect was transient. Our findings imply that fertilization in young Norway spruce stands, using the N150 dose (the typical dose used in Swedish forestry), may cause a transient burst in R_{ff} that is far outweighed by nutrient-driven increases in forest floor photosynthesis under favourable light conditions prior to canopy closure.

1. Introduction

Forests play a key role in the global climate system as they absorb huge amounts of CO_2 from the atmosphere and return an almost equal quantity through respiratory processes, with the difference bound as carbon (C) within various compartments but mainly in trees resulting in their vast contribution to terrestrial biomass storage (Artaxo et al., 2022).

Large parts of the world's forests are managed (Lesiv et al., 2022) and the scientific challenge is to understand and quantify how different forest management strategies affect the overall carbon balance (Canadell and Raupach, 2008). A fast-acting silvicultural measure to increase wood production and thereby rapidly sequester more CO_2 is forest fertilization (Bergh et al., 1999; Brockley, 2010; Hedwall et al., 2014). In the Fennoscandian region, where forests often grow on nutrient-poor soils, fertilization can be used and is then typically given as a single dose of N (nitrogen) fertilizer equivalent to 150 kg ha^{-1} of N late during the rotation period (Hedwall et al., 2014). Fertilization of young forests is less common, but the growing demand for forest products requires management options that can guarantee larger commodity flows in the future (Sathre et al., 2010; Kumar et al., 2020). Due to the greater nutrient requirements of vigorously growing juvenile trees,

Abbreviations: GPP, gross primary production; NEE, net ecosystem exchange; NFFE, net forest floor exchange; PPFD, photosynthetic photon flux density; R_{eco}, ecosystem respiration; R_{ff}, forest floor respiration.

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young stands show greater nitrogen use efficiency (the efficiency with which nitrogen is converted to biomass) than older stands that have reached canopy closure (Hyvönen et al., 2008). Early and repeated fertilization could thus provide a viable forest management option to meet the growing demand for forest raw materials. Indeed, a pioneering nutrient optimization study in young Norway spruce stands using a biannual fertilization regimen (125–150 kg ha^{-1} yr^{-1} of N), more than doubled stem volume yield compared to the unfertilized control (Svensson et al., 2023).

Fertilization not only enhances the production of forest biomass but also the amount of C stored in the soil (Johnson, 1992; Johnson and Curtis, 2001; Hyvönen et al., 2007; Mäkipää et al., 2023) through increased litterfall (Marshall et al., 2021; Blaško et al., 2022). Moreover, prior N addition studies have shown reduced rates of CO_2 emissions, likely caused by decreased decomposition of soil organic matter (Olsson et al., 2005; Ågren and Andersson, 2012; Yan et al., 2018; Jörgensen et al., 2021; Marshall et al., 2021), resulting from changes in soil microbial community composition and activity (Janssens et al., 2010; Ramirez et al., 2012), and high rates of N addition have also been suggested to alter the competitive balance between enzymatic lignin mineralization and non-enzymatic lignin oxidation in the soil (Bonner et al., 2019). However low levels of N addition (< 12 kg ha^{-1} yr^{-1} of N) may have minor effects on organic matter decomposition (Maaroufi et al., 2019).

The forest floor CO_2 fluxes comprise respiratory CO_2 losses from soil and ground vegetation (R_{ff}) as well as photosynthetic CO_2 uptake of the ground vegetation resulting in the net forest floor CO_2 exchange (NFFE). Even though fertilization enhances C fixation, *i.e.* gross primary production (GPP), a considerable fraction is respired back from the ecosystem to the atmosphere. The younger the stand (low leaf area index), the larger the contribution of the forest floor vegetation to NFFE, because it constitutes a relatively large proportion of the total biomass compared to the juvenile trees whose growth will eventually result in a closed canopy, blocking much of the light and thereby reducing forest floor vegetation.

This study aimed to determine the effect of fertilization on R_{ff} and NFFE in a young Norway spruce stand (*Picea abies* (L.) Karst.) in southern Sweden to evaluate this forest management tool in the context of climate change mitigation and the burgeoning demand for forest products. Our investigation was based on a one-year dose experiment (0, 150, 300, and 450 kg ha^{-1} of N) and a long-term forest fertilization trial (0 and 150 kg ha^{-1} of N). We anticipated a general increase in NFFE in response to fertilization, due to a growth stimulation of ground vegetation and reduced R_{ff} resulting from decreased decomposition. We further hypothesized that the magnitude of the fertilizer-induced reduction in R_{ff} would increase with increasing fertilizer quantity.

2. Material and methods

2.1. Study site

The experiments were located in Toftaholm, southern Sweden (N 57°0′, E 14°3′) with a humid continental climate, mean annual temperature of 7.0 °C, and mean annual precipitation of *ca* 750 mm during the years 2007–2016 (SMHI, 2017). The bedrock is mainly acid granite and the soil mainly mesic sandy moraine (SGU, 2022) with a CN ratio of about 25.

Soil scarification and planting with three-year-old seedlings of Norway spruce were carried out in 2005 and 2006, after salvage logging of wind-thrown forest, generating spruce-dominated stands with an admixture of naturally generated birch (*Betula pendula and B. pubescens*). Forest floor vegetation was dominated by grasses and mosses interspersed with forbs and raspberry (*Rubus idaeus*). For more details see Håkansson et al. (2021).

2.2. Experimental design

The experimental design corresponds to that of Håkansson et al. (2021) which presents results from measurements of CH_4 and N_2O fluxes from the forest floor.

To investigate the effects of N-fertilization on R_{ff}, two separate experiments were carried out in three adjacent stands with similar soil characteristics and land-use history, a dose experiment to ascertain potential fertilizer concentration effects (N0, N150, N300, and N450) applied at the start of the growing season, and a 4-year long trial using a conventional amount of N (long-term experiment, N150 application in year 1 and 3) (Table 1 and Table 2) from an optimal fertilization concept (Linder, 1995; Stockfors et al., 1997; Bergh et al., 2008). For the long-term experiment soil carbon stock in the top 30 cm of the soil (including organic layer) was measured to 83 ± 14 and 77 ± 15 ton C per hectare in the N0 and N150 treatment, respectively in year 2013.

The dose experiment took place in a stand with slightly lower basal area of Norway spruce, than in the stands of the long-term experiment (total basal area N0 = 4.2 ± 0.4, N150 = 3.8 ± 0.3 34 % and 42 % spruce respectively other part broadleaves Grelle et al. (2023)). A randomized complete block design was used, with six blocks placed 4–10 m apart, each with four circular plots (Ø 3 m). A circular collar (Ø 18.3 cm) was inserted into the soil (10 cm), at the center of each plot to measure R_{ff} and NFFE. Four fertilization treatments (N0, N150, N300, and N450) were allocated randomly to the plots within each block. Fertilizer (Table 1) was distributed evenly by hand across each plot in April 2016. During this procedure the collar was covered, directly after uncovered and separately fertilized to ensure the correct amount of fertilizer was applied on the soil within the collar.

The long-term experiment is a companion study of the study by Grelle et al. (2023) on net ecosystem exchange (NEE) and took place in two Norway spruce stands, one fertilized (N150) and one unfertilized (N0). Stand scale-level fertilization (> 20 ha; 150 kg ha^{-1} of N plus other nutrients in granular form) was applied using a helicopter in April of 2014 and 2016 (Table 1). Within each stand, 10 rectangular galvanized steel collars (Table 2) were installed at representative points (with respect to soil moisture, forest floor composition and cover and distance to the nearest tree) to measure R_{ff}. During the aerial fertilization the collars were covered with plastic foil, and later the same day uncovered, and the soil within manually fertilized to ensure that the correct amount of fertilizer was applied also within the relatively small collars.

2.3. Forest floor respiration (R_{ff})

Measurements of forest floor respiration (R_{ff}) comprised both heterotrophic respiration from soil as well as autotrophic respiration from ground vegetation and tree roots. In the dose experiment, R_{ff} measurements were made 1–5 times per month from April to November 2016 and in June 2017 (Table 2). In the long-term experiment, R_{ff} measurements were performed 1–3 times per month from 2014 to 2017 with the highest frequency during the growing season. In addition, R_{ff} was measured four times in July to September in 2013 prior to the start of the fertilization treatment.

For the R_{ff} measurements, we used two types of opaque chambers; one smaller, circular PVC chamber applied in the dose experiment, and one larger, rectangular chamber made of galvanized steel used in the long-term experiment (Table 2). Both chambers were equipped with a non-dispersive infrared gas analyzer (EGM-4, PP-Systems, Hitchin, UK). To ensure sufficient air circulation, each chamber featured a fan (Table 2). During each measurement, the chambers were placed on the soil collars (Table 2) as CO_2 concentration and air temperature inside the chamber were recorded every 4.2 s during 80- and 120-seconds long measurement periods in the dose and long-term experiment, respectively.

