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Annual climate variation modifies nitrogen induced carbon accumulation of *Pinus sylvestris* forests

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Running title: INTERACTION BETWEEN NITROGEN AND CLIMATE

Abstract

We report results from long-term simulated external nitrogen (N) input experiments in three northern *Pinus sylvestris* forests, two of moderately-high and one of moderately-low productivity, assessing effects on annual net primary production (NPP) of woody mass and its inter-annual variation in response to variability in weather conditions. A sigmoidal response of wood NPP to external N inputs was observed in the both higher and lower productivity stands, reaching a maximum of ~65% enhancement regardless of the native site productivity, saturating at an external N input of 4 – 5 g N m^{-2} yr^{-1}. The rate of increase in wood NPP and the N response efficiency (RE$_N$, increase in wood NPP per external N input) were maximized at an external N input of ~3 g N m^{-2} yr^{-1}, regardless of site productivity. The maximum RE$_N$ was greater in the higher productivity than the lower productivity stand (~20 *versus* ~14 g C g^{-1} N). The N induced enhancement of wood NPP and its RE$_N$ were, however, markedly contingent on climatic variables. In both of the higher and lower productivity stands, wood NPP increased with growing season precipitation (*P*), but only up to ~400 mm. The sensitivity of the response to *P* increased with increasing external N inputs. Increasing growing season temperature (*T*) somewhat increased the N-induced drought effect, whereas decreasing *T* reduced the drought effect. These responses of wood NPP infused a large temporal variation to RE$_N$, making the use of a fixed value unadvisable. Based on these results, we suggest that regional climate conditions and future climate scenarios should be considered when modeling carbon sequestration in response to N deposition in boreal *P. sylvestris*, and possibly other forests.

Key words: Carbon sequestration; Nitrogen deposition; Nitrogen Use Efficiency Precipitation; Temperature; Climate change; Heureka model; Nitrogen gradient; Scots pine;

INTRODUCTION

Increased nitrogen (N) deposition as a result of N fertilizer production and fossil fuel combustion has been credited with enhancing net primary production (NPP) of woody mass in N limited ecosystem (Townsend et al. 1996, Binkley and Högberg 1997, Pregitzer et al. 2008, de Vries et al. 2009, Gundale et al. 2014). Despite increasing understanding of the impact of N inputs on wood NPP (Tamm et al. 1999, Högberg et al. 2006, de Vries et al. 2014, Binkley and Högberg 2016), it is still unclear how N-induced responses of wood NPP interact with a changing climate.

Recently, a synthesis of data from N addition experiments suggested an increasing response of NPP from low to intermediate rates of external N input (the sum of N fertilization and background deposition) but a declining response of NPP at higher rates (de Vries et al. 2014). This declining response of NPP possibly reflects a decline of forest health and productivity from a nutritional imbalance (Oren et al. 1988, Oren and Schulze 1989). The different responses of NPP over the range of N input rates were also reflected in a wide range of the N response efficiency (RE$_N$, increase in wood NPP per external N input), serving as an index of the quantitative response of NPP to N deposition (Townsend et al. 1996, de Vries et al. 2009). In boreal forests, reported values of RE_N range from 14 to 56 g C g^{-1} N (Hyvönen et al. 2008, Gundale et al. 2014; but see Magnani et al. 2007) and in temperate forests from 15 to 60 g C g^{-1} N (Pregitzer et al. 2008, Thomas et al. 2010). These wide ranges were explained by not only a changing responsiveness of NPP over the range of external N inputs, including a negligible response at the low end of inputs (Gundale et al. 2011, de Vries et al. 2014), but also a species-specific response to external N inputs in context of succession, mortality, and a symbiotic relation with mycorrhizal fungi (Lilleskov et al. 2002, Magill et al. 2004, Thomas et al. 2010).

Although the empirically obtained shape of NPP response to external N inputs, and the position of sensitivity ranges, provide the best available summary of the response to N inputs, and account for the interactive effects of external N inputs and age on NPP (de Vries et al. 2014), it does not account for possible interactions with climate factors. For example, in boreal and temperate forests, natural and simulated variations in water availability alter the effect of N inputs on forest growth (Linder et al. 1987, Lim et al. 2015, Dziedek et al. 2016). In addition, a modeling experiment predicted (Thornton et al. 2007), and forest inventory data demonstrated (Solberg et al. 2009) that the sensitivity of NPP to N deposition depends on temperature and precipitation. Those findings are consistent with results from stable isotope analyses, indirectly suggesting that water stress of boreal *Pinus sylvestris* trees increases with N fertilization (Betson et al. 2007).

