

Long-term nitrogen addition raises the annual carbon sink of a boreal forest to a new steady-state

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ABSTRACT

The boreal forest is an important global carbon (C) sink. Since low soil nitrogen (N) availability is commonly a key constraint on forest productivity, the prevalent view is that increased N input enhances its C sink-strength. This understanding however relies primarily on observations of increased aboveground tree biomass and soil C stock following N fertilization, whereas empirical data evaluating the effects on the whole ecosystem-scale C balance are lacking. Here we use a unique long-term experiment consisting of paired forest stands with eddy covariance measurements to explore the effect of ecosystem-scale N fertilization on the C balance of a managed boreal pine forest. We find that the annual C uptake (i.e. net ecosystem production, NEP) at the fertilized stand was $16 \pm 2\%$ greater relative to the control stand by the end of the first decade of N addition. Subsequently, the ratio of NEP between the fertilized and control stand remained at a stable level during the following five years with an average NEP to N response of 7 ± 1 g C per g N. Our study reveals that this non-linear response of NEP to long-term N fertilization was the result of a cross-seasonal feedback between the N-induced increases in both growing-season C uptake and subsequent winter C emission. We further find that one decade of N addition altered the sensitivity of ecosystem C fluxes to key environmental drivers resulting in divergent responses to weather patterns. Thus, our study highlights the need to account for ecosystem-scale responses to perturbations to improve our understanding of nitrogen-carbon-climate feedbacks in boreal forests.

1. Introduction

Boreal forests cover 10–15% of the global land surface (Astrup et al., 2018; Brandt et al., 2013), store about one third of the global forest carbon (C) stock, and act as an important net C sink (Pan et al., 2011). However, their productivity is commonly limited by the low availability of soil nitrogen (N) (Bergh et al., 1999; Binkley and Högberg, 2016). As a consequence, forest N fertilization has been applied in some parts of the boreal region with the aim to increase tree growth (Hyvönen et al., 2008). Elevated N input has also resulted from globally rising N deposition due to anthropogenic activities during the past decades (Gruber and Galloway, 2008). Some studies have reported that increased N

availability enhances aboveground tree production as well as soil C storage in boreal forests by increasing photosynthesis and by limiting decomposition of soil organic matter (SOM) (Bonner et al., 2019; Fleischer et al., 2013; Hasegawa et al., 2021; Hyvönen et al., 2008; Olsson et al., 2005; Schulte-Uebbing et al., 2022). However, the N-induced C gain at the forest ecosystem-scale has remained unclear and under intensive debate over the past decades (de Vries et al., 2008; Flechard et al., 2020a; Högberg, 2007; Högberg, 2012; Magnani et al., 2007; Sutton et al., 2008). Specifically, Magnani et al. (2007) reported an unprecedented high response of forest net ecosystem production (NEP) to N wet deposition (725 g C per g N) based on surveys across a European N deposition gradient. Their estimate was later criticized by

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other studies which suggested that accounting for additional effects from site differences and dry N deposition results in a weaker C-N response of 30–70 g C per g total deposited N (de Vries et al., 2008; Högborg, 2012; Sutton et al., 2008). Nevertheless, owing partly to the lack of controlled empirical experiments at the ecosystem-scale, this debate is still unresolved.

When evaluating forest ecosystem C-N responses, it is important to recognize that the N effect on NEP depends on the separate responses from its component fluxes of gross primary production (GPP) and ecosystem respiration (R_{eco}), respectively (Chapin et al., 2006), which are currently highly uncertain in both magnitude and direction. Specifically, while GPP commonly increases after N addition (Jassal et al., 2010; Lee et al., 2020) due to enhanced canopy-scale photosynthesis caused by increased needle N content (Evans, 1989) and leaf area (Bergh et al., 1999; Linder, 1985), it may decrease under higher N addition rates due to nutrient imbalances (de Vries et al., 2014). Enhanced N supply may also increase the allocation of photosynthetically derived C towards aboveground wood production at the expense of belowground allocation (Högborg et al., 2010; Li et al., 2020; Lim et al., 2015) and enhance the plant carbon-use efficiency in producing woody biomass (CUE_w) (Vicca et al., 2012). Meanwhile, the effect of N addition on R_{eco} , i.e. the combined response of the autotrophic (R_a) and heterotrophic (R_h) components, also remains unclear. It is well documented that N addition leads to a decrease in soil R_h by decreasing decomposition of SOM (Bonner et al., 2019; Marshall et al., 2021; Olsson et al., 2005). In contrast, aboveground R_a may increase with fertilization to meet greater aboveground tree growth and maintenance requirements (Ryan et al., 1996; Stockfors and Linder, 1998). Moreover, belowground R_a has been reported to first increase and then decrease from moderate to high N addition rates. This “hump-shaped” response depends on the N-induced changes in tree belowground allocation of photosynthates, which regulates production and respiration from roots and mycorrhizal fungi (Hasselquist et al., 2012; Högborg et al., 2010; Olsson et al., 2005). Thus, a detailed understanding of how these various internal C cycle processes change with N supply on both short- and long-term (i.e. few years versus decadal) scales is crucial for assessing the impact of elevated N supply on the forest NEP.

Our current knowledge on N-induced changes in these various C fluxes relies primarily on compartmental C flux measurements conducted mainly at plot-scale trials (e.g. 0.04–0.25 ha) and focused on specific components of the whole forest ecosystem (e.g. soil or trees) (Forsmark et al., 2020; Maaroufi et al., 2015; Olsson et al., 2005; Xing et al., 2022). In comparison, estimates of whole ecosystem level responses are few (Eastman et al., 2021) and rarely assessed with ecosystem-scale flux measurements (e.g. eddy covariance). It therefore remains unclear how these separate component fluxes relate to each other quantitatively and, thus, affect total ecosystem-scale responses (i.e. within an area that includes all the organisms (i.e. above- and below-ground) and the abiotic pools with which they interact) (Chapin et al., 2011). Another shortcoming is that plot-scale experiments cannot capture ecosystem-scale feedbacks (i.e. changes in the energy and water balances) in response to N addition. Other study approaches based on exploring geographic gradients of N deposition (Magnani et al., 2007) and meta-analyses (Janssens et al., 2010; Liang et al., 2020) commonly suffer from the covariation with other confounding variables such as climate and site fertility (Flechard et al., 2020a; Flechard et al., 2020b). Moreover, biometric estimates based on conventional tree inventory and chamber methods are limited to annual or growing season scales, respectively, which excludes the possibility to investigate N addition effects on seasonal flux dynamics, particularly those occurring during the long-lasting winter periods in northern high latitudes. In comparison to these various methods, the eddy covariance (EC) technique can provide a direct net exchange estimate that integrates all vertical CO_2 fluxes at the ecosystem scale, with high temporal resolution (i.e. half-hourly) and all year-round (Baldocchi, 2003). Thus, the combination of large-scale fertilizer trials (i.e. N added via helicopter) and EC is optimal

for advancing our understanding of N addition effects on the forest ecosystem-scale C dynamics. However, while EC data have been used to calibrate models for the purpose of exploring forest C-N responses (Jassal et al., 2010; Lee et al., 2020), purely empirical ecosystem-scale N addition studies using EC at paired forest stands (i.e. control and fertilized) are lacking to date.

