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Long-term nitrogen fertilization increases drought sensitivity of gross primary productivity capacity in a boreal Scots pine forest

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Abstract. Nitrogen (N) is a key limiting element for plant photosynthesis in boreal forests. Thus, N fertilization is proposed as an effective management strategy to increase forest productivity and the associated carbon (C) sink in the N-limited boreal biome. However, there is a limited understanding of how N fertilization can affect the sensitivity of the C sink to drought stress, which is predicted to occur more frequently in the boreal region in a changing climate. This study was based on a 15-year controlled N fertilization experiment in a boreal Scots pine stand. Ecosystem light-saturated photosynthetic capacity (GPP2000) is a good indicator of forest photosynthesis response to environmental stress. Here, we used eddy covariance measurements of C fluxes data and environmental data from paired sites to investigate whether long-term N fertilization altered the drought sensitivity of the GPP2000. We found that long-term N fertilization significantly increased ecosystem GPP2000 even on dry days during summer (June, July, and August). However, a significantly divergent drought sensitivity of GPP2000 between the N Fertilized and Reference sites was detected. Specifically, N fertilization increased the sensitivity of GPP2000 to both atmospheric and soil drought to the extent that it may offset the positive effect of N fertilization on GPP2000. Moreover, using the random forest model, we found that the absolute GPP2000 difference between fertilization and control sites was mainly influenced by air and soil drought proxies, followed by canopy conductance rather than the air temperature. These results advance our understanding of the mechanisms of forest responses to drought with long-term N fertilization.

1 Introduction

Drought is projected to occur more frequently and intensively due to the ongoing climate warming (Kharin et al., 2018). Boreal forests, which store approximately 33% of global terrestrial carbon (C), are crucial in mitigating global warming (Bradshaw and Warkentin, 2015; Gauthier et al., 2015). However, boreal forests are increasingly at risk of drought due to amplified warming driven by climate feedbacks (Gauthier et al., 2015; Liu et al., 2023). Consequently, the C sink in boreal forests may be compromised by the increasing frequency of droughts (Baldocchi and Penuelas, 2019). Numerous studies have shown that drought is a key factor in forest functional stability. Therefore, understanding how boreal forests respond to drought is critical for predicting the C-climate feedback in future climate scenarios.

Drought occurs from the imbalance between the plant water supply and demand. During drought, trees reduce their stomatal conductance to avoid hydraulic failure at the cost of reducing photosynthesis (Parry et al., 2002). However, prolonged drought can significantly weaken C sequestration, induce C starvation, and finally, lead to tree mortality (McDowell et al., 2008, 2011). These drought effects are mediated by stomatal regulation. Stomata control water and C exchange in leaves and are indirectly affected by soil water availability via evapotranspiration (Keenan et al., 2013). Stomata are also sensitive to atmospheric vapor pressure deficits (VPD), especially at values close to 1 kPa at field conditions (Oren et al., 1999). Thus, both soil water availability and VPD should be considered when assessing the impact of drought on the forest ecosystem. Forest responses to drought vary due to different species compositions (Sturm et al., 2022; Chen et al., 2023; Zhong et al., 2023). One reason is that the response to drought stress is not always synchronized across species (Schnabel et al., 2021). These responses further depend on the water regulation strategies adopted by the species. For example, species with an isohydric strategy usually have quick stomatal closure to prevent water loss and keep leaf water potential, but reduce photosynthesis during drought (McDowell et al., 2008; Martínez-Vilalta and Garcia-Forner, 2017). In contrast, species with an anisohydric strategy delay the stomatal closure to maintain relatively high photosynthesis, but this leads to high fluctuations of leaf water potential, bringing the high risk of hydraulic failure and xylem embolism during prolonged droughts (McDowell et al., 2008). Drought also profoundly affects the root system. When the shallow soil is dry, plants can retain water by accessing deeper soil moisture. However, prolonged drought can damage root function by reducing root growth, limiting water uptake capacity, and further increasing the risk of hydraulic failure (Nardini et al., 2016). At the end of the prolonged drought, the dry soil can even be a water competitor of plant tissues due to a significant water potential difference (Nadezhdina et al., 2010)

Nitrogen (N) is crucial for photosynthesis and forest productivity, particularly in N-limited boreal forests. Thus, N fertilization is widely used in the boreal region to increase forest growth (Hyvönen et al., 2008). At the leaf scale, additional N can enrich the foliage N content, enhancing the efficiency of photosynthetic enzymes, stimulating leaf photosynthesis (Luo et al., 2021). At the stand scale, however, uncertainty exists since N addition changes the C allocation (Li et al., 2020). For example, N fertilization shifts more C into the aboveground biomass of the tree than the belowground biomass. Conversely, drought reduces the accumulated aboveground biomass more than the belowground biomass (Poorter et al., 2012; Eziz et al., 2017). At the ecosystem scale, N fertilization has been reported to increase gross primary productivity (GPP) (Zhao et al., 2022), which is a proxy to indicate the total amount of C fixed from the atmosphere to the ecosystem (Liang et al., 2020). The increased GPP allocates more C to aboveground biomass, triggering higher evapotranspiration without improving soil water access, which aggravates the forest drought sensitivity (Peng et al., 2024) and can diminish the benefits of N fertilization during droughts (Luo et al., 2020). However, a previous study reported that N fertilization can also mitigate the effects of drought (Zhang et al., 2021). These controversial findings highlight that it remains unresolved whether N fertilization increases or mitigates the drought sensitivity.