Both experimental and observational studies of N deposition suffer from inherent limitations (Oren et al. 1989). Manipulation experiments suffer from attempting to reproduce, over a short time period, an effect hypothesized to reflect a persistent low-dose burden. In observational studies, assembled data representing large geographical areas and, often, periods sufficiently long to capture the history of N deposition, may potentially lead to generalizable growth response to N deposition. However, other temporally and spatially varying and co-varying factors are likely to obscure or modify the response to N deposition when observational data are synthesized over large regions and long periods (Solberg et al. 2009, Etzold et al. 2014). Attempting to overcome the principle limitations of both experimental manipulations and observational studies, a few studies were designed to mimic N deposition, adding N at low rates (Tamm et al. 1999, Magill et al. 2004, Hyvönen et al. 2008, Pregitzer et al. 2008, Gundale et al. 2014). Such studies provide the most direct approach to investigating the effect of interaction between additions of N and variation in weather on forest growth and carbon (C) accumulation in plant biomass. These interactions can inform modelers what to expect as climate changes over landscapes receiving a range of external N inputs from deposition and fertilization. However, the scope of inference of each study is limited. A more generalized outcome can be generated through a synthesis that does not allow any site undue influence on the outcome and accounts for variables that can potentially affect the outcome (Norby et al. 2005, Stape et al. 2010; e.g., stand age and density, inherent site productivity, and prevailing climate).

Only few experiments have been systematically maintained (in terms of sustained inputs and measured response) over a long enough period to provide data for quantifying the interactive effects of N inputs and inter-annual variation in weather on ecosystem carbon fluxes (but see Mäkipää et al. 1999, Öquist et al. 2014). We combined results from three such studies on boreal *P. sylvestris* forests to examine the response of wood NPP to a wide range of external N input rates (spatial variability, 0.2 to 9.8 g N m^{-2} yr^{-1}), and how the sensitivity of the response is further affected by temperature and precipitation during the growing season (temporal variability). The three experiments lasted seven to eight years, with annual N addition of two to four levels (Nilsen and Abrahamsen 2003, From 2014, Lim et al. 2015). The multiple levels of N additions and large inter-annual variations in growing season weather conditions allowed us to quantify the response of productivity to a wide range of N input rates as the weather varies. Furthermore, the very low background N deposition rate (~0.2 g N m^{-2} yr^{-1}) in the study areas facilitated capturing the response of wood NPP at the low end of N availability. Using natural site productivity and stand age as covariates allowed synthesizing data across sites, providing a means to enlarge the scope to a range of stand development stages (30 to 160 years old stands). We hypothesized that (1) wood NPP will be responsive to external N inputs (spatial variability) in a non-linear form with a negligible response at the low end of external N input rates, and (2) the response will be more sensitive to precipitation (temporal variability) at higher rates of external N inputs than at lower rates.

METHODS

Setting

Three sets of partially published data (Table 1) were supplemented with additional data necessary to estimate net primary production (NPP) of woody mass to support the analyses. One of the study stands was in Norway (Åmli, *Ps*3) and two were in Sweden (Rosinedal, *Ps*8;

Åheden, *Ps*16). The *Ps* indicates *Pinus sylvestris* and the following number indicates stand age in decades. Thus, stand ages were about 30, 80, and 160 years old, and site indices were T23, T20, and T20 (T indicates species, *Pinus sylvestris*, and the following number is dominant height in meters at 100 years of age; Hägglund and Lundmark 1981) for *Ps*3, *Ps*8, and *Ps*16, respectively. The external nitrogen (N) input treatments were based on reference plots (background N deposition only), and plots receiving two annual N addition rates in *Ps*3 and *Ps*8 (3 and 9 g N m^{-2} yr^{-1} at *Ps*3, and 2 and 8.8 g N m^{-2} yr^{-1} at *Ps*8), and a reference and four N addition rates in *Ps*16 (0.3, 0.6, 1.25, and 5 g N m^{-2} yr^{-1}). The background N deposition was ~0.8 g N m^{-2} yr^{-1} at *Ps*3 (SFT 1998) and ~0.2 g N m^{-2} yr^{-1} at *Ps*8 and *Ps*16 (Phil-Karlsson et al. 2009). Rates of external N input were estimated as the sum of both N addition and background deposition, and the treatment is identified by the amount of external N input in g N m^{-2} yr^{-1} (e.g., N9 indicates plots had received an external N input of 8.8 + 0.2 = 9 g N m^{-2} yr^{-1}). Each treatment was replicated in four plots for eight years in *Ps*3, in three plots for eight years in *Ps*8, and in six or seven plots for seven years in *Ps*16. Detailed information on stands is given in Table 1, and further information on *Ps*3 can be found in Nilsen and Abrahamsen (2003), *Ps*8 in Lim et al. (2015), and *Ps*16 in Gundale et al. (2011) and From (2014).