The scarcity of empirical data at high temporal resolution and at ecosystem-level also limits our understanding of how N addition might alter the responses of ecosystem C dynamics to environmental drivers across multi-temporal scales. Specifically, N-induced shifts in the sensitivities of forest C fluxes may occur through changes in canopy light distribution, light use efficiency (LUE) and maximum photosynthetic rates (Kergoat et al., 2008; Lai et al., 2002), stomatal response to vapor pressure deficit (VPD) (Lai et al., 2002; Tarvainen et al., 2016), soil microbial biomass and heterotrophic respiration (Ågren et al., 2001; Arnebrant et al., 1996) and litter quality (Ågren et al., 2001), tree carbon allocation and CUE (Högborg et al., 2010; Li et al., 2020; Vicca et al., 2012), and soil water access in response to reduced root biomass (Lu et al., 2018). Detailed knowledge of how N addition and environmental drivers interact in regulating forest C fluxes is also important for improving Earth System Models to enable more accurate forecasts of climate and global change impacts on the boreal forest C balance (Drewniak and Gonzalez-Meler, 2017; Greaver et al., 2016).

In this study, we used empirical data from a unique experimental set up including paired stands with EC towers to evaluate the long-term (>1 decade) effects of ecosystem-scale N addition on the ecosystem C balance of a Scots pine (*Pinus sylvestris*, L.) forest in boreal Sweden. The main objectives were to determine the effects of long-term N addition on (1) the forest NEP and its underlying components (i.e. GPP and R_{eco}), and (2) the responses of these C fluxes to key environmental drivers.

2. Methods

2.1. Site description

The study was carried out at Rosinedalsheden experimental pine forest (*Pinus sylvestris* L.) in northern Sweden (64°10N, 19°45E) (Fig. 1). The site was regenerated by using *P. sylvestris* seed trees in 1920–1925, pre-commercially thinned in 1955 and thinned in 1976 and 1993, respectively (Lim et al., 2015). Based on measurements at the Svartberget field station (located 8 km from the study site), the most recent 30-year normal (1991–2020) of annual mean air temperature (T_a) and total precipitation are 2.4°C and 637 mm, respectively (Laudon et al., 2021). Snow cover commonly lasts from early November to late April. It is noteworthy that climatic conditions in the initial study year 2006 were within the range of those observed during the later study years 2015–2019 (Fig. A1, Table A1).

2.2. Experimental design

In 2006, an experiment was initiated to study the effect of N addition on ecosystem-scale C cycling. This experimental setup consisted of a fertilized and a non-fertilized control stand (at ~2 km distance). It is noteworthy that this large scale (i.e. 13 ha for each stand) experiment lacks real replicates, which is inherent in nearly all studies based on eddy covariance (Hill et al., 2017). Fertilizer was applied via helicopter to the N-addition stand over an area of 13 ha annually in summer (i.e. before the end of June), using Skog-Can fertilizer (Yara, Sweden) which was a solid pellet form, containing NH_4 (13.5%), NO_3 (13.5%), Ca (5%), Mg (2.4%), and B (0.2%) (Lim et al., 2015). The fertilized stand received 100 kg N $ha^{-1} yr^{-1}$ from 2006 through 2011, 50 kg N $ha^{-1} yr^{-1}$ from 2012 through 2014, and ~60 kg N $ha^{-1} yr^{-1}$ from 2015 through 2019, respectively. Fertilization rate was initially targeted to N-saturate the ecosystem. However, due to concerns about N leaching, the rate was reduced to 50 kg N ha^{-1} , when foliar N reached 2% in 2012, indicating N-saturation (Lim et al., 2015). In each of these two stands, an eddy

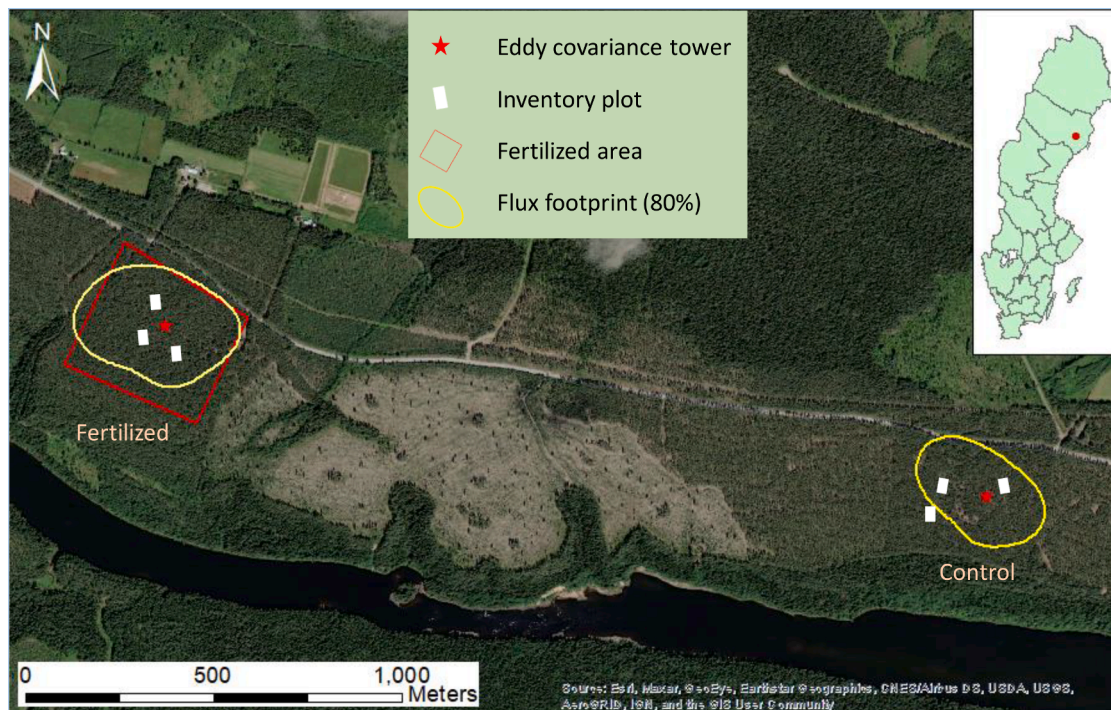


Fig. 1. Location of the eddy covariance flux towers and inventory plots at the fertilized and control stands, border of the fertilized stand, and the flux footprint climatology (80%) at two stands for the entire study period (March 2006 to February 2007, January 2015 to December 2019). The red dot at the top-right panel shows the location of the experiment forest in Sweden.

covariance (EC) tower was installed to measure the turbulent exchange of CO₂ and water vapor above the tree canopy.