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To accurately assess the long-term effects of N fertilization on forest responses to drought, GPP capacity at 2000 photosynthetic photon flux density (GPP2000) is a good proxy for forest productivity. By setting the light intensity at a high level, GPP2000 eliminates fluctuating light conditions, enabling the tracking of stress responses instead of light-induced responses, and thereby better reflects the inherent physiological state of the vegetation (Musavi et al., 2017; Chen et al., 2023; Gomarasca et al., 2024). In this study, we used eddy covariance (EC) tower-based measurements to track GPP2000 and droughts simultaneously over a 15-year controlled N fertilization experiment in paired boreal Scots pine forests in Northern Sweden. Using EC measurements of C fluxes and environmental data, we investigated whether long-term N fertilization alters the drought sensitivity of GPP2000. Specifically, we aimed to: (1) investigate whether long-term N fertilization altered key physiological parameters for forest photosynthesis (i.e. canopy conductance); (2) compare the response of GPP2000 to atmospheric drought and soil drought between the N-fertilized and control sites; (3) identify the key biotic and abiotic drivers responsible for GPP2000 differences between N-fertilized and control sites.

2Methods and Materials

2.1 Study sites

This study was conducted in a homogenous Scots pine (*Pinus sylvestris L.*) forest at Rosinedalsheden experimental forest, which includes a paired set of nitrogen fertilization experiment sites, 50 km from Umeå, northern Sweden (64°10′N, 19°45′E, 145m above sea level) (Figure 1). This forest comprises 90-year-old Scots pine (*Pinus sylvestris L.*) along the Vindeln River. Under the canopy, the dominant shrub species are bilberry (*Vaccinium myrtillus L.*), lingonberry (*Vaccinium vitis-idaea L.*), and the ground layer is characterized by mosses. The soil type is poorly fertilized fine sand with a 2–5 cm organic layer on the top (Hasselquist et al., 2012). During the past three decades, the mean annual temperature and precipitation are 2.4 °C and 637 mm, respectively (Laudon et al., 2021). See Lim et al., (2015) for more detailed information about the site description.

At the fertilized site, N was annually applied over an area of 13 ha at a rate of 100 kg N ha^{-1} per year from 2006 to 2011, and at a reduced rate of 50 kg N ha^{-1} per year due to concerns of N leaching since 2012 (Zhao et al., 2022). Granular Skon-Can fertilizer (Yara, Sweden) containing NH_4^+ (13.5%), NO_3^- (13.5%), Ca (5%), Mg (2.4%), and B (0.2%) were applied to the fertilized site in mid-June annually. The unfertilized site (hereafter, the reference site), located 2 km from the fertilized site, was designated as the reference site.

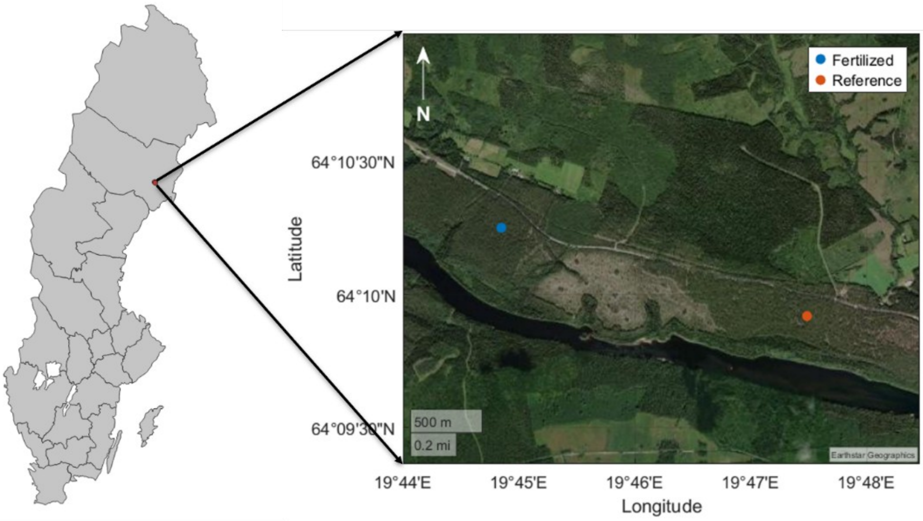

Figure 1: Location of the study area. Satellite imagery © Esri, Earthstar Geographics | Powered by Esri.

2.2 Eddy covariance measurements

In each paired site, CO_2 and H_2O fluxes have been measured above the canopy by an eddy covariance system since 2006. The eddy covariance system includes an ultrasonic anemometer Gill R3-100 (GILL Instruments Ltd, Lymington, UK) for detecting the three-dimensional wind components and sonic temperature, and an LI-7200 enclosed-path gas analyzer (LI-7200, LI-COR Environmental, Lincoln, USA) for measuring the mixing ratios of CO2 and H2O at the frequency of 20 HZ (Zhao et al., 2022). The raw data were processed and gap-filled by the same methods described by Zhao et al., (2022). To keep the primary flux source area constant, the measurement height was gradually adjusted to match the growing canopy height, starting in 2015. As a result, data from 2007 to 2014 were not included in this study.

2.3 GPP capacity calculation

The instantaneous rate of carbon flux between the atmosphere and the terrestrial ecosystem represents the balance between GPP and ecosystem respiration (Gilmanov et al., 2003). Thus, GPP can be defined as the sum of net ecosystem productivity and ecosystem respiration. The light response curve is widely used to estimate GPP. Here, the daily GPP2000 was estimated by a non-rectangular hyperbolic light response curve function using half-hourly GPP and incoming photosynthetic photon flux density (PPFD) (Gilmanov et al., 2003):

$$GPP = \frac{\alpha \cdot PPFD + P_{max} - \sqrt{(\alpha \cdot PPFD + P_{max})^2 - 4\alpha \cdot PPFD \cdot \theta \cdot P_{max}}}{2\theta} + R_d \qquad (1)$$

where α (mol CO_2 mol^{-1} per photon) is the initial slope of the ecosystem's light response curve, which indicates how efficiently the ecosystem uses the light for photosynthesis at low light levels. The greater α means higher efficiency at using low light. PPFD (µmol m⁻² s⁻¹) is the incoming photosynthetic photon flux density. P_{max} (µmol CO_2 m⁻² s⁻¹) is the maximum photosynthetic capacity at light saturation, indicating the maximum potential of ecosystem photosynthesis under ideal light conditions. θ is the convexity of the curve without unit, which indicates the sharpness of the curve between low-light levels and light-saturated levels. R_d (µmol CO_2 m⁻² s⁻¹) is daytime ecosystem respiration.