Climate data for *Ps*3 was obtained from the Nelaug observation station, ~20 km from the experimental stand (Åmli municipality, Norwegian Meteorological Institute, http://sharki.oslo.dnmi.no), and for *Ps*8 and *Ps*16 from the Svartbergets field station ~8 and 3 km from each site (Laudon et al. 2013).

Net primary production of woody mass

In this study, wood NPP was defined as the sum of NPP of stem wood, branches, and coarse-roots including stump.

Åmli (*Ps*3): Published data on annual volume increments (cf. Fig. 1 in Nilsen and Abrahamsen 2003) were obtained by image-digitalization using GraphClick (ver. 3.0.3, Arizona Software, 2012). Plots to which additional nutrients were added were used as replicates of the N addition, after finding no interactive growth response to N × other nutrient (two-way ANOVA, minimum $p = 0.139$ with Mg, $n = 8$). This provided a greater power to analyze the effect of external N inputs (Table 1). The NPP of stem was obtained from stem volume production multiplied by wood density and the carbon (C) content of wood of similar N treatments in *Ps*8 (N2.2 for N3.8 and N9 for N9.8), and NPP of stem was converted to wood NPP using a biomass expansion factor for each treatment obtained from the same stand (Vestgarden et al. 2004).

Rosinedal (*Ps*8): Annual wood NPP in the reference and N9 was taken from Lim et al. (2015), and wood NPP in N2.2 was estimated by analyzing raw data as in Lim et al. (2015). Briefly, wood NPP was the sum of NPP of woody components estimated from annual measurements of diameter at 1.3 m (DBH in m) and tree height (H in m) in mensuration plots (n = 3 for each treatment), and derived site-specific allometric equations from harvested trees. The NPP of stem wood was calculated by annual difference of stem volume multiplied by specific wood density in each year and the C content of stem wood (0.52). The NPP of branches was estimated by the sum of annual difference of branch biomass and annual branch replacement, determined based on the rate of upward movement of the live crown and branch biomass per meter of the live crown in the lowest stratum. The NPP of coarse-roots, including the stump, was estimated from annual difference of root biomass and stump multiplied by the C content of stem wood.

Åheden (*Ps*16): Wood NPP was estimated based on stem increment cores and national allometirc equations (Marklund 1988). Increment cores were taken from 30 or 35 trees (five per plot, six or seven replications for each treatment, see Table 1) in each of four levels of N addition and reference plots, reported as basal area increment (From 2014). For this study, measurements of DBH and H, taken together with tree coring, were used to generate a relation of DBH-H for each treatment. Using increment core-based annual DBH estimates, H was estimated for all trees. Estimated DBH and H were used with allometric equations to estimate dry mass of stem, branch, and coarse-root (including the stump) (Marklund 1988; a range of DBH in 0 – 45 cm). Wood NPP of each year was estimated by the sum of annual difference in standing biomass of the three woody components, multiplied by the wood C content of 0.52 as in *Ps*8 (Lim et al. 2015). Estimated wood NPP in plots receiving 5 g N m^{-2} yr^{-1} was reduced to 0.89 (cf. Lim et al. 2015) because high N addition reduces wood density in *P. sylvestris* (Mäkinen and Hynynen 2014).

In a large-scale field experiment with replicated plots, a large unintended spatial variability among plots may obscure the temporal (weather) and spatial (external N input) signals. In *Ps*16, except for N0.5 (minimum p = 0.486), stand density varied among replications (280 – 1030 stems ha^{-1}), which affected biomass production within each treatment (minimum R^2 = 0.67, maximum p = 0.040, Appendix S1: Table S1 and Fig. S1). The spatial standard deviation (SD) in *Ps*16 was 2.4 ± 0.4 times greater than the temporal SD, whereas in *Ps*3 and *Ps*8 it was only 0.46

± 0.5 of the temporal. To minimize the unintended variation, and thus reveal the climate and N contributions to spatial and temporal variations of wood NPP, we normalized wood NPP to the mean stand density (494 stems ha^{-1}) based on the relation of wood NPP-to-stand density in each treatment and year (Appendix S1: Fig. S1). When no significant relation with stand density emerged, the mean wood NPP across replications was used for normalizing. The mean relative stand density index for *Ps*16 (accounting for mean biomass of trees and stand density, Reineke 1933, Lim et al. 2015) was 0.58, similar to that for the other two stands ($p = 0.124$). Moreover, the decline of stand density from 80 to 160 year-old stand (45%) was similar to that predicted based on a stand dynamics model (47.5%, the Heureka, see *age related wood NPP* section). The normalization for density differences and predictability of behavior facilitate synthesis of data across sites.