Measurement campaigns started between 7am and 13pm. To prevent any bias in R_{ff} caused by its diurnal pattern, measurements were

Table 1
Total amount nutrients applied (kg per hectare) in the long-term experiment in 2014 and 2016 and the dose experiment in 2016. The trademark of applied fertilizers were (A) Skog-can + Yara Superfosfat P20 (kg), (B) YaraMila 23–3–8/*S* + *B* (kg) and (C) YaraBela N27, 27 % N.

Year	Experiment	Treatment	Fertilizer	N	P	K	S	B	Mg	Ca	Se
2014	Long-term	N150	A	150	111	–	6.67	0.11	13.3	27.8	–
2016	Long-term	N150	B	150	19.6	52.2	19.6	0.13	–	–	0.01
2016	Dose	N150	C	150	–	–	–	–	13.3	–	–
2016	Dose	N300	C	300	–	–	–	–	26.6	–	–
2016	Dose	N450	C	450	–	–	–	–	39.9	–	–

Table 2
Comparison of the basic materials and methods for the two experiments. As in Håkansson et al. (2021).

	Dose experiment	Long-term experiment
Planted (year)	2005	2005 + 2006
Year of fertilization treatment	2016	2014 + 2016
Fertilizer granulates	YaraBela N27	SkogCan+P20 (2014) YaraMila 23–3–8/*S* + *B* (2016)
Treatments (kg ha-1 of N)	N0, N150, N300, N450	N0, N150
Method of fertilizing the plot/stand	manually Ø 3 m	helicopter
Method of fertilizing the collar	manually	manually
Collar material, opaque	PVC	galvanized steel
Collar (cm^2)	263 (Ø 18.3 cm)	1880 (34.5 × 54.5 cm)
Chamber, opaque (m^3)	0.00363 (Ø 0.183 × 0.138 m)	0.0475 (0.365 × 0.565 × 0.23 m)
Chamber, transparent (m^3)	0.00425 (Ø 0.19 × 0.15 m	–
Airtight seal collar-chamber	rubber gasket	water
CO_2 flux measurements (seconds)	80	120
Period of CO_2 flux measurement	Apr. 2016 - Nov. 2016 + June 2017	July 2013 - Dec. 2017
Number of measurements (summer:winter)	22:2	46:16
Estimation of vegetation coverage	yes	no

performed within 15 min in each block in the dose experiment. In the long-term experiment one set of five steel collars were measured within 15 min, the order alternated between the two treatments and began with a fertilized set, and in general, one set from each treatment was measured within two hours. Soil moisture and soil temperature were measured simultaneously at a depth of 5 and 10 cm respectively, within 50 cm distance to the soil collars, using a ThetaProbe soil moisture sensor (ML2x, Delta-T, Cambridge, UK) and a temperature sensor (STP1, PP-systems, Hitchin, UK), respectively.

2.4. Net forest floor exchange (NFFE) and light response curves

In addition to the measurements of R_{ff} performed during dark conditions, measurements of net forest floor exchange of CO_2 (NFFE) were performed in the dose experiment in mid-June 2017 (14, 15, and 19th) with the purpose to create light response curves and estimations of accumulated NFFE for June 2017. During these measurements, a transparent chamber, equipped with a separate light sensor (photosynthetic active radiation, PAR, µmol m^{-2} s^{-1}) and temperature sensor, was connected to an infra-red gas analyzer (CPY-5, TRP-3 Temperature/PAR Probe, EGM-4, PP-Systems, Amesbury, USA) was placed on the circular collars. To vary light conditions, the intensity of the sunlight was adjusted by covering the chamber and the PAR sensor with shade cloths of non-woven fabric (up to 3 layers).

2.5. Global radiation

Global radiation (W m^{-2}) was measured continuously at the site and means were presented as half-hourly means. To be able to calculate the accumulated NFFE per treatment over a 1-month period, the global radiation data was converted (see section 2.8) to photosynthetic photon flux density (PPFD, µmol m^{-2} s^{-1}) using a multiplication factor of 2.3 (Kaukoranta et al., 2017).

2.6. Biomass of forest floor vegetation

In the dose experiment, an ocular estimation of vegetation coverage was made within each collar and surrounding area (Ø 1 m) in May and August 2016 as well as in May 2017. For biomass estimation, the aboveground vegetation was harvested within each collar and a surrounding belt of 80 mm after the last flux measurements in July 2017. At the same time, two soil cores (Ø 80 mm × 100 mm depth) per collar were collected for the estimation of root biomass. The above-ground vegetation samples were oven-dried at 50 °C for 72 h and 103 °C for 24 h until dry and then the dry mass was weighed. The root biomass samples were processed in the same way after all soil was thoroughly washed away in tap water.

2.7. Data analysis

All statistical computations and graphics were performed using the R software (R Core Team, 2022).

Forest floor CO_2 fluxes (both R_{ff} and NFFE) were calculated from the linear slope of CO_2 concentration change against measurement time. If the correlation for the linear slope was below 0.9, an extra control was done to investigate the reason for it. If it was caused by an individual outlier, the outlier was removed, and the linear slope was calculated from the remaining values. If it was caused by a flat slope, the value was discarded if the standard deviation of the CO_2 concentration was high (indicating noise) but kept if it was low (natural behaviour for a low flux). Prior to further analysis, the CO_2 fluxes were corrected for air temperature and air pressure, and the potential difference in active chamber volume caused by different heights of collar insertion (Håkansson et al., 2021). The regional mean air temperature for the measurement days of the long-term experiment was calculated from hourly values obtained from the nearby weather station Ljungby A (SMHI, 2017) and for the dose experiment calculations were made from half-hourly values obtained from eddy-flux towers in two adjacent stands (Grelle et al., 2023).

To estimate accumulated R_{ff} per treatment and measurement period for the dose experiment, values per measuring frame and date of measurement were used. Each date represented a period corresponding to half the time span between the previous and next measurement date, except the first and last date, which represented the period from the first and last date of the measurement period, respectively, as well as half the period to the nearest measurement date (Håkansson et al., 2021). For the long-term experiment, the start and end of the year was used instead of the first and last date of measurements, hence resulting in R_{ff} per treatment and year.

Fertilization treatment effects on R_{ff} and biomass were tested using generalized linear mixed models, fitted with penalized quasi-likelihood estimation using the *glmmPQL* function in the *MASS* package (Venables and Ripley, 2002). R_{ff} was modelled as a function of fertilizer treatment, year and their interaction, with block as a random effect in the dose experiment and soil collar as a random effect in the long-term experiment. Biomass was only assessed in the dose experiment and analyzed as a function of fertilizer dose (0, N150, N300, N450). A gamma error distribution with log-link was used in case of the two R_{ff} models and the gaussian distribution for the biomass data. Autocorrelation plots of the model residuals indicated serial correlation in the R_{ff} measurements in both the dose and the long-term experiment, which we accounted for by incorporating an autocorrelation structure (autoregressive order 1 covariance structure). Significant treatment effects were followed up with a *post hoc* analysis based on Tukey contrasts (R package *emmeans*, Lenth (2022)).

A nonlinear mixed-effects model (NLME) fitted by maximum likelihood estimation with 'block' as a random term was used to model the net forest floor exchange rate (NFFE) as a function of the photosynthetic photon flux density (PPFD) based on a rectangular hyperbola (Pinheiro et al. (2022), R package *nlme,* Falge et al. (2001)):

$$NFFE = \frac{\alpha \times Asym \times PPFD}{\alpha \times PPFD + Asym} + R_{ff} \tag{1}$$

where α is the light-use efficiency (μmol CO_2 m^{-2} s^{-1} / μmol quanta m^{-2} s^{-1}) given by the initial slope of the light response curve, *Asym* is the maximum CO_2 assimilation under light-saturating conditions (μmol m^{-2} s^{-1}), *PPFD* is the photosynthetic photon flux density (μmol m^{-2} s^{-1}) and R_{ff} is the respiration of forest floor (μmol m^{-2} s^{-1}). Graphical model validation tools, *i.e.*, a Tukey-Anscombe plot (standardized residuals *vs.* fitted values) and a quantile-quantile plot, indicated no gross deviations from homoscedasticity or normality, respectively. One extremely low measurement was excluded as an outlier indicated by Rosner's outlier test (R package *EnvStats*, Millard (2013)).