To get the parameters for Eq. (1), we only considered the daytime data, with PPFD above 4 µmol m⁻² s⁻¹. The relatively low PPFD threshold was applied to determine daytime because of high-latitude summertime conditions, where the midnight sun phenomenon results in limited duration of low light levels. Our method ensured sufficient data coverage for accurate parameter estimation in Eq. (1), particularly for α. We then applied a 7-day moving window with a 1-day step across the whole measurement period to slice the data. Each slice of data was used to fit Eq. (1). In high-latitude areas, summer is short and cloudy. Besides, in natural fields, the ideal light situation is hardly reachable. So, P_{max} may not represent the real maximum photosynthesis capacity (Reichstein et al., 2012). Thus, we further recomputed GPP with a fixed PPFD of µmol m⁻² s⁻¹ by Eq. (1), which represents GPP2000. The parameters (α, θ, and P_{max}) and GPP2000 were assigned on the middle day of the 7-day moving window. We only kept those parameters with R^2 between measured and estimated GPP greater than 0.6. Finally, the daily GPP2000 time series was produced.

2.4 Drought detection

To compare the forest response to dryness between treatments, the same baseline should be addressed. Therefore, in this study, we applied the same historical precipitation records from a local weather station for the last 30 years (1991-2022) as the reference precipitation to detect the dry days based on precipitation anomalies at the two sites. Precipitation anomaly for each site was calculated using the following formula:

$$P_{anomaly,i} = \frac{P_{i,j} - \mu_i}{\sigma_i} \tag{2}$$

where $P_{i,j}$ means precipitation on the day i of year j; μ_i is the mean value of the precipitation for the day i across all years in the historical dataset; σ_i is the standard deviation of precipitation for the day i across all years in the historical dataset.

The dry days were defined as $P_{anomaly} < 0$. We further divided dry days into two severity categories based on the $P_{anomaly}$ to check the forest response to dryness under different drought severities. If $P_{anomaly} < 0$ and $P_{anomaly} >= -0.5$, the day was defined as minor dry; if $P_{anomaly} < -0.5$, the day was defined as severely dry (Li et al., 2021). After identifying dry days on the same baseline, two drought proxies were further used to quantify the dryness. We considered both atmospheric and soil water deficits since drought is usually accompanied by complex atmospheric and soil water stress and can hardly be separated from each other. Vapor pressure deficit (VPD) was used to measure the atmospheric water stress. For soil water deficit, we used the soil water availability index (WAI) rather than other water stress proxies, such as soil water content, the Standardized Precipitation Evapotranspiration Index (SPEI), or climatic water balance, which were widely used as drought proxies. Reasons were listed: First, soil water measurements at the eddy covariance site are usually taken at only a few points, which hardly represent water availability at the ecosystem scale (Luo et al., 2020). Moreover, soil water content was not available at the beginning of the experiment. Second, comparisons of SPEI across sites have been reported to be problematic, as SPEI is a site-specific standardized drought proxy (Piedallu et al., 2013; Slette et al., 2019; Zang et al., 2019). Third, the climate water balance considers only precipitation and potential evapotranspiration, ignoring recharge processes, which could introduce uncertainty in detecting drought events. Instead, WAI is based on a dynamic bucket model, which has been reported to better represent water stress at the ecosystem scale than VPD, precipitation, or other remotely sensed indices, since it integrates water recharge and loss from previous time steps (Tramontana et al., 2016). Daily WAI can be calculated as follows:

$$WAI(t) = WAI(t-1) + R(t) - E(t) \tag{3}$$

where $WAI(t-1)$ is soil water availability at the time of $t-1$; $R(t)$ means water recharge, which is calculated as the minimum value between precipitation (P) and water deficit:

$$R(t) = min[P(t), 100 - WAI(t-1)] \tag{4}$$

where $P(t)$ is precipitation at the time of t. $100 - WAI(t-1)$ means soil water deficit at the time of $t-1$. We also assumed that the initial water storage (first day of the year) was 100 mm

In Equation (3), $E(t)$ means evapotranspiration, which is calculated as a minimum value between potential evapotranspiration (PET) and water supply (SET):

$$E(t) = min[PET(t), SET(t)] \tag{5}$$

The PET is calculated via the *Bigleaf* package (Knauer et al., 2018). The SET is calculated as a fraction of WAI (Luo et al., 2020):

$$SET(t) = k \cdot WAI(t-1) \tag{6}$$

where k is a constant, we set it as 0.05.

2.5 Drought sensitivity

Simple linear regression was used to analyze the relations between GPP2000, VPD, WAI, and the interaction between VPD and WAI:

$$\mathrm{GPP2000} = a + b \cdot VPD + c \cdot WAI + d \cdot VPD{:}WAI + \varepsilon \tag{7}$$

where GPP2000 is the standardized light-saturated photosynthesis GPP; VPD is the standardized vapor pressure deficit; WAI is the soil water availability index; $VPD{:}WAI$ means interaction between VPD and WAI; a, b, c, d are coefficients; ε is the error term. The standardized method used for GPP2000 and VPD was:

$$z = \frac{x - \mu}{\sigma} \tag{8}$$

where x means GPP2000 or VPD across sites. μ is the mean value of GPP2000 or VPD across sites. σ is the standard deviation of GPP2000 or VPD across sites.

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In particular, the obvious non-linear relationship between GPP2000 and WAI at both sites followed the light response curve. We designed a water response curve to show the sensitivity of GPP2000, along with WAI variations, which is below:

$$\text{GPP2000} = \beta \cdot \left(1 - e^{\frac{-\gamma \cdot WAI}{\beta}}\right) \tag{9}$$

where β is the maximum GPP2000, indication the maximum GPP2000 can be reached in an ideal soil water condition; γ is the slope between WAI and GPP2000 when GPP2000 decreasing sharply along the decreased WAI (shown as the black line in Figure S1), the greater γ means the higher sensitivity of GPP2000 to the low WAI.