The mean tree height (mean \pm standard error) based on three inventory plots (1000 m² per plot) increased significantly ($P < 0.05$) from 16.4 (± 0.1) and 14.7 (± 0.2) m in 2006 to 19.1 (± 0.1) and 18.4 (± 0.2) m in 2019 at the control and fertilized stands, respectively. The corresponding leaf area index (LAI) was 2.3 and 1.8 m² m⁻² in 2006 and 2.7 and 3.1 m² m⁻² in 2013 (Lim et al., 2015). The understory vegetation consists mainly of bilberry and cowberry (*Vaccinium myrtillus L.* and *Vaccinium vitis-idaea L.*), and a ground layer of mosses (Hasselquist et al., 2012). The soil is fine sand, and the soil type is a weakly developed podsol with an organic mor-layer ranging in thickness from 2 to 5 cm (Hasselquist et al., 2012). The ground surface around the towers is rather flat up to a distance of ~ 200 m from the tower with a maximum elevation difference of ~ 2 m, and the maximum elevation differences within 300 m and 1000 m distance from the tower are 24 m and 114 m, respectively (Jocher et al., 2017).

2.3. Eddy covariance measurements

From March 2006 to February 2007, an EC system was installed at 18 and 17 m height above the ground level at the control and fertilized stand, respectively. The EC system consisted of a Gill R3-100 (Gill Instruments Limited, Hampshire, UK) sonic anemometer for detecting the three-dimensional wind components and sonic temperature and an open-path LI-7500 (LI-COR Environmental, Lincoln, USA) gas analyzer for measuring H₂O and CO₂ mixing ratios at 20 Hz frequency. From March 2007 to June 2014, the EC measurement height was not adjusted to the increasing height of the growing trees which resulted in bad data due to insufficient measurement height. Data from these years were therefore not considered in this study.

From July 2014 to February 2020, H₂O and CO₂ mixing ratios were measured with a gas analyzer (LI-7200, LI-COR Environmental, Lincoln, USA) at 20 Hz frequency (Jocher et al., 2017) and the EC measurement heights were raised to adjust for the continuous increase in tree height

(Table A2). The step-wise rise of the measurement height ensured that the main flux source area (i.e. fetch distance) remained somewhat constant and limited to the area of interest. Based on footprint estimates using a two-dimensional Flux Footprint Prediction model (Kljun et al., 2015), for nearly all of the available half hourly flux data (i.e. 94%), at least 80% of the contributing source area was located within the fertilized area (Fig. 1).

In 2014, a second EC system was installed below the forest canopy at 2.5 m height near the base of the above-canopy EC flux tower at each stand. These below-canopy systems (CPEC 200, Campbell Scientific, Inc., USA) consisted of a closed-path infrared gas analyzer (IRGA, EC155, Campbell Scientific, Inc., USA) and a three-dimensional ultrasonic anemometer (CSAT3A, Campbell Scientific, Inc., USA). Data from the below- and above-canopy EC systems were used to determine periods of decoupling of below- and above-canopy air mass flow based on a comparison of the standard deviation of vertical wind velocities (σ_w) below- and above-canopy (Jocher et al., 2017; Thomas et al., 2013; see further details below).

2.4. Data processing, quality control, and gap-filling of EC data

The EC raw data were processed using the EddyPro® software (version 7.0.6, LI-COR Biosciences, USA) to obtain the 30-min average turbulent fluxes of CO₂. As part of the processing, we applied the following corrections implemented in Eddypro: double coordinate rotation was used to align the sonic anemometer with the local wind streamlines (Wilczak et al., 2001), block averaging was used to determine the turbulent fluctuations over each 30-min averaging period (Gash and Culf, 1996), and time lags between sonic and gas analyzer were determined by automatic time lag optimization method. The high-pass (Moncrieff et al., 2004) and low-pass (Moncrieff et al., 1997) filtering corrections were applied, respectively. The “0-1-2 system” flagging policy (Mauder and Foken, 2004) was selected for quality check of the half-hourly flux data where “0” represents the best quality flux data, “1” stands for good data quality for general analysis (e.g. annual

carbon budget), and “2” indicates data with low quality that were subsequently removed from the dataset.

To filter out spikes occurring due to biophysical (e.g. fast changes in turbulence conditions) and instrumental (e.g. water drops on sonic anemometer or the open-path gas analyzer mirrors) reasons (Papale et al., 2006), half-hourly CO₂ flux data were discarded if the value of a specific data point was outside the common range (defined as mean \pm 3 \times standard deviation) over a 14-day moving window. Half-hourly CO₂ flux data were also discarded during post-Eddypro filtering for periods when mean vertical wind speed was $> 0.2 \text{ m s}^{-1}$ or $< -0.3 \text{ m s}^{-1}$ due to sonic malfunctioning.

For periods with weak turbulent mixing, the below-canopy airflow can be decoupled from the vertical exchange with the above canopy air masses. During these periods, CO₂ may either accumulate in the air volume below the EC sensor height or be removed outside the area of interest by horizontal advection (Belcher et al., 2012). Canopy CO₂ storage and advection fluxes are not accounted for by the turbulent EC measurements above the forest canopy (Goulden et al., 1996), and thus need to be estimated separately based on concentration profile measurements (Montagnani et al., 2018). Since continuous concentration profile measurements are lacking at our study sites, we routinely apply the decoupling filtering method (Thomas et al., 2013) to account for storage and advection effects (Jocher et al., 2017), by investigating the site-specific correlations of σ_w between below- and above-canopy measurements: if air masses below and above the canopy are fully coupled then this relation is linear. During fully coupled periods, storage and advective fluxes can be considered negligible (Jocher et al., 2017; Thomas et al., 2013). Thus, the half-hourly CO₂ flux data above-canopy in 2015–2019 was discarded when half-hourly below- and above-canopy σ_w was below either one of their respective σ_w threshold values (Figs. A2a, A3a).