Age related wood NPP

To account for age-related wood NPP dynamics between site indices, and thus further hone the comparison among the three stands of different developmental stage, we generated age-related wood NPP dynamics for the two site indices of the study stands (T20 and 23) and stands representing low (T15) and high (T23) site fertilities, using the Heureka Forestry Decision Support System (Wikström et al. 2011, Fahlvik et al. 2014). The growth simulator in the Heureka includes a set of empirical sub-models for predicting growth and mortality based on data mainly from the National Forest Inventory in Sweden. An individual-tree dataset from pre-commercial thinning experiments in *P. sylvestris* forests was used as inputs to the growth simulator (Karlsson and Ulvcrona 2010). Input variables were an initial stand density of 2500 stems ha^{-1}, a mean height of 3.5 m, and stand age of 14 years for T28 and of 33 years for T15. Stand development was simulated up to an age of 160 years without any additional management.

Statistical analyses

We examined the two sources of variability of wood NPP (Fig. 1) – spatial variability in relation to external N inputs (hypothesis 1) and temporal variability in relation to growing season temperature (T) and precipitation (P) (hypothesis 2) – after the three stands were categorized as moderately-high and moderately-low productivities based on the age-site index curves (Fig. 2) and comparison of wood NPP in reference plots among the stands using analysis of variance (ANOVA) with a significance level at $p < 0.05$ (Eq. 1).

$$NPP_{ijk} = \mu + \alpha_i + \varepsilon_{ijk} \qquad \text{(Eq. 1)}$$

where NPP_{ijk} is the wood NPP of *k*th reference plot (*k* = 1 – 4 for *Ps*3, 1 – 3 for *Ps*8, and 1 – 6 for *Ps*16) in site *i* (*i* = *Ps*3, *Ps*8, and *Ps*16) in *j*th year, μ is a grand population mean, α is the effect of site, and ε is the residual.

For spatial variability, determining the form of response of wood NPP to external N inputs, the response was fitted using a four-parameter logistic growth function to determine the response along continuous external N inputs (Eq. 2).

$$NPP_{ijk} = \gamma_0 + \frac{\gamma-\gamma_0}{1+e^{-\alpha\cdot(N_i-\beta)}} + \varepsilon_{ijk} \qquad \text{(Eq. 2)}$$

where NPP_{ijk} is the wood NPP in *k*th of replication at a rate of external N input of *i* (*i* = 0.8, 3.8, and 9.8 g N m^{-2} yr^{-1} for *Ps*3, 0.2, 2.2, and 9 g N m^{-2} yr^{-1} for *Ps*8, and 0.2, 0.5, 0.8, 1.45, and 5.2 g N m^{-2} yr^{-1} for *Ps*16) in year *j*. The γ_0 is the minimum asymptote, γ is the maximum asymptote, α is the growth rate, β is the point of inflection when a rate of increase in wood NPP is maximized, and ε is the residual. Observed minimum and maximum wood NPP were used for initial values of γ_0 and γ, respectively, and then initial values for α and β were approximated using a linearized Eq. 2 [$\ln\left(\frac{\gamma-\gamma_0}{NPP_{ijk}-\gamma_0} - 1\right) = \alpha\cdot\beta - \alpha\cdot N_{ijk}$]. When the logistic growth function in each stand was not different from the function of data pooled across sites (ANOVA with a significance level at $p < 0.05$), sites were merged into a single population.