2.6 Canopy conductance calculation and its sensitivity to vapor pressure deficit

The half-hourly canopy conductance (Gs) was calculated by the Penman-Monteith equation (Monteith, 1965):

$$\frac{1}{Gs} = \frac{1}{G_a}\left[\frac{\rho_a \cdot G_a \cdot D + \Delta(R_n - G)}{\gamma \cdot \lambda ET} - \frac{\Delta}{\gamma} - 1\right] \tag{10}$$

where ρ_a is air density. D is the vapor pressure deficit. Δ is the slope between saturation vapor pressure and air temperature. R_n is net radiation. G is soil heat flux. G_a is the aerodynamic conductance calculated by Thom's function (Thom, 1972):

$$\frac{1}{G_a} = \frac{u}{u_*^2} + 135u_*^{-0.67} \tag{11}$$

where u is wind speed. $u_*$is the friction velocity.

To investigate the instinctive sensitivity of Gs to VPD at both sites, following the method reported by (Xu et al., 2023), the upper envelopes of Gs and VPD were applied during the summer at both the fertilized and reference sites. First, all half-hourly Gs were grouped into VPD intervals starting at 0.6 kPa with a 0.2 kPa step. Second, for each VPD class, the mean and standard deviation of Gs was calculated. Third, the upper envelopes of Gs was determined by the sum of the mean and the standard deviation of each VPD class. Finally, the sensitivity of Gs to VPD based on an empirical function (Oren et al., 1999) to the upper envelopes were performed:

$$Gs = -m \cdot ln(VPD) + G_{cref} \tag{12}$$

where m is a parameter for quantifying the sensitivity of Gs to VPD, the greater m means more sensitive to Gs to VPD. G_{cref} means reference canopy conductance at 1 kPa VPD. To compare the difference of m between fertilized and reference sites, a 7-day moving window with a 1-day running step method was applied to Eq. (12) over the summer at both sites.

2.7 Random forest model

The random forest (RF) model (Breiman, 2001) is an ensemble tree-based machine learning method widely used in ecology to assess variable importance in regression or classification (Brieuc et al., 2018). For the regression model, RF first randomly resamples the input data for each regression tree (as specified by the *ntree* parameter). Then, RF randomly selects a subset of predictors to test at each node, searching for the best combinations of features and split thresholds that minimize error in the

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resulting child nodes (as indicated by the parameter *mtry*). To avoid overfitting, the nodesize parameter controls the depth of the RF model. Finally, an RF model with default settings was applied in this study (*ntree* = 500, *mtry* = $\sqrt{\text{numbers of input variables}}$, *nodesize* = 5). To evaluate the importance of the difference in variables for modulating the variation of $\mathrm{GPP2000}$ between sites ($\Delta\mathrm{GPP2000}$), four factors were considered as input variables: differences in (a) air temperature (Tair), (b) VPD, (c) Gs, and (d) WAI between the fertilized and reference sites. For input variables that were not significant in the T-test for differences across sites ($p > 0.05$), we used the variable's mean across sites instead (Fig. S2).

2.8 Statistical analysis

All statistical analyses were performed in R (R Core Team, 2024) with significant levels of 0.05. The Wilcoxon Rank-Sum and Signed-Rank Tests were used to compare biotic variables (WAI, VPD, and Tair) and the abiotic variable (Gs) between the fertilized and reference sites. These comparisons were used in the *'compare_means'* function in the '*ggpubr'* package (Kassambara, 2023). Linear regression for drought sensitivity analysis was applied using the *'lm'* function. All non-linear regressions (e.g., Eq. 1, 9, 12) were fitted using the *'nls'* function in the *'minpack.lm'* package (Elzhov et al., 2023). The importance of variables for modulating $\Delta\mathrm{GPP2000}$ was determined using the RF model with the default setting in the *'ranger'* package (Wright and Ziegler, 2017). The significance of that variable was also assessed using 100 permutations of the RF model by the *'importance_pvalues'* function in the *'ranger'* package. The positive and negative effects of those variables were assessed by partial dependence plots using the *'pdp'* package (Greenwell, 2017).