Since no below-canopy EC systems were installed in 2006–2007, we applied a single-level decoupling filtering method based on only the above-canopy thresholds (determined by the two-level approach in 2015–2019) to detect and remove half-hourly flux data during low turbulence conditions in that first year. A separate analysis suggested that the single-level filter (Figs. A2b, A3b) captured 83% and 81% of the decoupled data flagged by the two-level filter (Figs. A2a, A3a) in the 2015–2019 dataset at the fertilized and control stands, respectively. Furthermore, the differences in annual CO₂ fluxes between the single- and two-level decoupling filtering methods were small (i.e. 3% for annual NEP and GPP, 5% for annual R_{eco} averaged over 2015–2019 at both stands). Thus, the half-hourly CO₂ flux data above-canopy in 2006–2007 were discarded when half-hourly above-canopy σ_w was below the corresponding σ_w thresholds. The above-canopy σ_w thresholds from 2015–2019 were applied in 2006–2007 since we found that in 2006–2007, the nighttime CO₂ flux becomes independent of turbulent mixing strength when exceeding the same above-canopy σ_w threshold as in 2015–2019 (Fig. A4).

After the filtering of spikes and periods with low turbulence, some outliers remained (primarily during winter). Thus, the 5% highest and lowest half-hourly CO₂ flux from November to March as well as remaining spikes during rainy days were also removed. After applying all quality control steps, 43% and 48% of the half-hourly CO₂ flux data during the entire study periods (Mar 2006–Feb 2007, 2015–2019) remained as good quality data at the fertilized and control stand, respectively.

Gaps in the half-hourly CO₂ flux data were filled using the marginal distribution sampling (MDS) approach (Reichstein et al., 2005) implemented in the REddyProc online tool (Wutzler et al., 2018). The same online tool was used to partition the gap-filled NEE into GPP and R_{eco} using the nighttime-based flux partitioning method (Reichstein et al., 2005). According to Wutzler et al. (2018), R_{eco} during nighttime was represented by only the modeled values without considering the measured nighttime NEE data (i.e. representing R_{eco} during the night). GPP was computed as the difference between R_{eco} and NEE (i.e. GPP =

R_{eco} – NEE). From August 9 to September 11 in 2016 the malfunction of the gas analyzer resulted in a large gap at the fertilized stand for which the ReddyProc online tool could not provide reasonable estimates. Instead, we used the PRELES model which was calibrated by EC and meteorology data from the study site (Tian et al., 2021) to model GPP (RMSE of predicted GPP is $0.71 \text{ g C m}^{-2} \text{ day}^{-1}$). R_{eco} during this long-gap period at the fertilized stand was re-estimated following the respiration-temperature equation recommended by Wutzler et al. (2018), in which the parameter R_{ref} (reference respiration at 15 °C) during this long-gap period at the fertilized stand was modeled based on the relationship between R_{ref} at the two stands during one month before and after the gap period. Finally, the PRELES modeled GPP was then combined with the re-estimated R_{eco} to determine NEE during this long-gap period at the fertilized stand.

The uncertainty of the annual NEE, GPP, and R_{eco} due to random measurement errors and the uncertainty introduced by the gap-filling procedures was estimated using Monte Carlo simulations (100 repetitions) following the procedures described in Richardson and Hollinger (2007). The standard deviation (\pm SD) of the resulting 100 annual sums was used as a measure for the uncertainty in the annual flux sums.

2.5. Meteorological and soil measurements

At each site, a suite of environmental measurements was conducted. This includes photosynthetic photon flux density (PPFD, Apogee SQ110 in 2014–2017, LiCor LI-190 in May 2017–2019), relative humidity (RH) and T_a (Rotronic Hygroclip in 2014–2017, Thies Clima probe in May 2017–2019), precipitation (Campbell ARG100), snow depth (Campbell SR50 in 2014–2017, Campbell SR50A in May 2017–2019), soil temperature (T_s, Campbell 107) and soil water content (SWC, Delta-T SM 300 in 2014–2017, Campbell CS655 in May 2017–2019). The above-canopy PPFD, RH and T_a, and precipitation were measured at the same height as the concurrent EC. T_s and SWC were measured at the depths of 15 cm and 50 cm respectively. The measurements of PPFD, RH, T_a, T_s, and SWC in 2014–2017 were corrected by cross-comparison during an overlapping period (May–Dec in 2017) based on the measurements from new sensors from May 2017 to 2019. Due to the lack of meteorological and soil measurements at the Rosinedal sites in 2006–2007, all meteorological data (global radiation, T_a, RH) were taken from measurements at the Svartberget climate station 8 km from the study site. Global radiation data was then converted into PPFD (PPFD = 2.07 * global radiation; Papaioannou et al., 1993).

2.6. Statistical analysis

Eddy covariance studies commonly suffer from a lack of replication and a statistical evaluation with true replicates is therefore not possible. However, using a paired-stand approach with both pre-treatment and parallel control data is likely the best experimental approach to achieve when applying the EC technique to address treatment effects on the ecosystem C balance. One-way ANOVA (two-tailed) was used to test significant differences in the annual C fluxes between the two stands based on the Monte Carlo simulations (100 repetitions). Bivariate Pearson Correlation (two-tailed) was used to test significance in the correlations. Statistical tests were performed using IBM SPSS version 26 (IBM Corp, Armonk, NY). Post-Eddypro filtering of the eddy covariance flux data, and mathematical fits of flux differences between the two stands against environmental drivers were conducted using the Matlab software (Matlab R2019b, Mathworks, USA).

3. Results

3.1. N addition effects on the boreal forest ecosystem C balance

Our EC data revealed that the fertilized stand initially had a lower annual NEP than the control stand in the first year of ecosystem-scale N

addition (i.e. 2006), whereas the NEP of the fertilized stand exceeded that of the control stand after one decade of N addition (Fig. 2a). Specifically, the ratio of annual NEP at the fertilized and control stands ($NEP_F:NEP_C$) increased from 0.92 in 2006 to 1.07 ± 0.02 (mean \pm SE) in 2015–2019, indicating that the N-induced gain in the net C uptake was $16 \pm 2\%$ during the first decade (Fig. 2a). After one decade of N addition, however, the $NEP_F:NEP_C$ ratio did not further increase but remained at a stable level during the following five years (i.e. 2015–2019).