To test for an overall treatment effect, a likelihood ratio test was used to compare an NLME with common parameter estimates to a varying-parameter NLME, allowing individual parameter estimates for each level of N treatment (0, 150, 300, 450 kg ha^{-1} y^{-1} of N). A *post hoc* analysis using Tukey contrasts was performed for each of the three model parameters to allow all pairwise comparisons and the resulting *P*-values were adjusted for multiplicity using the false discovery rate method (Benjamini and Hochberg, 1995). The delta method (Bolker, 2008) was used to compute 95 % prediction intervals around the nonlinear model fits.

Block-level NLME model predictions based on global radiation data from the on-site meteorological station were used to calculate accumulated NFFE for each N treatment level over the whole of June 2017, the month in which the light response measurements were conducted.

3. Results

3.1. Weather conditions, soil moisture and R_{ff} in the dose experiment

Global radiation (Fig. 1a) measured in the stand in 2016 showed the highest levels during the summer months May-July (max value 1100 W m^{-2} on the 6th of June) and the mean monthly air temperature (Fig. 1b) varied narrowly between 13 and 16 °C from June to October with one peak in maximum temperature each month and more stable lowest values. Rain fell regularly but rarely exceeded 10 mm d^{-1} from mid- April to mid-May followed by a low precipitation period until the start of July coinciding with a strong rainfall event of around 25 mm (Fig. 1c). The second half of July remained nearly rainless until another heavy rainfall (> 20 mm) occurred in the beginning of August followed by a relatively dry period until the end of September (Fig. 1c). Soil temperature remained below 10 °C until mid-May followed by a rapid increase to around 15 °C in the beginning of June and stayed roughly at this level throughout the summer to decrease at the end of September (Fig. 1d). The opposite trend was seen for soil volumetric water content (VWC in Fig. 1e), which decreased from spring values between 25 and 30 % in a quasi-linear fashion down to values below 5 % in the beginning of June and began to rise again in late September. Two VWC peaks, one in July and one in August, coincided with heavy showers (20–25 mm). Pre-growing season R_{ff} rates were around 2–3 μmol m^{-2} s^{-1} in all treatments of the dose experiment and reached maxima of around 8 up to 15 μmol m^{-2} s^{-1} in mid to late summer with the largest values seen in the N300 treatment, followed by the N450 and N150 treatments and the smallest values in the control (Fig. 1f).

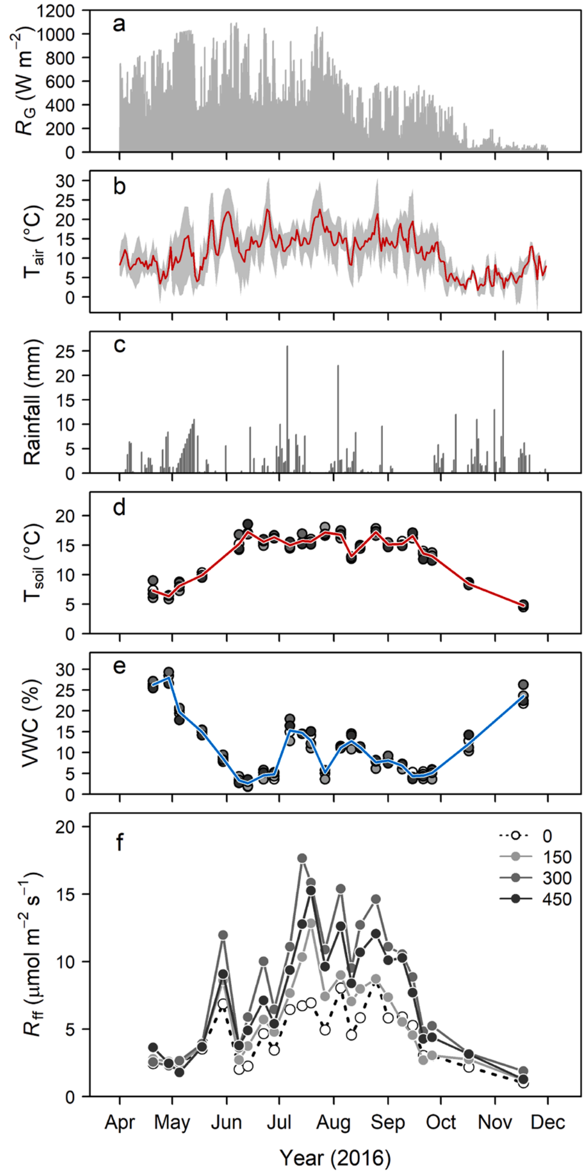

Fig. 1. Overview of meteorological data and forest floor respiration (R_{ff}) in the dose experiment, where fertilization was conducted on April 18, 2016. Global radiation (a) and mean daily air temperature (b), sampled at stand level (Grelle et al., 2023), the red line represents the daily mean values, and the grey polygon indicates daily minima and maxima. Daily rainfall (c) from the nearby weather station Ljungby A (SMHI, 2018), Soil temperature (d), soil volumetric water content (e), and mean R_{ff} (f) sampled across 6 blocks in the dose experiment on each measurement day. N addition (f) in kg ha^{-1} of N.

3.2. Weather conditions, soil moisture and R_{ff} during the long-term experiment

On average, daily means of air temperature (T_{air}) ranged from 13 °C in summer (May-October) to 2 °C in winter (Fig. 2a) across the years of the long-term experiment. Exceptionally high temperatures (> 20 °C) occurred occasionally in May-August during the study years, except for 2017 where the highest daily T_{air} was 19.3 °C. Daily precipitation was somewhat lower from early 2015 to early 2017 with the exception of a few days of heavy rain around 25 mm d^{-1} in 2015 and 2016 respectively (Fig. 2b). Soil temperature (Fig. 2c), measured at the same time as the R_{ff} measurements, varied with the seasons between lows of 2 °C in December-January to around 15 °C in June-September, with slightly higher summer temperatures in 2014 and 2016. VWC in the upper 5 cm (Fig. 2d) was highest outside of the growing seasons, and briefly dropped below 10 % during the peak growing season, apart from the summer 2016 when low VWC prevailed almost through the entire growing season. VWC was on average 6 % lower in the N150 than the N0 throughout the years of measurements with two exceptions. R_{ff} in the long-term experiment was highest during growing seasons reaching maxima between 10 and 19 μmol m^{-2} s^{-1} (Fig. 2e) and declined to around 1–4 μmol m^{-2} s^{-1} during winter. The highest R_{ff} values, of 12–19 μmol m^{-2} s^{-1}, were reached in the N150 treatment during the growing seasons of 2014 and 2015, *i.e.*, in the first two years after fertilization.

3.3. Forest floor respiration (R_{ff}) response to fertilization (in both experiments)

In the dose experiment, the GLMM showed a significant effect of fertilization on R_{ff} (L = 85.56, df = 3, P < 0.001). A *post-hoc* analysis showed that there was a statistically significant difference between N0 as well as N150 to N300 and N450, however no significant difference between N300 and N450 (Fig. 3). Compared to the N0, the N150, N300 and N450 treatments caused significant increases in R_{ff} by 23, 81 and 55 %, respectively, and differ significantly from each other except for the N300 and N450 (Fig. 3).

In the long-term experiment, the four initial chamber measurements (in 2013), indicate that there was an initially higher R_{ff} in the area which was later fertilized (Fig. 2). The fertilized treatment also showed a higher R_{ff} in the first two years after fertilization (2014 and 2015). The

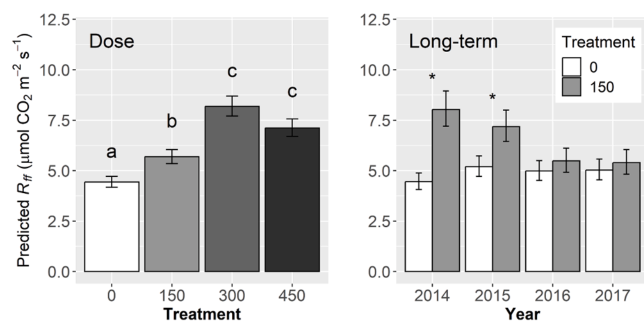

Fig. 3. Predicted forest floor respiration (R_{ff}) in the dose experiment 2016, and the long-term experiment, based on measurements with opaque chamber. Error bars indicate standard errors. Different lower- case letters and *, respectively, indicate statistically significant differences at P < 0.05. Fertilization treatments are presented as kg ha^{-1} of N.