3. Results

3.1 Environmental variables and GPP capacity during summer at the Fertilized and Reference sites

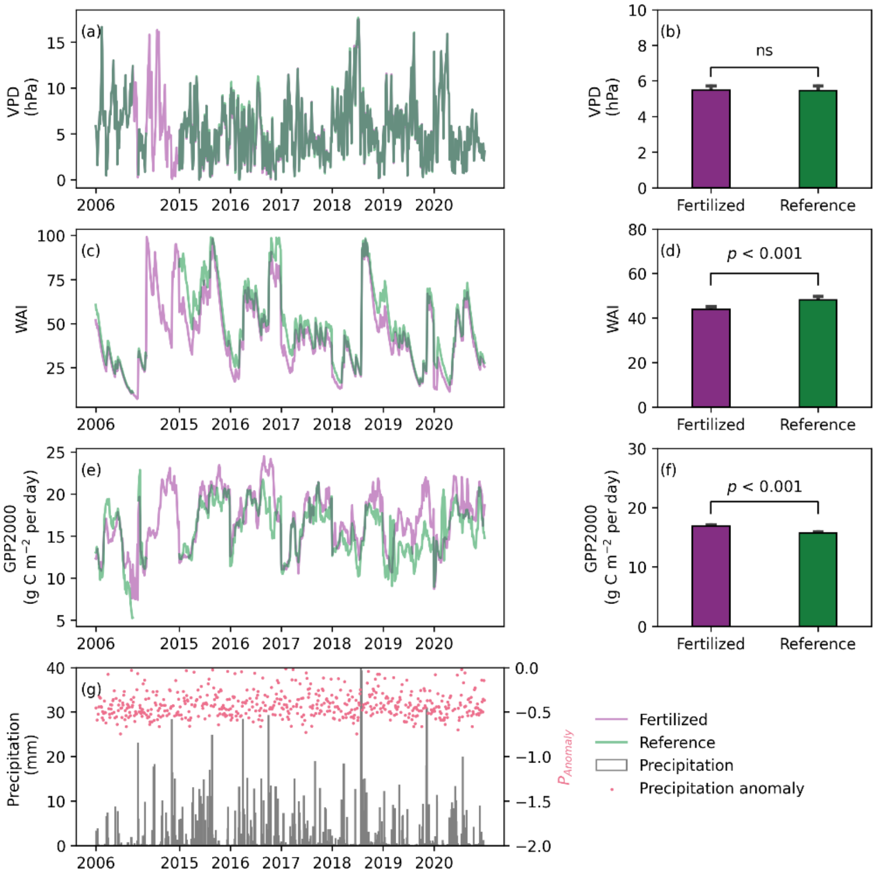

Figure 2: Variations and comparisons of environmental variables and GPP2000 on the fertilized and reference sites. VPD means vapor pressure deficit. WAI means soil water availability index. GPP2000 means GPP capacity at PPFD of 2000 µmol m^{-2} s^{-1}. $P_{Anomaly}$ means the daily precipitation anomaly relative to the historical mean values. Here, precipitation anomalies are only shown when values are negative, indicating dry days.

VPD in both sites also showed a similar pattern and no significant difference between sites ($p > 0.05$) (Fig. 2a, Fig. 2b). Generally, WAI in the Reference site was significantly higher than the Fertilized site ($p < 0.001$) (Fig. 2d), and with a similar pattern over the years (Fig. 2C). Moreover, the long-term daily variation of GPP2000 showed that GPP2000 at the Fertilized site was higher than GPP2000 in the Reference site, especially in the summer peak (Fig. 2e). And the mean value of GPP2000 at both sites also indicated a significantly high GPP2000 at the fertilized site compared to the reference site ($P < 0.001$) (Fig. 2f). During the study period, the mean precipitation was 2.1mm per day. The maximum precipitation was recorded on July 28th, 2018, with a value of 40 mm per day. The minimum $P_{Anomaly}$ was -0.74, indicating the maximum rainwater deficit over the years, was detected on July 15, 2006 (Fig. 2g).

3.2 Divergent drought sensitivity of GPP2000 between the Fertilized and Reference sites

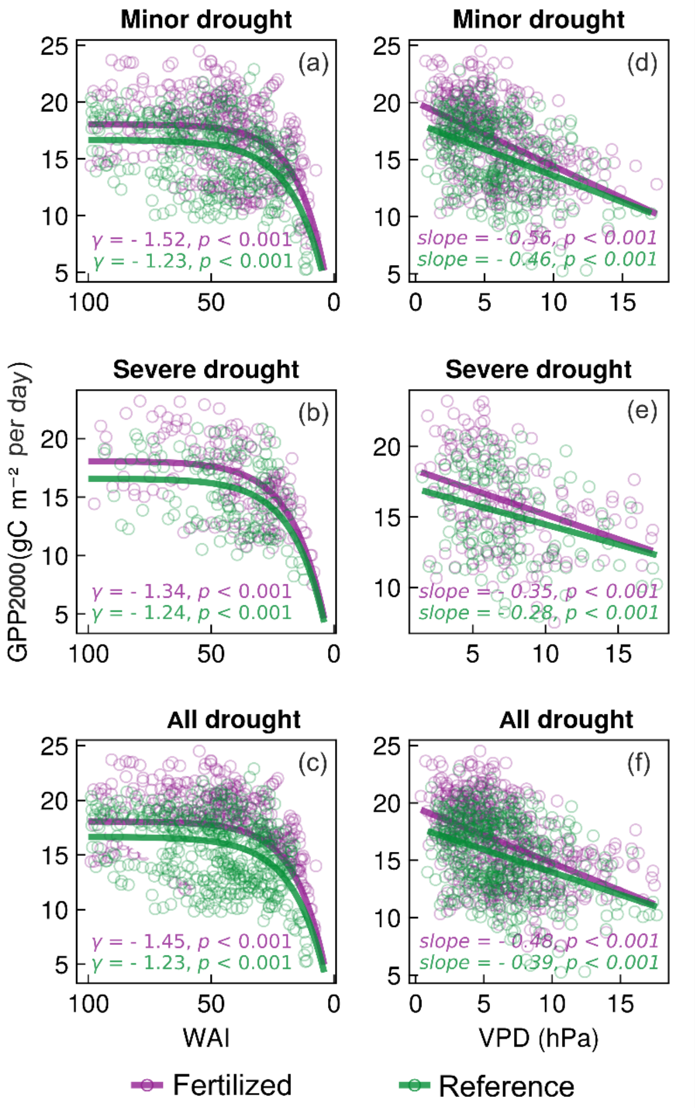

Figure 3: GPP capacity response to different drought stress at the fertilized and reference sites. Minor drought means $P_{anomaly} \in$ [-0.5, 0); Severe drought means $P_{anomaly} <$ -0.5. All drought means combining all data from days with $P_{anomaly} < 0$.

In all drought scenarios, GPP2000 at the Fertilized site clearly shows greater sensitivity to either soil (WAI) or atmospheric (VPD) water stress than at the Reference site, with a similar declining pattern. In addition, the fertilized site showed slightly higher productivity than the Reference site. The sensitivities of GPP2000 to WAI, which was presented as γ, were -1.52, -1.34, and -1.45 g C m^{-2} per day at minor (Fig. 3a), severe (Fig. 3b), and overall drought (Fig. 3c) scenarios in the Fertilized site, respectively, whereas with the values of -1.23, -1.24, and -1.23 g C m⁻² per day at the Reference site, respectively. For the sensitivity of GPP2000 to VPD, GPP2000 in the Fertilized site showed slightly more sensitivity to VPD than the Reference site, with the slope of -0.56, -0.35, and -0.48 g C m⁻² hPa⁻¹ per day at minor (Fig. 3d), severe (Fig. 3e), and overall drought (Figure 3f) scenarios in the Fertilized site, respectively. And with the values of -0.46, -0.28, and -0.39 g C m⁻² hPa⁻¹ per day at the Reference site, respectively.