The initial between-site difference in annual NEP in 2006 was caused by greater GPP at the control stand while R_{eco} was similar between the two stands (Fig. 2b, c). Following a decade of N addition, both GPP and R_{eco} were significantly higher at the fertilized stand than control in 2015–2019. Specifically, the ratio of annual GPP between the two stands ($GPP_F:GPP_C$) increased from 0.97 in 2006 to 1.13 ± 0.01 in 2015–2019, while the ratio of annual R_{eco} ($R_F:R_C$) increased from 0.99 to 1.16 ± 0.02 (Fig. 2b, c). As with the site-differences in annual NEP, the ratios for annual GPP and R_{eco} between the two stands did not further increase and remained relatively stable after one decade of N addition (i.e. in 2015–

2019). Based on these results, when taking the initial difference between the two stands (i.e. year 2006) into account, the N-induced C gain was 7 ± 1 and 24 ± 2 g C per g N for NEP and GPP in 2015–2019, respectively (Fig. 2a, b). It is further noteworthy that N addition did not alter the ecosystem-level CUE ($CUE_e = NEP/GPP$), which for the fertilized and control stand was 0.31 and 0.33 in 2006, and on average 0.28 ± 0.01 and 0.29 ± 0.01 during 2015–2019, respectively (Fig. A5).

In the first year of N addition (i.e. 2006), monthly NEP was higher at the control stand during most of the growing season with the maximum difference occurring in June (Fig. 3a). Meanwhile, no clear site-differences were noted in the non-growing season in 2006. Long-term N addition not only reversed the sign but also shifted the timing of the peak site-difference of monthly NEP into August (Fig. 3a). Similar patterns were also observed in monthly GPP (Fig. 3b). In comparison, long-term N addition also caused higher R_{eco} at the fertilized stand throughout the entire year with the peak difference occurring in June, whereas no differences were noted in 2006 (Fig. 3c).

In 2015–2019, the fertilized stand showed both higher summer C

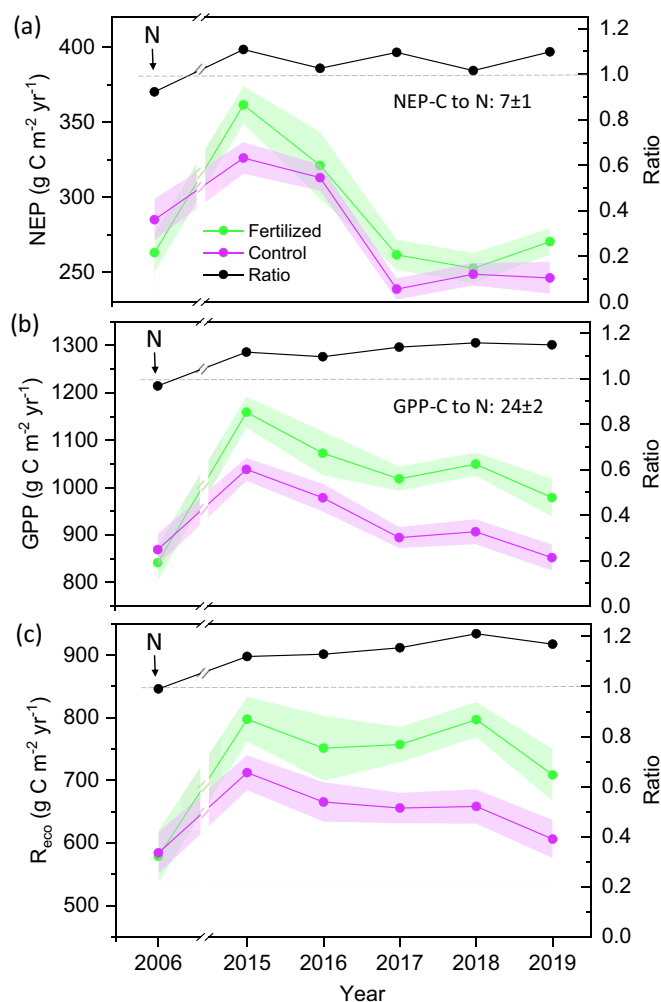


Fig. 2. Annual net ecosystem production (NEP), gross primary production (GPP) and ecosystem respiration (R_{eco}) at the fertilized and control stands and the response ratio (fertilized/control) in 2006 (i.e. Mar 2006–Feb 2007) and 2015–2019. Shaded areas indicate the uncertainties (i.e. standard deviation, SD) in the annual cumulative carbon fluxes estimated from the Monte Carlo simulations. All the annual fluxes were significantly ($P < 0.05$) different between two stands except for R_{eco} in 2006 ($P = 0.28$). Inserted in panels a) and b) are the 5-year mean \pm SE (2015–2019) response ratios of NEP-C to N and GPP-C to N, respectively, expressed in g C per g added N $ha^{-1} yr^{-1}$ (see Table A3 for annual response values).