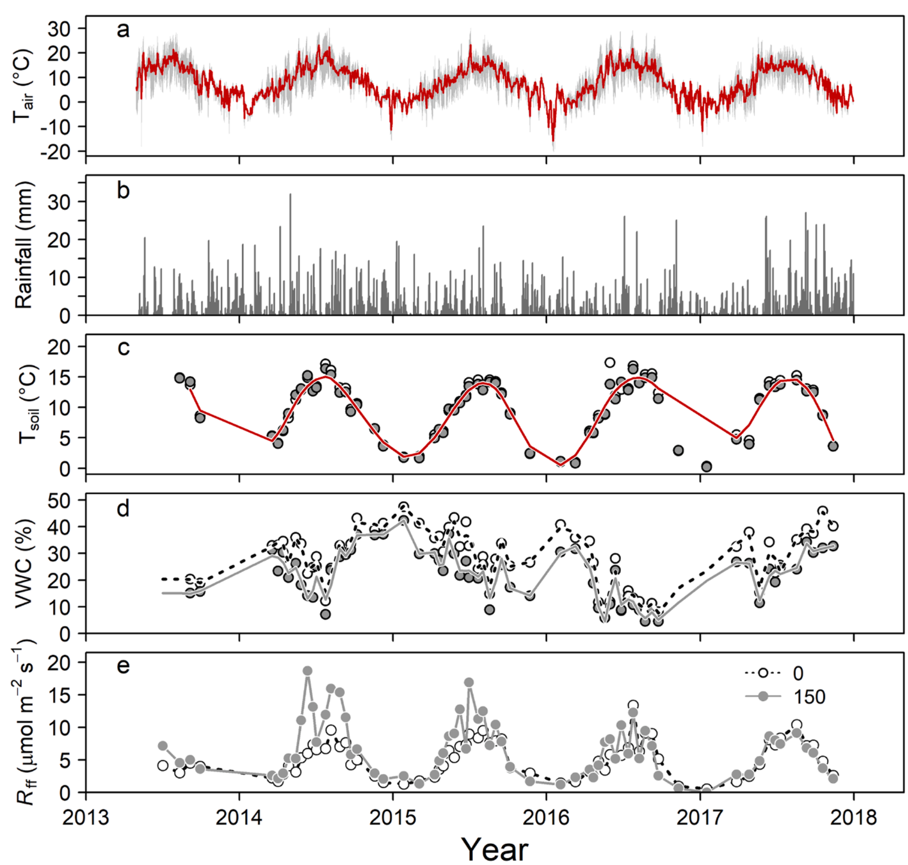

Fig. 2. Overview of meteorological data and forest floor respiration (R_{ff}) in the long-term experiment. Mean daily air temperature, T_{air} (a), the red line represents the daily mean values, and the grey polygon indicates daily minima and maxima. Daily rainfall (b), soil temperature (c), soil volumetric water content, (VWC) (d), and mean forest floor respiration (R_{ff}) (e) sampled across 10 plots per treatment in the long-term experiment on each measurement day. N addition (d and e) in kg ha^{-1} of N. T_{air} and rainfall data were from the nearby weather station Ljungby A (SMHI, 2018).

GLMM approach showed significant effects of fertilization ($L = 17.19$, $df = 1$, $P < 0.001$), but no significant effect of year ($L = 5{,}57$, $df = 3$, $P = 0.13$), however showed a significant interaction between fertilization and year ($L = 34.16$, $df = 3$, $P < 0.001$) on R_{ff}. A *post-hoc* analysis showed that R_{ff} was significantly higher by *ca.* 60 % in the fertilized treatment in 2014, the year of the first fertilization, and by 23 % in 2015 with no significant differences in the two following years (Fig. 3). When comparing the two experiments, the stimulation of R_{ff} in response to adding N150 was considerably smaller in the dose experiment (23 %) compared with the response in the long-term experiment (60 %) in the first year of fertilization.

In the dose experiment, accumulated R_{ff} for the measurement period (April to November 2016) varied from 33 to 60 tons of CO_2 ha^{-1} with the lowest and highest emissions obtained in the NO and the N300 treatment, respectively (Table 3). Accumulated R_{ff} measurements for the whole year in the long-term experiment varied across the study years from 54 to 64 tons of CO_2 ha^{-1} yr^{-1} in unfertilized treatment and from 54 to 93 ton in the fertilized treatment (Table 4).

3.4. *Net forest floor exchange (NFFE) with incoming light; photosynthesis, light response curves, and global radiation*

The nonlinear mixed effects (NLME) modeling approach, based on the transparent chamber measurements of the dose experiment, showed that N addition had a significant overall effect on the light response of NFFE ($L = 74.83$, $df = 9$, $P < 0.001$). A *post-hoc* procedure showed that all N additions resulted in significantly higher light-use efficiency (α) than the control (N0), but they did not differ significantly from each other (Fig. 4, Table 5). Maximal NFFE rates increased significantly in the highest N additions (N300 and N450) compared to the N0, but there were no differences between the N150 and the N0. The largest maximal NFFE of 13 μmol m^{-2} s^{-1} was seen in the N300 treatment (Fig. 4, *Asym* parameter). The R_{ff} estimates for the two highest N treatments did not differ significantly from each other but significantly exceeded N0 values by 84 and 66 %, respectively (Table 5). R_{ff} in the N150 treatment did not differ significantly from the N0 treatment but was 32 and 25 % lower compared to the two higher N levels, and these differences were significant, although only marginally for N450 (Table 5).

The NLME model was used to predict accumulated NFFE based on solar radiation data for the whole of June 2017, the month in which the light response recordings were taken (Fig. 5). Without N addition, the ecosystem took up 2.7 t ha^{-1} of CO_2 during this period. The N150 treatment raised this figure by 27 % but this difference was not statistically significant. The two remaining N additions (N300 and N450) increased net ecosystem CO_2 uptake significantly by 96 % and 64 %, respectively, relative to the N0 treatment.

3.5. *Biomass of forest floor vegetation*

In the dose experiment, visual inspection showed that all plots had a vegetation cover (grass and herbs) of >95 % of the total plot surface area on all three assessments (May and August 2016, May 2017). The total (above- and belowground) dry weight ranged from 1.78 and 1.71 kg m^{-2} in the N0 and the N150 treatment, respectively, to about 2.2 kg m^{-2} in the N300 and N450 treatments.

Table 3
Accumulated forest floor respiration including confidence interval (CI) for the measurement period (April-November) of the dose experiment.

Treat (kg ha^{-1} of N)	CO_2 (ton ha^{-1} $period^{-1}$)	
	Mean	CI
N0	33	3
N150	40	4
N300	60	11
N450	51	9

Table 4
Accumulated forest floor respiration including confidence interval (CI) for the measurement years of the long-term experiment.

Accumulated forest floor respiration (R_{ff}) including confidence interval (CI) for each year of the long-term experiment (Håkansson et al., 2021).	CO_2 (ton ha^{-1} yr^{-1})			
	Control (N0)		Fertilized (N150)	
Year	Mean	CI	Mean	CI
2014	58	21	93	19
2015	64	20	78	15
2016	54	13	54	9
2017	61	19	55	11

Fertilization had a significant effect ($L = 11.14$, $df = 3$, $P = 0.011$) on aboveground forest floor biomass (Fig. 6) and a *post-hoc* analysis showed that there was a significantly ($P = 0.05$) larger biomass (25 %) in the N300 than in N150 treatment while the remaining pairwise comparisons were insignificant (Fig. 6). Understory plants showed a tendency towards greater belowground biomass with increasing levels of fertilizer, but this trend was not statistically significant ($L = 4.011$, $df = 3$, $P = 0.25$) (Fig. 6).

On average, the below-ground biomass was about twice as high as the above-ground biomass.

4. Discussion

Forest fertilization as a silvicultural tool to increase woody biomass yield has long been used in Sweden to release northern forests from nutrient-limitation (Lindkvist et al., 2011) although the effects on R_{ff} have rarely been quantified (Metcalfe et al., 2013). In this study, we assessed the first half-year impact of different doses of N on R_{ff} as well as the longer-term effect of two N additions in four years in nutrient-limited boreal Norway spruce stands. In the dose experiment, both R_{ff} and NFFE were enhanced by fertilization treatment, indicating that forest fertilization at higher doses may increase the C sink strength of the understory, at least initially before canopy closure. An initial stimulation of R_{ff} was supported by the results from the long-term study, but this effect gradually vanished over the years.