3.3 Differences in physiological parameters between the Fertilized and the Reference site

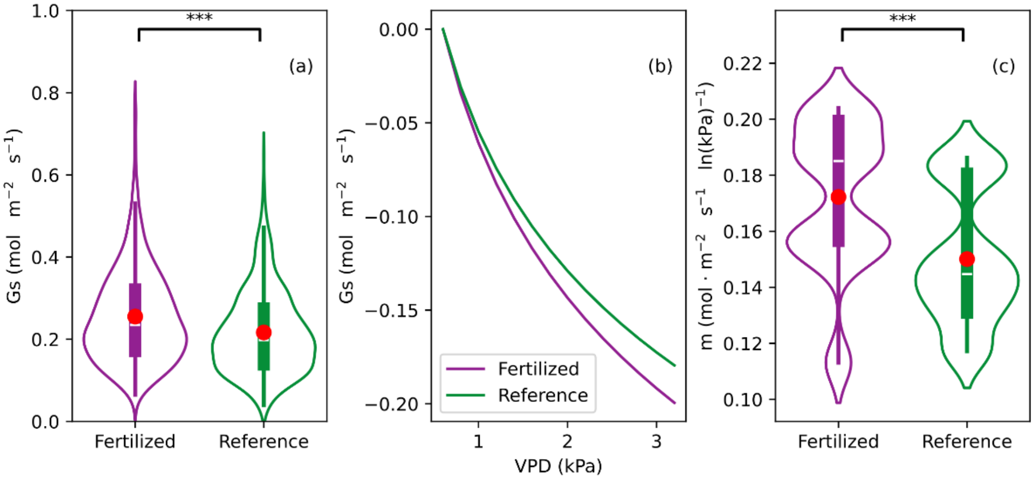

Figure 4: Comparisons of physiological variables between the Fertilized and Reference sites during dry days in summer ($P_{anomaly} < 0$). (a) Comparisons of canopy conductance (Gs). (b) Comparisons of the relationship between Gs and VPD on the two sites. (c) Comparisons of Gs sensitivity to VPD (m) using 7-day moving windows methods between the Fertilized and Reference sites during the whole summertime. The red dots represent the mean values in each group. * means p < 0.001.**

The Gs in the Fertilized site was found to be significantly higher than those in the Reference site ($p < 0.001$), with a mean value of Gs 0.26 mol m⁻² s⁻¹ and 0.22 mol m⁻² s⁻¹ at the Fertilized and Reference sites, respectively (Fig. 4a). The VPD response curve of Gs also indicated that Gs at the Fertilized site was more sensitive to rising VPD than those at the Reference site, with an m of -0.12 at the Fertilized site compared with -0.11 at the Reference site during dry days (Fig. 4b). Similarly, cross the whole summer period (Tab. s1). With 7-day moving windows, the overall Gs sensitivity (m) also showed that Gs at the Reference site was significantly more sensitive than at the Reference site (Fig. 4c).

3.4 Biotic and abiotic controls on the difference of GPP capacity between the Fertilized and Reference sites

The random forest model shows that the ΔWAI is the most crucial factor, contributing around 34% to regulating the difference in GPP2000 between the two sites. Other factors, for example, VPD and ΔGs played key roles in regulating the

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difference in GPP2000, contributing to 29% and 22%, respectively. However, Tair had no significant impact on the difference in GPP2000 between sites (ns).

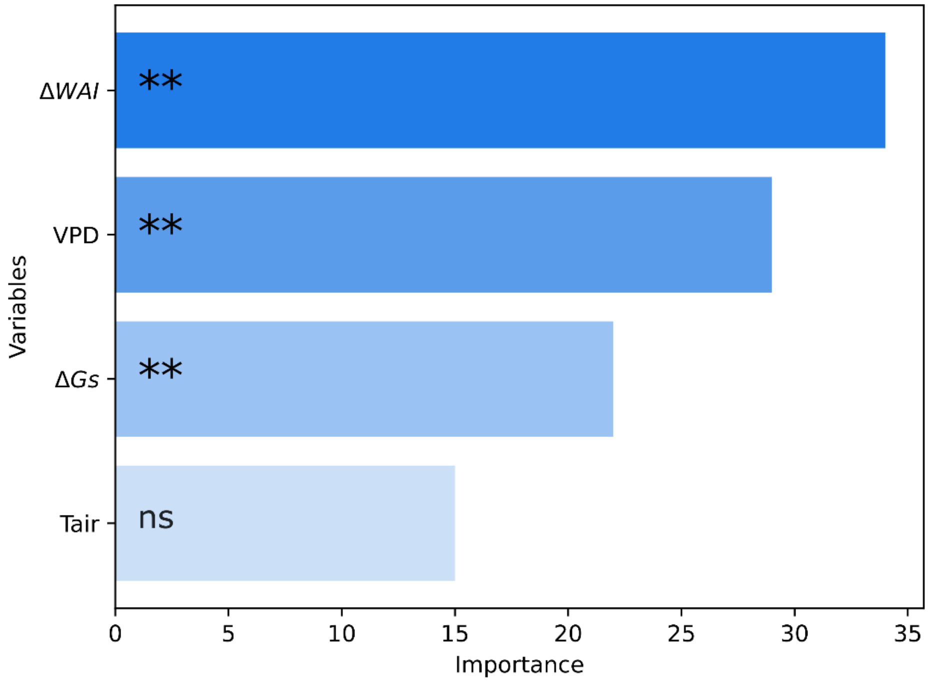

Figure 5: Variable importance for modulating the N fertilization-induced GPP capacity difference at Rosinedalsheden experimental forest using the random forest method. ** means $p < 0.01$. ns means $p > 0.05$. The mean value is used if the variables between the Fertilized and Reference sites have no significant difference. Otherwise, the differences in variables between sites were applied. Here, VPD and Tair were applied using mean values across sites. WAI, and Gs were applied with the differences between variables across sites. ΔWAI means the difference in soil water availability across sites. VPD is vapor pressure deficit. ΔGs is the difference in canopy conductance across sites. Tair is the air temperature.