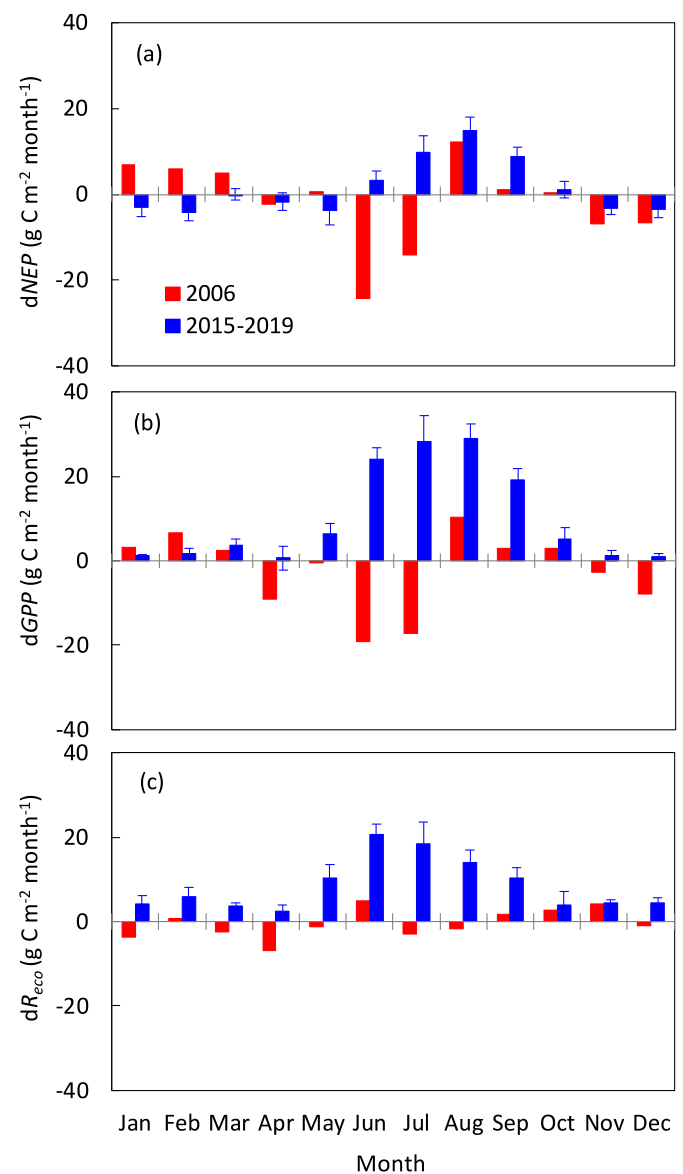


Fig. 3. Monthly flux difference in (a) net ecosystem production (NEP), (b) gross primary production (GPP), and (c) ecosystem respiration (R_{eco}) between the fertilized and control stands in 2006 (i.e. Mar 2006–Feb 2007) and 2015–2019 (5-year average \pm SE). Positive means higher flux at the fertilized stand.

uptake and higher winter C loss than the control stand (Fig. 3a), resulting in a strong ($R^2 = 0.87$) seasonal coupling (Fig. 4). This cross-seasonal feedback resulted in lower annual $NEP_{F:NEP_C}$ ratios compared to those observed for GPP and R_{eco} ratios during 2015–2019 (Fig. 2, Table A3).

3.2. N addition effects on the sensitivity of forest C fluxes to environmental drivers

Our data further showed that long-term N addition altered the responses of the forest C balance to environmental drivers. In the first year of N addition (i.e. 2006), the daily NEP and GPP increased more at the control stand compared to the fertilized stand with higher PPFD, T_a , and VPD, with the GPP difference leveling out at high T_a (Figs. 5a–f, A6a–f). In comparison, the difference in R_{eco} between the two stands in 2006 showed no significant correlations with environmental factors (Figs. 5g–i, A6g–i). After one decade of N addition, the daily NEP was higher at the fertilized stand with the difference showing a unimodal optimum-curve relationship with PPFD, T_a , and VPD (i.e. with the greatest difference occurring at intermediate PPFD, T_a , and VPD) (Figs. 5a–c, A6a–c). The decline in the NEP site-difference during hot and dry summer periods (i.e. with high PPFD, T_a , and VPD) in 2015–2019 occurred because the site-difference in R_{eco} continued to further increase whereas the site-difference in GPP declined under these conditions (Figs. 5d–i, A6d–i).

4. Discussion

4.1. Long-term N addition raises the boreal forest C sink to a new steady-state

Our findings based on paired EC measurements confirm empirically that N addition in boreal forest causes a sustained increase in NEP. However, our long-term observations further demonstrate a non-linear progression of the N-induced gain in NEP which reached a new steady state of $16 \pm 2\%$ after one decade. This observation supports the non-linear response observed for tree growth (Binkley and Högberg, 2016; Högberg et al., 2006; Li et al., 2020; Xing et al., 2022) and soil C stock (Xu et al., 2021) in previous plot-scale trials and meta-analysis studies. However, the N-induced C gain at the ecosystem scale of 7 g C per g N observed during the later part of the period we studied was considerably lower than the estimate of > 700 by Magnani et al. (2007) and the more recently reported numbers of 18–70 g C per g N (de Vries et al., 2008;

Högberg, 2007; Högberg, 2012; Hyvönen et al., 2008; Sutton et al., 2008; Xing et al., 2022). In support of the ongoing debate, our results thus clearly support the notion that the C to N response estimate by Magnani et al. (2007) was far too high. Given that our fertilized stand is likely close to a N-saturated system after one decade of N addition, our findings further provide new evidence suggesting that the N-induced ecosystem C gain diminishes in the long-term to even lower values (i.e. well below 10 g C per g N) than expected from the range of 18–70 g C per g N observed in these previous plot-scale studies limited to one decade and conducted in non-N-saturated systems (de Vries et al., 2008; Högberg, 2007; Högberg, 2012; Sutton et al., 2008; Xing et al., 2022). Thus, while our study corroborates a sustained increase in NEP following N addition, the observed non-linearity in its response trajectory highlights the need for long-term studies to adequately evaluate the consequences of changes in N supply for the C sequestration capacity of boreal forest ecosystems (Binkley and Högberg, 2016).

Our study unfortunately cannot provide information on the C balance response to N addition during the initial treatment years due to the lack of reliable EC data from 2007 to 2014. However, a study based on plot-scale inventory measurements reported that in the initial year (i.e. 2006) the aboveground net primary production (ANPP) and NPP were similar between the two stands but significantly increased from 2007 to 2013 at the fertilized stand (Lim et al., 2015). This indicates an initial steady increase of the net C sink due to N addition towards the divergent levels observed in our EC data from 2015–2019.

The long-term stabilization of the N-induced increase in NEP observed in our Scots pine forest resulted from the concurrent increases in both NEP component fluxes, i.e. GPP and R_{eco} . In the short term, a relatively faster response of GPP following the N-induced increases in LAI and, thus an increased light harvest (Lim et al., 2015; Tian et al., 2021), likely explains the initially greater increase in NEP following N addition. Over time, however, greater biomass and litter production due to higher GPP likely caused a subsequent increase in R_{eco} which eventually compensated for some of the higher GPP and thereby constrained the NEP differences between the two stands (Fig. 2). Furthermore, our long-term EC flux measurements revealed the novel observation that long-term N-fertilization not only enhanced the forest C uptake in summer but also increased the C emission during winter (Fig. 3a), suggesting a counterbalancing feedback mechanism between growing and non-growing season C cycle dynamics. A possible explanation for this cross-seasonal coupling is that greater aboveground tree biomass production and litter production following N addition increased aboveground tree R_a (Grant et al., 2010; Lai et al., 2002) and the supply of substrate (e.g. above-ground litter input increased by 77% at the fertilized stand at our site based on unpublished data) for microbial decomposition during the subsequent non-growing season period (Forsmark et al., 2020). Our empirical results support the predictions of a modeling study that simulated increased summer C uptake and winter C emission following N addition compared to the control stand in a temperate pine forest in northern USA (Lai et al., 2002). Further noteworthy is the N-induced shift in the timing of the peak between-site difference in monthly NEP from June (in 2006) into August (2015–2019). This result is in line with previous studies reporting sustained tracheid production (Kalliokoski et al., 2013) and greater C allocation towards storage in aboveground tree components (Högberg et al., 2010) in N-fertilized plots compared to control stands during the late summer period. Overall, our findings demonstrate that the N-induced increase in boreal forest NEP caused by an initial imbalance of production and respiration components stabilizes at a new steady state due to the inherent coupling of production and respiration at seasonal and multi-annual scales.