4.1. *Forest floor respiration (R_{ff})*

Contrary to expectations, our experiments showed that R_{ff} was 23 % higher in the dose experiment and 60 % greater in the long-term experiment (both statistically significant), in the year of the first fertilization with 150 kg ha^{-1} of N. R_{ff} in the dose experiment was also significantly increased in the N300 and N450 treatments (81 and 55 %, respectively). An increase in R_{ff} following fertilization is in line with a field experiment on Douglas-fir in the Pacific Northwest of the United States showing that N fertilization (single dose of 200 kg ha^{-1} of N) resulted in a significant short-term (3–4 months) increase in R_{ff} (Jassal et al., 2010), due to an increase in autotrophic soil respiration followed by a small decrease in heterotrophic respiration. A stimulated biomass production can also be a possible explanation in our experiments since the belowground biomass of ground vegetation tended to be higher in the plots with the highest N additions. We also observed a significantly higher photosynthetic CO_2 uptake of the forest floor vegetation in these high-N treatments, which may result in higher autotrophic respiration and thus an overall increase in R_{ff} (Högberg et al., 2010). Another possible reason for greater R_{ff} in response to fertilization is an initial stimulation in heterotrophic respiration by releasing the soil microbial community from N limitation. Such a stimulation of microbial respiration is likely to wane with progressive C limitation related to the exhaustion of labile C pools, eventually leading to the oft-observed depression of soil respiration later on. However, other studies found that the R_{ff} rates remained unaffected by fertilization, *e.g.* in a Norway spruce stand in Finland (200 kg ha^{-1} of N, Maljanen et al. (2006)), in a

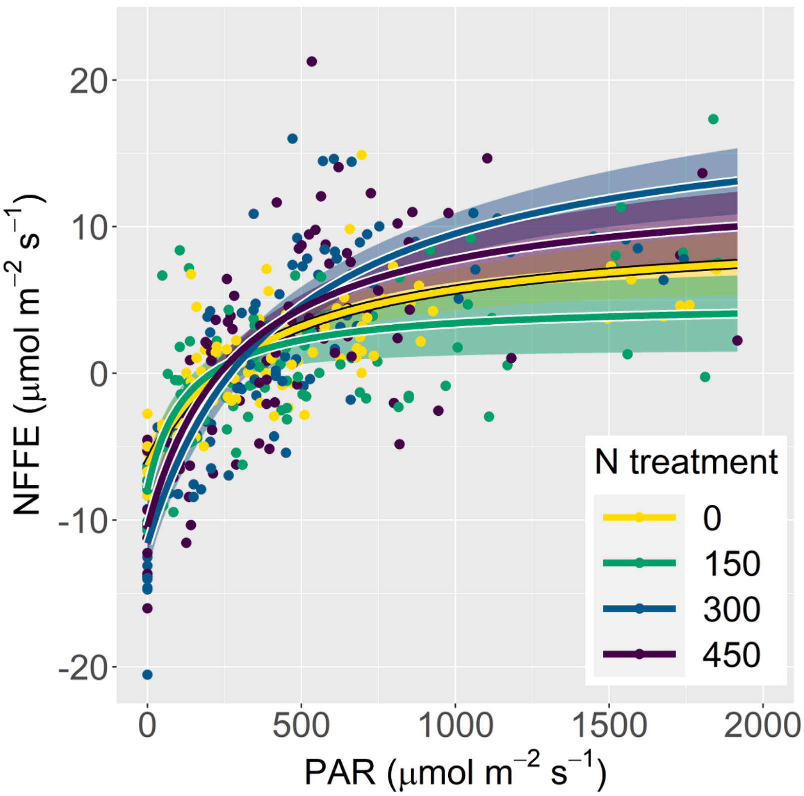

Fig. 4. Net forest floor exchange (NFFE) in the dose experiment based on data from transparent chambers (filled symbols) and global radiation from a pyranometer in a Eddy-flux mast in another experiment the stand (Grelle et al., 2023). Curves represent nonlinear mixed effects model fits. Shaded areas correspond to the 95 % confidence interval of the model predictions. Treatments denote fertilizer applications in kg ha^{-1} of N.

subalpine spruce (*Picea asperata*) plantation in northern China (250 kg ha^{-1} of N, Li et al. (2019)) and, in a 70-year-old Scots pine (*Pinus sylvestris*) forest in northern Sweden after five years of annual fertilization (100 kg ha^{-1} yr^{-1} of N, Hasselquist et al. (2012)). In a black spruce (*Picea mariana*) forest in Alaska, N-fertilization (initially 200, then 100 kg ha^{-1} yr^{-1} of N) caused changes in soil microbial community composition and in the soil enzymatic profile without effects on total R_{ff} (Allison et al., 2008). Even under high soil N availability and simultaneous atmospheric CO_2 enrichment (effectively eliminating any C limitation), R_{ff} remained unstimulated in a Norway spruce stand in Switzerland (Mildner et al., 2015).

In our long-term experiment, the N150 treatment had a lower soil VWC throughout the measurement period as well as a somewhat higher R_{ff} from the start. It is, however, not possible to distinguish if the lower soil VWC and the higher R_{ff} observed in the N150 treatment during the first years was a true fertilization effect or a consequence of pre-treatment differences or a combination of both, since this stand level experiment did not include true replicates. Regardless of the underlying causes, such differences in VWC may affect microbial activity and hence heterotrophic respiration more strongly in the fertilized than in the control plots because soil moisture can become limiting more rapidly in the former during periods of low water supply, such as in 2016 when the second fertilization was applied in the long-term experiment. On the other hand, high VWC ($\geq$ 35 %) may periodically impede soil gas diffusivity and thus soil gas exchange resulting in a temporary accumulation of CO_2 in the soil pore space and suboxic conditions restricting respiratory metabolism (Bader and Körner, 2010), which may have sporadically occurred in the control plots. However, the pre-treatment differences were also observed in eddy flux-based NEE measurements, with higher uptake in the area designated for the N0 treatment (Grelle et al. 2023), which makes us believe that the observed increase in R_{ff} in the long-term experiment overestimates the real fertilization effect, but this does not fundamentally change our conclusions (see below).

In the following years, R_{ff} in the control remained steady but decreased gradually in the fertilized plots, indicating that the potential initial stimulation (in excess of the pre-treatment difference) was short-lived. Similarly, a roughly 40 % decrease in R_{ff} has been reported in a long-term experiment with repeated N fertilization in Norway spruce stands in northern Sweden (Olsson et al., 2005). In a 34-year-old mixed forest in northwest China with *Pinus koraiensis* as dominant conifer, Geng et al. (2017) observed significant increases in soil respiration related to low-dose fertilization with 10 kg ha^{-1} yr^{-1} of N, while high rates of 140 kg ha^{-1} of N even caused a strong reduction in R_{ff}. Such nonlinear responses of R_{ff} (or its components) to increasing soil N supply are consistent with our theoretical understanding of optimal C allocation in forest trees (Franklin et al., 2012) where higher levels of available soil N tend to increase the above ground parts of vegetation at the expense of the fine roots and this is also supported by empirical evidence by Högberg et al. (2010), who showed a 60 % reduction in belowground C allocation one year after fertilization with 100 kg ha^{-1} of N in a young boreal Scots pine forest. Considering these findings, the transient response observed in our long-term study likely reflects the shift from an initial nutrient-driven stimulation of belowground C allocation, fuelling autotrophic respiration, towards a reduction in C fluxes to belowground sinks with an ensuing decrease in autotrophic respiration and thus total R_{ff}. Indeed, in the long-term experiment, R_{ff} had already decreased in 2015 and remained unchanged after the second fertilization in 2016, which may be indicative of such a C limitation caused by a microbially-driven depletion of the labile soil C reserves and a lack of replenishment due to reduced tree C allocation belowground that had presumably set in by this time (Högberg et al., 2010). However, precipitation patterns may have also had an effect as soil water availability was very low during much of the 2016 growing season (Fig. 2). This moisture limitation has probably impaired soil metabolism, delayed the

Table 5
Results of a post-hoc analysis applied to a nonlinear mixed effects model for net forest floor exchange (NFFE) as a function of light intensity (PPFD) and N addition (0, 150, 300, 450 kg ha^{-1} y^{-1} of N). α = light-use-efficiency, Asym = asymptote, the maximum NFFE under light saturation, R_{ff} = forest floor respiration. ˙ $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, P_{adj} = multiplicity-adjusted P-values (false discovery rate method). The numerator and denominator degrees of freedom of the F-statistic were $df_{num} = 1$ and $df_{den} = 403$.