For temporal variability, determining the interactive effect between a rate of external N input and climate variables (*T* and *P*), we analyzed the variability using a multiple linear regression after setting the external N input as a categorical variable (*N*) (Eq. 3). In the regression, the interactive effects between *T* and *P*, and *T* and *N* in each site were removed after verifying that these interactions did not occur based on at $p < 0.05$ (minimum p = 0.230 for $T \times P$, 0.720 for $T \times N$).

$$NPP_{ijk} = \alpha + \beta_N \cdot N_i + \beta_T \cdot T_j + \beta_P \cdot P_j + \beta_{NP} \cdot N_i \cdot P_j + \varepsilon_{ijk} \qquad \text{(Eq. 3)}$$

where NPP_{ijk} is the wood NPP in *k*th replication at a rate of external N input (*N*) of *i* (*i* = six levels for the higher productivity, and five levels for the lower productivity stand) in year *j* (*j* = 1 – 8 for the higher productivity, and 1 – 7 for the lower productivity stand), $N \cdot P$ is the interaction between *N* and *P*, α is intercept, β are coefficients to be estimated, and ε is the residual. To quantify each impact of *T* and *P* on *NPP*, we discriminated Eq. 3 into Eq. 4 for *T* and Eq. 5 for *P*.

$$NPP_{ijk} = \alpha_1 + \beta_{N1} \cdot N_i + \beta_T \cdot T_j + \varepsilon_{Tijk} \qquad \text{(Eq. 4)}$$

where $\varepsilon_{Tijk} = \alpha_2 + \beta_{N2} \cdot N_i + \beta_P \cdot P_j + \beta_{NP} \cdot N_i \cdot P_j + \varepsilon_{ijk}$ (Eq. 5)

When an intercept was not different among levels of external N input (determined by the coefficient, β_{N1} in Eq. 4), the levels were merged into a single population.

Residuals bias of each function was checked using predicted values. Parameters were estimated using R (ver. 3.2.2) with the *nls* function for the logistic growth function, the *aov* for analysis of variance, the *HSD.test* in the *agricolae* package for multiple comparisons using the Tukey test, and the *lm* for multiple linear regressions.

RESULTS

Response of wood NPP to external N inputs

Net primary production (NPP) of woody mass in reference plots was not different between *Ps*3 and *Ps*8, but wood NPP of these stands was greater than that of the much older stand, *Ps*16 (Fig. 2, Eq. 1, $p < 0.001$; 177.6 ± 45.0 g C m^{-2} yr^{-1} for *Ps*3, 169.4 ± 31.8 for *Ps*8, and 84.3 ± 4.4 for *Ps*16, mean ± SD). Wood NPP of reference plots in *Ps*3 and *Ps*8 positioned at a similar rate, one before and the other after the peak wood NPP due to the age difference and a slight difference in site index. The much older stand (*Ps*16) had a lower wood NPP, as expected based on the generic age-related dynamics irrespective of site index (Fig. 2). Therefore we considered *Ps*16 as an example of moderately-low productivity stands, likely caused by advanced age. Based on both stand development dynamics and wood NPP of reference plots in *Ps*3 and *Ps*8, we considered these to represent moderately-high productivity stands. We note that, although both age and site quality affect stand productivity, *if* these two stands of different age and site quality respond similarly to external N inputs and weather, it would suggest that the potential of wood NPP to response to external N inputs depends on the current production rate.

Wood NPP at the three stands responded to external N inputs in a sigmoidal fashion, showing negligible responses to a low level of external N input, well fitted with a logistic growth function (Fig. 3a). Because the individual functions of *Ps*3 and *Ps*8 were not different from the function of their pooled data ($p = 0.501$), we used a single logistic growth function for the higher productivity stands, keeping a separate function for the lower productivity stand (*Ps*16, $p < 0.001$ for model difference between the higher and lower productivity stand). The two curves were similarly shaped (Fig. 3a) but displaced downward for the lower productivity stand. The fit for the higher productivity stands generated a minimum asymptote (γ_0) of 152.1 g C m^{-2} yr^{-1}, a maximum asymptote (γ) of 262.8 g C m^{-2} yr^{-1}, a growth rate (α) of 0.83 g C g^{-1} N, and a point of inflection (β) at an external N input of 2.3 g N m^{-2} ($R^2 = 0.42$, $p < 0.001$). The fit for the lower productivity stand, *Ps*16, produced γ_0 of 73.8 g C m^{-2} yr^{1}, γ of 149.7 g C m^{-2} yr^{-1}, α of 0.93 g C g^{-1} N, and β of 2.5 g N m^{-2} yr^{-1} ($R^2 = 0.79$, $p < 0.001$). The response of wood NPP to external N inputs, in both relative and absolute terms, reached maximum rates at a similar N input rate, ~5 g N m^{-2} yr^{-1}, in the intermediate-age (*Ps*8) and the older (*Ps*16) stands, both of which shared an age-related wood NPP curve (Fig. 3a, 81.9 ± 27.2 g C m^{-2} yr^{-1} in *Ps*8 *vs.* 58.4 ± 19.2 for in *Ps*16 for absolute; 48.2 ± 13.8 % *vs.* 68.7 ± 24.5 % for relative).