Previous plot-scale studies exploring the N response of respiration fluxes in boreal forests were mainly focused on soil respiration and reported a wide range of its responses including positive (Liu et al., 2021), insignificant (Forsmark et al., 2020; Liu et al., 2021) and negative (Forsmark et al., 2020; Maaroufi et al., 2015; Olsson et al., 2005) effects.

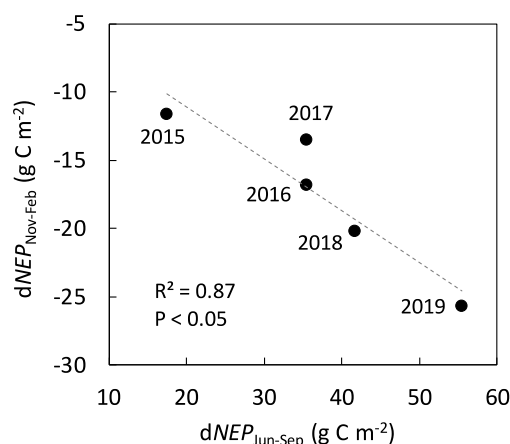


Fig. 4. Regression relationship of differences in total net ecosystem production (NEP) between the fertilized and control stands for winter (Nov-Feb) versus summer (Jun-Sep) periods in 2015–2019. Note that winter in one year represent the period from November in this year to February in the next year (e.g. winter 2019 represents the period from November 2019 to February 2020).

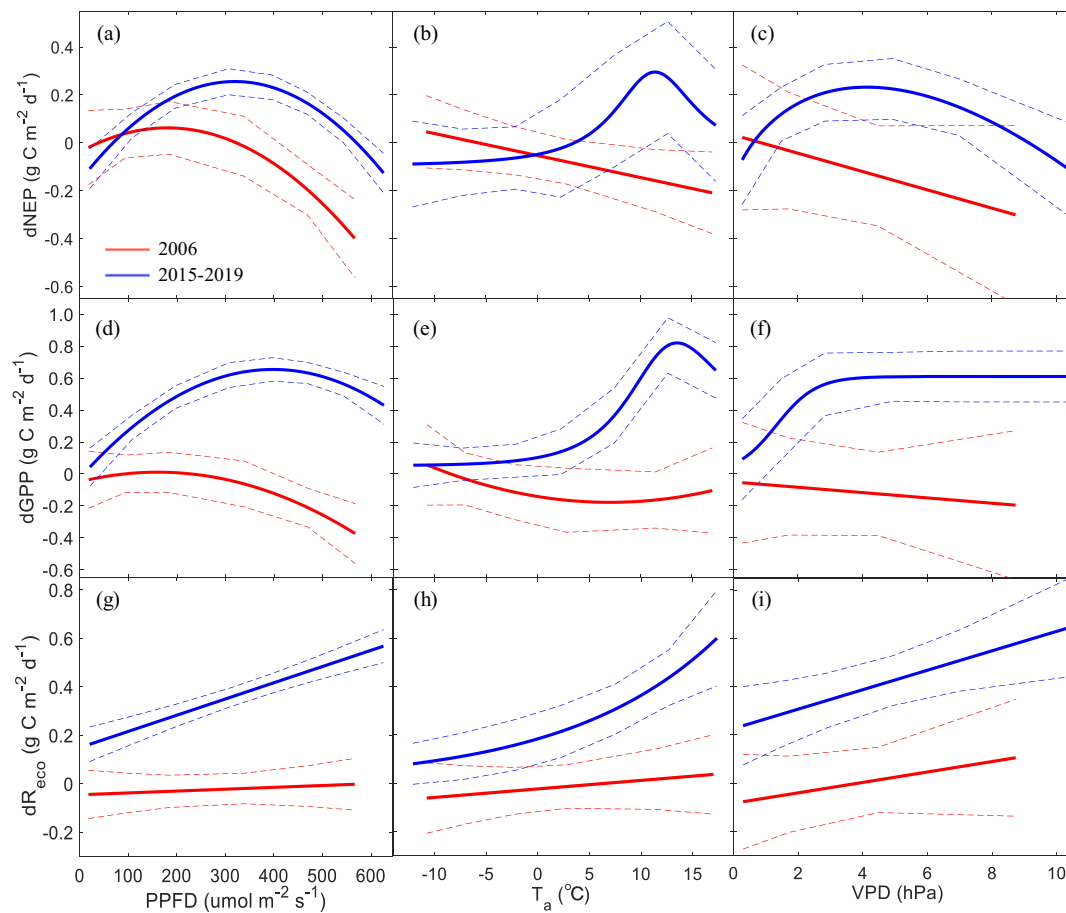


Fig. 5. Difference in the daily (a–c) net ecosystem production (NEP), (d–f) gross primary production (GPP) and (g–i) ecosystem respiration (R_{eco}) between the fertilized and control stands against daily average photosynthetic photon flux density (PPFD), air temperature (T_a), and vapor pressure deficit (VPD) in 2006 (i.e. Mar 2006–Feb 2007) and 2015–2019. The solid lines are mathematical fits to bin-averaged data (shown in Fig. A6) in 2006 and 2015–2019, respectively. The dash lines are 95% confidence limits.

Altogether, these contrasting observations indicate that the soil respiration-N response may largely vary with different N input levels and treatment duration (de Vries et al., 2014; Xing et al., 2022; Xu et al., 2021), forest floor vegetation (Dirnböck et al., 2014; Metcalfe et al., 2013) and soil C stock (Hyvönen et al., 2008; Olsson et al., 2005). At our site, previous studies observed a decrease in soil respiration in year 6 (Metcalfe et al., 2013) and year 7–9 (Marshall et al., 2021) following the beginning of N addition. These results are corroborated by additional data from our study site showing N induced inhibition of soil C decomposition (Bonner et al., 2019) and a concomitant increase in lignin derivatives (aromatic, methoxy/N-alkyl C) relative to that of carbohydrates (O-alkyl C) in the soil organic layer (Hasegawa et al., 2021), together suggesting a significantly increased rate of soil C accumulation. This would imply that the N-induced increase in R_{eco} observed in our study was caused by a substantial increase in aboveground R_a , possibly caused by greater aboveground tree woody and foliar biomass production (Lim et al., 2015) combined with increased N content in the biomass (needle N content nearly doubled at the fertilized site, Tarvainen et al. (2016)). This finding highlights the need for an improved understanding of aboveground R_a , as well as belowground R_a and R_h dynamics for evaluating consequences from altered N supply on the forest ecosystem C balance and allocation patterns.