4. Discussion

4.1 Nitrogen fertilization increases canopy conductance and sensitivity to drought

Results from the long-term N fertilization experiment showed that the photosynthesis capacity was significantly increased (Fig. 2). Meanwhile, Figure 4 clearly shows the Gs was also significantly increased, whereas GPP2000 and Gs had no significant difference at the beginning of the N fertilization experiment (Fig. s4). Both VPD and WAI during the drought period have significant negative effects on GPP capacity in fertilization and reference sites, but without interactions (Tab. s2). The overall drought sensitivity in the fertilization site was higher than in the reference site. This finding is consistent with other studies that used isotope and tree growth analyses and observed higher drought sensitivity under N fertilization

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(Betson et al., 2007; Lim et al., 2015). Many studies have reported that Gs behavior is the key factor in controlling photosynthetic processes at the canopy level (Parry et al., 2002; Van Der Molen et al., 2011). Here, during drought, the reduction in Gs at both sites decreases GPP capacity, further supporting the conclusions of Zhang et al. (2020) and aligning with a light-use efficiency-based model study in the same area (Tian et al., 2021). These studies suggested that reduced Gs directly reduced GPP capacity during drought. In addition, the significantly higher canopy conductance at fertilization sites compared to the control area can be attributed to increased leaf area. During the experiment, the leaf area index in the fertilization site was 22% and 31% higher than the Reference site in 2015 and 2018, respectively (Lim et al., 2015; Tian et al., 2021). Usually, N fertilization is reported to improve foliage N content, increase individual leaf area, and produce more leaves in a single canopy, and it also changes tree canopy structure vertically and horizontally, leading to increased light interception and increased crown projection. This has also been shown in different forest ecosystems (Zhu et al., 2020). Furthermore, it is essential to acknowledge that, unlike at the leaf scale, the relationship between Gs and leaf area is defined as multiplicative at the canopy level, as illustrated by the Jarvis-Stewart Equation (Jarvis et al., 1997; Stewart, 1988). Consequently, a larger leaf area typically results in greater Gs.

Our study further compared the sensitivity of Gs to VPD between the Fertilization and Reference sites using the upper envelope method, accounting for the direct impact of VPD on Gs. This method revealed a clearer Gs response to VPD, excluding impacts from other environmental factors (Xu et al., 2023). Our results clearly showed that although Gs at both sites decreased during drought, Gs at the fertilization site were more sensitive to VPD than at the reference site, indicating that long-term N fertilization altered Gs sensitivity to VPD. This finding contrasts with an earlier study conducted in a loblolly pine plantation (Domec et al., 2009), suggesting the relative sensitivity of Gs was not influenced by N fertilization. The difference might be partly explained by the amount of N applied per unit area (g N m^{-2}). In their study, the amount of N applied was 2 times greater than in this study (11.2 VS 5.0 g N m^{-2}). The higher applied N content changed the sensitivity of canopy Gs to VPD. Previous studies also reported a similar finding that higher nitrogen availability generally leads to increased maximum stomatal conductance, which correlates with greater sensitivity to VPD, but as N continues to increase, the sensitivity of Gs to VPD can be less pronounced (Liao et al., 2022; Flo et al., 2022). In this study, the significant difference in Gs sensitivity induced by N fertilization may also imply different water use strategies between treatments. Results of the sensitivity comparisons of Gs to VPD between sites suggested that the fertilization site was likely to exhibit more active water-conservation behavior during drought, as indicated by a more rapid decrease in Gs with increasing VPD. This behavior closely resembles isohydric regulation; the rapid response of Gs has been reported to reduce hydraulic efficiency and photosynthesis, but can help avoid xylem conduits from embolization (McDowell et al., 2008; Blackman et al., 2009; Berkelhammer et al., 2020). However, a study of 70 woody species has revealed that plant water regulation is a continuum rather than a dichotomy between isohydric and anisohydric, highlighting the complexity of this process. Thus, more studies along water potential gradients are suggested to better show the diverse water use strategies across species and their responses to environmental changes.

Another important reason for the differing Gs sensitivity may be the varying WAI levels at the two sites. During the drought, a significant difference in ecosystem WAI between the two sites was observed, suggesting lower plant water availability at the fertilization site. This can be due to feedback from higher mean Gs levels at the fertilization site during the drought, leading to greater water loss from the ecosystem via the canopy as leaf area increases. Different C allocation strategies may provide another plausible explanation for the significantly low WAI at the fertilization site. N fertilization can directly change the C allocation, in which more C is allocated aboveground than belowground. Moreover, the fine-root system at the Fertilization site was reported to have lower production and a faster turnover than at the Reference site, leading to a thick organic layer and limiting soil water-holding capacity (Leppälammi-Kujansuu et al., 2014; Tian et al., 2021). In turn, the weak water-holding capacity further triggers a rapid Gs response to VPD to maintain the tree's hydraulic safety (Sperry et al., 2016).