Comparison	*F*	*P*	P_{adj}
$\alpha_{N150} - \alpha_{N0}$	4.592	0.033	0.051˙
$\alpha_{N300} - \alpha_{N0}$	7.484	0.006	0.013*
$\alpha_{N450} - \alpha_{N0}$	9.461	0.002	0.006**
$\alpha_{N300} - \alpha_{N150}$	1.339	0.248	0.298
$\alpha_{N450} - \alpha_{N150}$	0.565	0.453	0.453
$\alpha_{N450} - \alpha_{N300}$	0.729	0.394	0.417
$Asym_{N150} - Asym_{N0}$	3.161	0.076	0.105
$Asym_{N300} - Asym_{N0}$	28.064	< 0.001	< 0.001***
$Asym_{N450} - Asym_{N0}$	10.101	0.002	0.005**
$Asym_{N300} - Asym_{N150}$	51.894	< 0.001	< 0.001***
$Asym_{N450} - Asym_{N150}$	28.652	< 0.001	< 0.001***
$Asym_{N450} - Asym_{N300}$	6.420	0.012	0.021*
$R_{ff\ N150} - R_{ff\ N0}$	1.659	0.198	0.255
$R_{ff\ N300} - R_{ff\ N0}$	23.114	< 0.001	< 0.001***
$R_{ff\ N450} - R_{ff\ N0}$	14.404	< 0.001	0.001***
$R_{ff\ N300} - R_{ff\ N150}$	8.928	0.003	0.007**
$R_{ff\ N450} - R_{ff\ N150}$	4.518	0.034	0.051˙
$R_{ff\ N450} - R_{ff\ N300}$	1.009	0.316	0.355

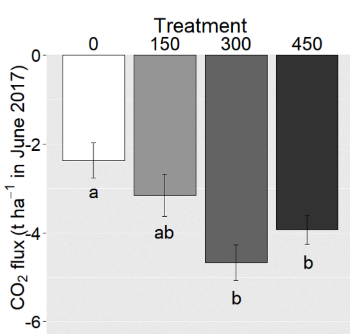

Fig. 5. Accumulated net forest floor CO_2 exchange (NFFE) in the dose experiment, in June 2017. Negative numbers denote an uptake of CO_2. Error bars indicate standard errors and different lower- case letters indicate statistically significant differences at $P < 0.05$. Treatments are presented as kg ha^{-1} of N.

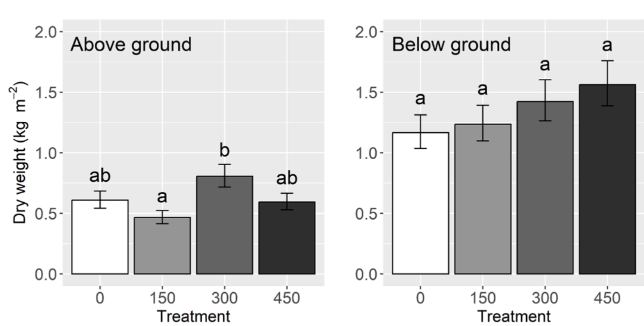

Fig. 6. Predicted dry weight for above- (left) and belowground (right) understory vegetation in the dose experiment based on a sampling in July 2017. Error bars indicate standard errors and different lower- case letters indicate statistically significant differences ($P < 0.05$). Treatments are presented as kg ha^{-1} of N.

dissolution of the fertilizer granules and hampered nutrient dispersion and plant uptake in the soil, which may thus have diminished potential nutrient effects on R_{ff}.

4.2. Net forest floor exchange (NFFE); photosynthesis, light response curves, and global radiation

In June 2017, our estimates of net forest floor exchange (NFFE), which in contrast to R_{ff} include the CO_2 uptake by forest floor vegetation, showed a net uptake of CO_2 and that fertilization with 300 kg ha^{-1} of N doubled this uptake (Fig. 5). Eddy flux estimates of the stand-level net uptake of the fertilized area in 2014 (first fertilization) amounted to *ca.* 18 Mg CO_2 ha^{-1} yr^{-1} (Grelle et al., 2023), indicating that this young spruce plantation has absorbed a far greater amount of CO_2 than that emitted by the forest floor. In the first 20 years after establishment, planted conifer (other than pine) and pine forests in the boreal region have been reported to remove 4.5 (±1) (mean ± 95 confidence interval) and 10.2 (±4.9) Mg CO_2 ha^{-1} yr^{-1} from the atmosphere, respectively (Bernal et al., 2018). Although the different time scales hamper a direct comparison, and a large spatial variability in forest-floor CO_2 fluxes has been seen across boreal landscape (Martínez-García et al., 2022), our findings imply that even with the initial burst in R_{ff}, fertilization may have increased stand-level C uptake 1.8- to 4-fold in the first year. In comparison, a 40-year-old boreal Norway spruce forest has shown a reduction in maximum soil CO_2 respiration of 36 %, 15 years after the start of a long-term nutrient optimization experiment (Olsson et al., 2005). No change in total soil respiration has been reported for a mature *Picea mariana* forest in central Alaska, 3 years after N or N + P addition (Allison et al., 2008). However, both studies lack early measurements; therefore, an initial nutrient-driven stimulation of soil metabolism, and thus soil respiration, cannot be ruled out. Studies on mineral forest soils investigating the early response of soil respiration rates under nutrient enrichment are scarce. At the Harvard forest research site, N addition in a mature red pine (*Pinus resinosa*) stand caused a rapid reduction in soil CO_2 respiration by 21–25 % in the first treatment year, with a further decrease to 41 % after 13 years of continuous N fertilization (Bowden et al., 2004). With regard to our study, this means that the magnitude of the positive fertilization effect on forest C uptake can be expected to increase with time, assuming a long-lasting fertilizer effect (Bennett et al., 2011) and a rapid return to pretreatment R_{ff} levels (as observed here) or even a further decline as has frequently been reported elsewhere (Fig. 5).

Our light response data indicate that under favourable light conditions CO_2 assimilation in the understory was constrained by limited N availability (Håkansson et al., 2021). The nutrient-driven stimulation of forest floor photosynthesis at light intensities > 250 μmol m^{-2} s^{-1} in the N300 and N450 treatments more than compensated the increases in R_{ff} under elevated nutrient supply translating into a net CO_2 uptake under well-lit conditions. It is possible that this effect on photosynthesis will decline as nutrient availability decreases with time after fertilization. However, light levels reaching the forest floor are bound to decrease with increasing tree canopy closure (Hedwall et al., 2010), and the fertilizer effect (should it last longer) on forest floor photosynthetic C uptake will thus probably become largely irrelevant over time due to light limitation. Together with the waning stimulation of R_{ff} these changes are unlikely to turn the forest stand from a C sink into a C source. Unexpectedly, the N150 treatment failed to enhance photosynthesis in the forest floor vegetation, and we speculate, as Thébault et al. (2014) have done for trees in alpine environments, that an N-limited soil microbial community outcompeted forest floor vegetation for N and thus prevented a positive fertilizer effect on photosynthesis at this level of nutrient enrichment.

4.3. Conclusions

Our chamber-based study indicates that negative fertilization effects on the greenhouse gas balance of young boreal spruce stands in the form of increased R_{ff} are transient (1–2 years) and already far outweighed by nutrient-driven increases in forest floor photosynthesis, not to mention the probably large stimulation of canopy C uptake. Together with the reported large gains in stem wood yield, our findings from the understory vegetation, imply that repeated fertilization of young nutrient-limited Norway spruce stands, enhances aboveground C sequestration and following investigations into changes in soil C pools will show whether this holds true at the whole stand-level. However, as repeated nutrient additions entail an increased risk of N-leaching, or as N_2O emissions (short-lived increase in this experiment, see Håkansson et al. (2021) and Bergh et al. (2008)), and changes in forest biodiversity and soil microbial communities, such factors and their broader ramifications should be carefully considered in forest management planning. The positive dose-dependent relationship between fertilizer application and R_{ff} represents an immediate, presumably short-lived response and calls for longer-term studies using varying fertilizer doses with and without labile C additions to unravel the complex interplay between nutrient availability, belowground C allocation and biotic and abiotic soil processes. The resultant information can help guide forest planning and management.

CRediT authorship contribution statement

Charlotta Håkansson: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Per-Ola Hedwall:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Martin Karl-Friedrich Bader:** Writing – review & editing, Visualization, Validation, Formal analysis. **Monika Strömgren:** Writing – review & editing, Validation, Methodology, Funding acquisition, Data curation, Conceptualization. **Magnus Axelsson:** Writing – review & editing, Investigation. **Johan Bergh:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Data availability

Data will be made available on request.

References

Allison, S.D., Czimczik, C.I., Treseder, K.K., 2008. Microbial activity and soil respiration under nitrogen addition in Alaskan boreal forest. Glob. Chang. Biol. 14 (5), 13. https://doi.org/10.1111/j.1365-2486.2008.01549.x.