For the years 2012–2014, chamber- and inventory-based studies have estimated annual R_h at 232 ± 8 and 277 ± 22 $\text{g C m}^{-2} \text{y}^{-1}$ (Marshall et al., 2021) and net primary production (NPP) at 522 ± 31 and 381 ± 29 $\text{g C m}^{-2} \text{y}^{-1}$ (unpublished data, Lim et al., 2015) at our fertilized and control stands, respectively. The net C balances (290 and 104 g C m^{-2}

y^{-1} at fertilized and control stands) derived from these biometric estimates (i.e. $\text{NEP} = \text{NPP} - R_h$) are similar to our EC-based NEP estimates and support the greater C sink-strength noted at the fertilized stand. Furthermore, these biometric data indicate that the N-induced net C gain at the ecosystem level observed in the EC measurements occurred primarily due to increased tree biomass production, and only to a relatively smaller part due to the reduced R_h . This implies that the long-term fate of this additional C gain strongly depends on forest management choices and future climatic constraints on forest growth.

4.2. Long-term N addition alters environmental response of boreal forest C balance

Our long-term EC data provided a unique opportunity to investigate the N addition effect on the responses of forest ecosystem C fluxes to environmental drivers. In 2006, the greater NEP and GPP in the control stand at high PPFD, T_a , and VPD were likely due to greater responses from the initially higher tree biomass and LAI (i.e. 18% for stand density and 22% for LAI, Lim et al., 2015). In contrast, we found that long-term N addition resulted in higher GPP at the fertilized stand particularly at medium levels of PPFD, T_a , and VPD, which may reflect N-induced changes in tree canopy structure (possibly causing a shift in the diffuse light fraction) and increases in photosynthetic capacity (Liang et al., 2020; Tarvainen et al., 2016). For instance, a modeling study identified greater ecosystem light interception (through increased LAI) and LUE in our fertilized stand (Tian et al., 2021). These divergent responses might also further explain the observed temporal shift of the peak in monthly

NEP and GPP differences between the sites towards the late summer when the fertilized stand may benefit from the more frequent medium levels of PPFD and T_a compared to the earlier summer or autumn periods when lower and high PPFD and T_a prevail during which conditions the differences between the control and fertilized stand diminish (Fig. 3a, b). The leveling and eventual decline of the positive effects of N addition on GPP at high PPFD, T_a , and VPD levels implies that the response of stomata and/or root water uptake at the fertilized stand was more sensitive to drought conditions caused by decreased fine roots production and altered root distribution (Henriksson et al., 2021; Ryan et al., 1996; Tian et al., 2021). It is noteworthy that our analysis was limited to exploring the single factor responses without accounting for additional confounding effects from variable interactions. A more comprehensive multi-factorial model analysis at our site however previously identified that the N-induced increase in GPP is reduced under high PPFD and VPD most likely due to the reduced stomatal conductance at the fertilized stand (Tian et al., 2021).

Similar to the responses of GPP, the sensitivity of R_{eco} to environmental drivers increased after one decade of N addition, likely due to higher R_a from greater aboveground tree biomass. In contrast to the decline of GPP difference at high T_a , PPFD, and VPD, however, the difference in R_{eco} between the two stands continuously increased with higher T_a , PPFD, and VPD in 2015–2019. Together, this explains the observed decrease in the N-induced net C gain (i.e. the site-difference in NEP) at high T_a , PPFD, and VPD, e.g. during the 2018 drought year. Our empirical results support a modeling study that suggested the largest increase in NEP after N addition in a temperate pine forest to occur under cooler T_a during which R_{eco} decreases more than GPP (Lai et al., 2002). Other studies also reported that the responses of forest soil respiration (Song et al., 2020) and aboveground NPP (Lim et al., 2017) to fertilization were affected by precipitation. However, since precipitation effects are primarily exerted through changes in radiation and soil moisture levels (Öquist et al., 2014), a detailed understanding of how N addition interacts with these primary environmental drivers (i.e. PPFD, T_a , VPD) is a key prerequisite for improving our understanding on climate change impacts on the boreal forest C cycle. In addition to these observed changes in C cycle responses to climatic factors, it is important to note that increased N supply might also amplify the positive effects of increasing atmospheric CO_2 concentration (iCO_2) on the terrestrial carbon sink (Norby et al., 2010; Walker et al., 2021). Overall, the N-induced shifts in the responses of ecosystem C fluxes to environmental factors observed in our study highlight the importance of incorporating such interactive effects between N supply and multiple environmental drivers (incl. iCO_2) into Earth System Models to improve predictions of nitrogen-carbon-climate feedbacks in the boreal biome.

5. Conclusions

Our study based on paired eddy covariance measurements assessed the responses of ecosystem-scale C balance and its component to nitrogen addition for a boreal pine forest ecosystem over a 15 year period of ecosystem-scale fertilization. The results showed that the net ecosystem production (NEP) increased following one decade of N-fertilization by 16%, but increase stabilized during the subsequent five years, during which the N-induced NEP-C gain was 7 g C per g N. This is considerably lower than previous estimates reported in the plot-scale trials and non-N-saturated forest ecosystems. This non-linear long-term response resulted from a cross-seasonal feedback between N-induced increases in both growing-season C uptake and winter C emission. Gross primary production and ecosystem respiration also increased by fertilization but their increases stabilized after one decade. We further found that long-term fertilization caused a divergence in the sensitivity of ecosystem C fluxes to environmental drivers, highlighting the importance of incorporating such interactive effects between N supply and climate into modeling. These findings indicate that present-day ecosystem models based on plot-scale data are likely to fail in accurately simulating future

forest nitrogen-carbon-climate feedbacks.

Author contributions

P.H., S.L., and T.L. designed the field experiment. P.Z. and M.P. conceived the analysis. P.Z. collected and processed the data, performed the analysis, and wrote the paper. M.B.N. and M.O.L. contributed to data collection. J.C., J.R., G.J., and X.T. contributed to the processing of the data. M.P. contributed to the performing of the analysis and writing of the paper. T.N., T.L., P.H., and S.L. provided financial support. All authors participated in interpreting the results and provided feedback on the paper.

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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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2022.109112.

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