4.2 Biotic and abiotic factors regulate the GPP2000 between sites

The results of the RF model clearly showed that the N-induced difference in GPP capacity between sites during drought was primarily driven by drought proxies (e.g., WAI and VPD). Moreover, the N-induced improvement of GPP capacity can be offset by the increasing drought stress (Fig. s2). This finding is consistent with a previous study, which found that N fertilization altered plant osmotic adjustment and offset the improvement in photosynthesis achieved by additional N (Graciano et al., 2005). WAI, which integrates water loss and soil water recharge, indicates how much water remains available for plant use. WAI further emphasizes soil water rather than VPD (Fig. 5) as the dominant driver of site-to-site N-induced differences in GPP capacity during dry days. Especially when the fertilization site has a similar WAI level to the reference site, the gap in GPP capacity between the two sites reaches the maximum (Fig. s2). The preeminent role of WAI in C fluxes was also reported in the dryland ecosystem of the USA, particularly at daily or sub-daily timescales (Kannenberg et al., 2024). The reasons can be that, even with high VPD, the root system can continue to absorb water from different soil layers, and that photosynthesis can remain active even as canopy conductance decreases. However, when soil water falls below a safe threshold, water transport can be cut off and stomata further close, even under better N conditions; if the soil water supply is not timely, the tree dies (Sperry et al., 2002). Additionally, N fertilization increased the GPP capacity and the net C accumulation of the forest (Zhao et al., 2022), which further contributes the biomass accumulation; the larger biomass and extensive leaf areas can also intercept more precipitation and transport more water into the air, consequently weakening soil water storage at the Fertilization site (Fig. 1d; Fig. s3) (Martínez-García et al., 2024). Conversely, VPD variability is homogeneous across sites, especially those in close proximity (Fig. 2b). This observation underscores the significant role of WAI and may suggest that VPD plays a comparatively lesser role in regulating GPP capacity across sites. Other studies also reported similar results that the dominant drivers of soil water are controlling Gs and further impacting C and water fluxes during drought (Niu et al., 2023; Li et al., 2024), highlighting the mediating role of Gs in regulating GPP capacity. However, a recent global study reported that the negative sensitivity of forest productivity to increasing VPD is observed across the full soil-water range, highlighting the dominant controlling role of VPD on C fluxes and canopy conductance over soil water (Fu et al., 2022). These controversial studies suggested that more studies should be conducted regarding the co-effects of VPD and soil water conditions on forest productivity. Our results also showed that Tair did not play a significant role in the GPP2000 difference between sites, further confirming the soil water as a primary limiting factor. This result was in line with the study from Dannenberg et al., (2022), who reported that during the drought, the low soil water contributed about 50% to the regional reduction of primary production, followed by the VPD, whereas the Tair contributed only a minor amount. The reason may be that Tair is also an essential factor in photosynthesis. Tair is usually correlated with VPD, increasing evapotranspiration and, indirectly, soil water and forest productivity, except during extreme heat waves. Additionally, the current air temperature is generally below the optimal temperature for photosynthesis, especially in boreal regions (Park et al., 2019). Tair is not necessarily as important as drought proxies during the drought.

4.3 Implications and limitations

N fertilization is a common management practice in the boreal region to increase forest productivity. However, our results suggest that the benefits of nitrogen fertilization may be offset by drought. Fertilization significantly increased photosynthesis but also enhanced the sensitivity of GPP capacity to both atmospheric and soil drought. This indicates that the positive effects of nitrogen fertilization on forest productivity may be increasingly suppressed in future climate conditions. Moreover, our findings highlight that fertilization strategies may need to be adjusted according to site-specific hydrological conditions to ensure sustainable forest productivity. In addition, climate warming may increase soil nitrogen availability through enhanced nitrogen mineralization. Warmer soil temperatures can accelerate microbial decomposition and nutrient cycling, thereby increasing nitrogen availability even without external fertilization (Melillo et al., 2002). Such climate-driven increases in nitrogen availability may trigger ecosystem responses akin to fertilization, potentially boosting photosynthetic capacity while also increasing drought sensitivity.

Despite these insights, several limitations should be acknowledged. Firstly, this study was conducted at a single experimental site dominated by Scots pine, which may limit the generality of the findings across other boreal forest types with different species compositions, soil conditions, and climatic regimes. What's more, soil water availability was represented by WAI, derived from a bucket model rather than from direct measurements at the ecosystem scale. Although WAI integrates both water recharge and loss processes and has been shown to perform well at ecosystem scales, we believe that uncertainties in modeled soil water availability may still influence the results. Last, key plant physiological processes, such as plant hydraulic traits, were not directly included in this study. These processes play important roles in determining drought responses and could help explain the mechanisms underlying the increased drought sensitivity under nitrogen fertilization (Zhang et al., 2020). Future research should explore diverse forest ecosystems and fertilization practices while measuring plant hydraulic traits, thereby improving our understanding of how nutrient availability and water limitations affect forest carbon uptake in a changing climate.

5. Conclusions

This study highlights that long-term N fertilization increased the sensitivity of forest GPP and Gs to drought. N fertilization increased both the atmospheric and soil drought sensitivity of the Scots pine forest. The canopy conductance at the fertilization site was more sensitive to VPD than the reference site. The compound effect of WAI and VPD was not found. Moreover, drought might offset the positive effect of N fertilization on forest productivity. Furthermore, the random forest model showed that the N-induced difference in GPP2000 between the Fertilized and Reference sites was mainly driven by drought proxies (WAI and VPD), followed by Gs rather than Tair. Overall, these results advance our understanding of the mechanisms by which forests respond to drought under long-term N fertilization.

Code and data availability

The historical precipitation data can be found at https://data.fieldsites.se/portal/; The dataset and code supporting the conclusions of this article can be found at DOI: 10.5281/zenodo.19520619.

Supplement link

The link to the supplement will be included by Copernicus, if applicable.

Author contributions

Liang Chen: conceptualization (lead), formal analysis (lead), methodology (lead), visualization (lead), writing – original draft (lead). **Matthias Peichl:** resources (lead), conceptualization (equal), writing – review and editing (equal). **Yunpeng Luo:** formal analysis (equal), writing – review and editing (equal). **Peng Zhao:** data curarion (lead), writing – review and editing (equal). **Alisa Krasnova:** conceptualization (equal), writing – review and editing (equal). **Frank Berninger**: conceptualization (equal), writing – review and editing (equal), supervision (lead).

Competing interests

The authors declare no competing interests.

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