Artaxo, P., Hansson, H.-C., Andreae, M., Bäck, J., Alves, E., Barbosa, H., Bender, F., Bourtsoukidis, E., Carbone, S., Chi, J., Decesari, S., Despres, V., Ditas, F., Ezhova, E., Sandro, F., Hasselquist, N., Heintzenberg, J., Holanda, B., Guenther, A., Makshtas, A., 2022. Tropical and boreal forest – atmosphere interactions: a review. Tellus B 74, 140. https://doi.org/10.16993/tellusb.34.

Ågren, G., Andersson, F., 2012. Terrestrial ecosystem ecology principles and applications. Forest. Chronicle 88, 11. https://doi.org/10.5558/tfc2012-066.

Bader, M., Körner, C., 2010. No overall stimulation of soil respiration under mature deciduous forest trees after 7 years of CO_2 enrichment. Glob. Chang. Biol. 16, 14. https://doi.org/10.1111/j.1365-2486.2010.02159.x.

Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate - a practical and powerful approach to multiple testing. J. R. Stat. Soc. Ser. B 57, 13. https://doi.org/10.2307/2346101.

Bennett, J., Blevins, L., Barker, J., Blevins, D., Prescott, C., 2011. Increases in tree growth and nutrient supply still apparent 10 to 13 years following fertilization and vegetation control of salal-dominated cedar hemlock stands on Vancouver Island. Canad. J. Forest Res. 33, 10. https://doi.org/10.1139/x03-069.

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. For. Ecol. Manage. 119 (1), 51–62. https://scholar.google.se/scholar?hl=en&q=The+effect+of+water+and+nutrient+availability+on+the+productivity+of+Norway+spruce+in+northern+and+southern+Sweden.&btnG=&as_sdt=1%2C5&as_sdtp=.

Bergh, J., Nilsson, U., Grip, H., Hedwall, P.-O., Lundmark, T., 2008. Effects of frequency of fertilisation on production, foliar chemistry and nutrient leaching in young Norway spruce stands in Sweden. Silva Fennica 42 (5), 13. http://www.metla.fi/silvafennica/full/sf42/sf425721.pdf.

Bernal, B., Murray, L.T., Pearson, T.R.H., 2018. Global carbon dioxide removal rates from forest landscape restoration activities. Carbon N YCarbon Balance Manag. 13 (1), 22. https://doi.org/10.1186/s13021-018-0110-8.

Blaško, R., Forsmark, B., Gundale, M., 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, 14. https://doi.org/10.1016/j.scitotenv.2022.156327.

Bolker, B.M., 2008. Ecological Models and Data in R. Princeton University Press. https://math.mcmaster.ca/~bolker/emdbook/index.html.

Bonner, M.T.L., Castro, D., Schneider, A.N., Sundström, G., Hurry, V., Street, N.R., Näsholm, T., 2019. Why does nitrogen addition to forest soils inhibit decomposition? Soil Biology (Basel) Biochem. 137, 9. https://doi.org/10.1016/j.soilbio.2019.107570.

Bowden, R.D., Davidson, E., Savage, K., Arabia, C., Steudler, P., 2004. Chronic nitrogen additions reduce total soil respiration and microbial respiration in temperate forest soils at the Harvard Forest. For. Ecol. Manage. 196 (1), 14. https://doi.org/10.1016/j.foreco.2004.03.011.

Brockley, R., 2010. Effects of repeated fertilization in a young spruce stand in central British Columbia. Canad. J. Forest Res. 40, 11. https://doi.org/10.1139/X10-123.

Canadell, J.G., Raupach, M.R., 2008. Managing forests for climate change mitigation. Science (1979) 320 (5882), 3. https://doi.org/10.1126/science.1155458.

Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Gross, P., Grünwald, T., Hollinger, D., Jensen, N.-O., Katul, G., Keronen, P., Kowalski, A., Lai, C.-T., Wofsy, S., 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. Agric. For. Meteorol. 107, 27. https://doi.org/10.1016/S0168-1923(00)00225-2.

Franklin, O., Johansson, J., Dewar, R.C., Dieckmann, U., McMurtrie, R.E., Brännström, Å., Dybzinski, R., 2012. Modeling carbon allocation in trees: a search for principles. Tree Physiol. 32 (6), 19. https://doi.org/10.1093/treephys/tpr138.

Geng, J., Cheng, S., Fang, H., Yu, G., Li, X., Si, G., He, S., Yu, G., 2017. Soil nitrate accumulation explains the nonlinear responses of soil CO_2 and CH_4 fluxes to nitrogen addition in a temperate needle-broadleaved mixed forest. Ecol. Indic. 79 (28–36), 9. https://doi.org/10.1016/j.ecolind.2017.03.054</bib.

Grelle, A., Hedwall, P.-O., Strömgren, M., Håkansson, C., Bergh, J., 2023. From source to sink – recovery of the carbon balance in young forests. Agric. For. Meteorol. 330, 9. https://doi.org/10.1016/j.agrformet.2022.109290.

Hasselquist, N.J., Metcalfe, D.B., Högberg, P., 2012. Contrasting effects of low and high nitrogen additions on soil CO_2 flux components and ectomycorrhizal fungal sporocarp production in a boreal forest. Glob. Chang. Biol. 18 (12), 10. https://doi.org/10.1111/gcb.12001.

Hedwall, P.-O., Gong, P., Ingerslev, M., Bergh, J., 2014. Fertilization in northern forests – biological, economic and environmental constraints and possibilities. Scand. J. Forest Res. 29 (4), 301–311. https://doi.org/10.1080/02827581.2014.926096.

Hedwall, P.-O., Nordin, A., Brunet, J., Bergh, J., 2010. Compositional changes of forest-floor vegetation in young stands of Norway spruce as an effect of repeated fertilisation. For. Ecol. Manage. 259 (12), 7. https://doi.org/10.1016/j.foreco.2010.03.018.

Hyvönen, R., Persson, T., Andersson, S., Olsson, B., Ågren, G.I., Linder, S., 2008. Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. Biogeochemistry. 89 (1), 17. https://doi.org/10.1007/s10533-007-9121-3.

Hyvönen, R., Ågren, G.I., Linder, S., Persson, T., Cotrufo, M.F., Ekblad, A., Freeman, M., Grelle, A., Janssens, I.A., Jarvis, P.G., Kellomäki, S., Lindroth, A., Loustau, D., Lundmark, T., Norby, R.J., Oren, R., Pilegaard, K., Ryan, M.G., Sigurdsson, D.B., … Wallin, G. (2007). The Likely Impact of Elevated [CO2], Nitrogen Deposition, Increased Temperature and Management on Carbon Sequestration in Temperate and Boreal Forest Ecosystems: a Literature Review. (3), 463. http://search.ebscohost.com.proxy.lnu.se/login.aspx?direct=true&db=edsjsr&AN=edsjsr.4131179&lang=sv&site=eds-live&scope=site.

Håkansson, C., Hedwall, P.-O., Strömgren, M., Axelsson, M., Bergh, J., 2021. Effects of fertilization on soil CH_4 and N_2O fluxes in young Norway spruce stands. For. Ecol. Manage. 499, 119610. https://doi.org/10.1016/j.foreco.2021.119610.

Högberg, M.N., Briones, M.J.I., Keel, S.G., Metcalfe, D.B., Campbell, C., Midwood, A.J., Thornton, B., Hurry, V., Linder, S., Näsholm, T., Högberg, P., 2010. Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. New Phytol. 187 (2), 485–493. https://doi.org/10.1111/j.1469-8137.2010.03274.x.

Janssens, I.A., Dieleman, W., Luyssaert, S., Subke, J.A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A.J., Grace, J., Matteucci, G., Papale, D., Piao, S.L., Schulze, E.D., Tang, J., Law, B.E., 2010. Reduction of forest soil respiration in response to nitrogen deposition. Nat. Geosci. 3 (5), 7. https://doi.org/10.1038/ngeo844.

Jassal, R.S., Black, T.A., Trofymow, J.A., Roy, R., Nesic, Z., 2010. Soil CO_2 and N_2O flux dynamics in a nitrogen-fertilized Pacific Northwest Douglas-fir stand. Geoderma 157 (3), 118–125. https://doi.org/10.1016/j.geoderma.2010.04.002.

Johnson, D.W., 1992. Effects of forest management on soil carbon storage [Article]. Water Air Soil Pollut. 64 (1–2), 38. https://doi.org/10.1007/BF00477097.

Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta analysis. For. Ecol. Manage. 140 (2), 12. https://doi.org/10.1016/S0378-1127(00)00282-6.

Jörgensen, K., Granath, G., Lindahl, B., Strengbom, J., 2021. Forest management to increase carbon sequestration in boreal Pinus sylvestris forests. Plant Soil 466, 14. https://doi.org/10.1007/s11104-021-05038-0.

Kaukoranta, T., Jokinen, K., Näkkilä, J., & Särkkä, L. (2017). *LED-belysning i växthus* (14). (Forskning i naturresurser och bioekonomi Issue. N. (Luke). http://urn.fi/URN:ISBN:978-952-326-372-7.

Kumar, A., Adamopoulos, S., Jones, D., Amiandamhen, S.O., 2020. Forest Biomass Availability and Utilization Potential in Sweden: a Review [journal article]. Waste BioMass Valorizat. 16. https://doi.org/10.1007/s12649-020-00947-0.

Lenth, R.V. (2022). *emmeans: estimated marginal means, aka least-squares means*. In https://CRAN.R-project.org/package=emmeans.

Lesiv, M., Schepaschenko, D., Buchhorn, M., See, L., Dürauer, M., Georgieva, I., Jung, M., Hofhansl, F., Schulze, K., Bilous, A., Blyshchyk, V., Mukhortova, L., Brenes, C.L.M., Krivobokov, L., Ntie, S., Tsogt, K., Pietsch, S.A., Tikhonova, E., Kim, M., Fritz, S., 2022. Global forest management data for 2015 at a 100 m resolution. Sci. Data 9 (1), 14. https://doi.org/10.1038/s41597-022-01332-3.

Li, D., Liu, Q., Yin, H., Luo, Y., Hui, D., 2019. Differential responses and controls of soil CO_2 and N_2O fluxes to experimental warming and nitrogen fertilization in a subalpine coniferous spruce (Picea asperata Mast.) plantation forest. Forests. 10, 16. https://doi.org/10.3390/f10090808.

Linder, S., 1995. Foliar analysis for detecting and correcting nutrient imbalances in norway spruce. *Ecol. Bull.* (44), 178–190. http://www.jstor.org/stable/20113161.

Lindkvist, A., Kardell, Ö., Nordlund, C., 2011. Intensive forestry as progress or decay? An analysis of the debate about forest fertilization in Sweden, 1960–2010. Forests. 2 (1), 35. https://www.mdpi.com/1999-4907/2/1/112.

Maaroufi, N., Nordin, A., Palmqvist, K., Hasselquist, N., Forsmark, B., Rosenstock, N., Wallander, H., & J Gundale, M. (2019). *Anthropogenic nitrogen enrichment enhances soil carbon accumulation by impacting saprotrophs rather than ectomycorrhizal fungal activity*. https://doi.org/10.1111/gcb.14722.

Maljanen, M., Jokinen, H., Saari, A., Strömmer, R., Martikainen, P., 2006. Methane and nitrous oxide fluxes, and carbon dioxide production in boreal forest soil fertilized with wood ash and nitrogen. Soil. Use Manage 22, 7. https://doi.org/10.1111/j.1475-2743.2006.00029.x.

Marshall, J.D., Peichl, M., Tarvainen, L., Lim, H., Lundmark, T., Näsholm, T., Öquist, M., Linder, S., 2021. A carbon-budget approach shows that reduced decomposition causes the nitrogen-induced increase in soil carbon in a boreal forest. For. Ecol. Manage. 502, 12. https://doi.org/10.1016/j.foreco.2021.119750.

Martínez-García, E., Nilsson, M.B., Laudon, H., Lundmark, T., Fransson, J.E.S., Wallerman, J., Peichl, M., 2022. Overstory dynamics regulate the spatial variability in forest-floor CO_2 fluxes across a managed boreal forest landscape. Agric. For. Meteorol. 318, 14. https://doi.org/10.1016/j.agrformet.2022.108916.

Metcalfe, D., Eisele, B., Hasselquist, N., 2013. Effects of nitrogen fertilization on the understory carbon balance over the growing season in a boreal Pine forest. Biogeosciences Discuss. 10, 21. https://doi.org/10.5194/bgd-10-14093-2013.

Mildner, M., Bader, M.K.-F., Baumann, C., Körner, C., 2015. Respiratory fluxes and fine root responses in mature Picea abies trees exposed to elevated atmospheric CO_2 concentrations. Biogeochemistry. 124 (1), 16. https://doi.org/10.1007/s10533-015-0084-5.

Millard, P.S. (2013). *EnvStats: An R Package for Environmental Statistics*. Springer New York. https://doi-org.proxy.lnu.se/10.1007/978-1-4614-8456-1.

Mäkipää, R., Abramoff, R., Adamczyk, B., Baldy, V., Biryol, C., Bosela, M., Casals, P., Curiel Yuste, J., Dondini, M., Filipek, S., Garcia-Pausas, J., Gros, R., Gömöryová, E., Hashimoto, S., Hassegawa, M., Immonen, P., Laiho, R., Li, H., Li, Q., Lehtonen, A., 2023. How does management affect soil C sequestration and greenhouse gas fluxes in boreal and temperate forests? – a review. For. Ecol. Manage. 529, 24. https://doi.org/10.1016/j.foreco.2022.120637.

Olsson, P., Linder, S., Giesler, R., Högberg, P., 2005. Fertilization of boreal forest reduces both autotrophic and heterotrophic soil respiration. Glob. Chang. Biol. 11 (10), 9. https://doi.org/10.1111/j.1365-2486.2005.001033.x.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Team, R.C. (2022). *nlme: linear and Nonlinear Mixed Effects Models*. In R package version 3.1-155. https://CRAN.R-project.org/package=nlme.

R Core Team, 2022. R: a language and environment for statistical computing. R Found. Stat. Comput. https://www.r-project.org/.

Ramirez, K.S., Craine, J.M., Fierer, N., 2012. Consistent effects of nitrogen amendments on soil microbial communities and processes across biomes. Glob. Chang. Biol. 18 (6), 10. https://doi.org/10.1111/j.1365-2486.2012.02639.x.

Sathre, R., Gustavsson, L., Bergh, J., 2010. Primary energy and greenhouse gas implications of increasing biomass production through forest fertilization. Biomass Bioenergy 34 (4), 10. https://doi.org/10.1016/j.biombioe.2010.01.038.

SGU, 2022. Geological Survey of Sweden. Geological survey of Sweden. Retrieved 07.07.2022 from. https://www.sgu.se/produkter/kartor/kartvisaren/jordkartvisare/jordarter-125-000-1100-000/,https://apps.sgu.se/kartvisare/kartvisare-berg-50-250-tusen.html.

SMHI. (2017). *Swedish Meteorological and Hydrological Institute*. Retrieved March 31 2017, from https://www.smhi.se/klimatdata/meteorologi/ladda-ner-meteorologiska-observationer#param=airtemperatureInstant,stations=period,selectedDate=2017-12-01,stationid=63510.

SMHI. (2018). *Swedish Meteorological and Hydrological Institute*. Retrieved July 5 2018, from http://www.smhi.se/klimatdata/meteorologi/nederbord.

Stockfors, J., Linder, S., Aronsson, A., 1997. Effects of Long-Term Fertilisation and Growth on Micronutrient Status in Norway spruce Trees. Swedish Univesity of Agricultural Sciences, Faculty of Forestry. https://res.slu.se/id/publ/125760.

Svensson, C., Bader, M.K.-F., Forsmark, B., Nilsson, U., Lundmark, T., Nordin, A., Bergh, J., 2023. Early and Repeated Nutrient Additions Support Far Greater Stemwood Production in Norway Spruce than Traditional Late-Rotation Fertilisation. For. Ecol. Manage. 10. https://doi.org/10.2139/ssrn.4499954. Article FORECO-D-22-00459.

Thébault, A., Clement, J.-C., Ibanez, S., Roy, J., Geremia, R., Pérez, C., Buttler, A., Estienne, Y., Lavorel, S., 2014. Nitrogen limitation and microbial diversity at the treeline. Oikos. 123, 11. https://doi.org/10.1111/j.1600-0706.2013.00860.x.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Springer. https://doi.org/10.1007/978-0-387-21706-2.

Yan, T., Qu, T., Sun, Z., Dybzinski, R., Chen, A., Yao, X., Zeng, H., Piao, S., 2018. Negative effect of nitrogen addition on soil respiration dependent on stand age: evidence from a 7-year field study of larch plantations in northern China. Agric. For. Meteorol. 262, 10. https://doi.org/10.1016/j.agrformet.2018.06.029.