Using the parameter values from the logistic fits, we calculated the response efficiency (RE$_N$) over increasing external N inputs (de Vries et al. 2009). Because wood NPP at an external N input of 0 cannot be defined – all sites received N through atmospheric deposition (Table 1) – we calculated the differences from wood NPP of reference plots, and related it to N added through treatments ($\Delta C/\Delta N$). The RE$_N$ of the higher productivity stands showed a peak of 19.6 g C g^{-1} N near the point of inflection at an external N input of 3.2 g m^{-2} yr^{-1}, whereas that of the lower productivity stand had a similar pattern with a peak of 14.0 g C g^{-1} N at an external N input of 3.5 g N m^{-2} yr^{-1} (Fig. 3b).

Interactive effect of external N inputs and climate variations on wood NPP

Regardless of stand productivity, wood NPP increased with increasing *T*, ($p < 0.001$ for the higher and $p = 0.044$ for the lower productivity stand; Table 2, Fig. 4a, b), but the sensitivity of NPP to *T* was unrelated to the rate of external N input; coefficients were not different among the populations within each productivity stand (minimum $p = 0.316$). The magnitude of the sensitivity was, however, a six-fold greater in the higher than that in the lower productivity stand (25.9 g C per 1 °C for the higher productivity *vs.* 4.7 for the lower productivity stand). The relations in the lower productivity stand were statistically grouped into two populations (N0.2 – N1.45 and N5.2, $p < 0.001$ for the difference between populations, Table 2), with an offset of 57.03 ± 5.21 g C m^{-2} yr^{-1} (Fig. 4a). In the higher productivity stands, the relations were grouped into three populations (N0.2 – N0.8, N2.2 – N3.8, and N9 – N9.8, p = 0.310, 0.187, and 0.656 for the difference among external N inputs within a population, respectively; $p < 0.001$ for the difference among populations, Table 2), with an offset of 50.8 ± 8.0 g C m^{-2} yr^{-1} between N0.2 – N0.8 and N2.2 – N3.8, and an additional offset of 39.0 ± 8.0 g C m^{-2} yr^{-1} between the latter population and N9 – N9.8 (Fig. 4b). In both productivity stands, the remaining temporal variations after that explained by *T* were greater in higher rates of external N input than in lower rates (see RMSE in Table 2).

Using the slopes to normalize the temperature-dependent response to that expected at the mean growing season *T* (12.2 °C in *Ps*3, and 11.5 in *Ps*8 and *Ps*16), remaining temporal variations were assessed against the variation in *P*. In both *Ps*8 and *Ps*16 (Fig. 4c, d, and Table 2), where $P < \sim 400$ mm, wood NPP was sensitive to *P* under high external N inputs, but not under low external N inputs (< 2.2 g N m^{-2} yr^{-1}). The slope under N9 was steeper (0.97 ± 0.21 g C m^{-2} mm^{-1}, $p = 0.014$) than those under N2.2 and N5.2, whereas slopes under N2.2 and N5.2 were similar (0.50 ± 0.10 *vs.* 0.36 ± 0.11 g C m^{-2} mm^{-1}, $p = 0.686$). At $P > 400$ mm (*Ps*3), the inter-annual variation of wood NPP was unrelated to *P* (Fig. 4d).

DISCUSSION

The long-term effect of N deposition on biomass production in forest ecosystems has been studied extensively, with the effects ranging from negative to positive (Oren et al. 1989, Schulze 1989, Tamm et al. 1999, de Vries et al. 2009, Thomas et al. 2010). In a recent comprehensive synthesis, de Vries et al. (2014) have shown that the response to external N inputs (the sum of N fertilization and background deposition) varies with forest age, reflecting the age-dependence of forest growth (Vitousek and Reiners 1975, Goulden et al. 2011), and that increasing external N inputs may generate a positive, roughly sigmoidal response. Our results (Figs. 2 and 3a) for stands in moderately-high productivity, intermediate-age stage (*Ps*3 and *Ps*8), as well as moderately-low productivity, older stage (*Ps*16), principally support these observations. The production in the old stand was less sensitive to site fertility than in the young stands (Fig. 2), and the response to external N inputs was grouped by annual net primary production (NPP) of woody mass under reference conditions (Fig. 3a), rather than by age or site fertility (these were dissimilar in the two intermediate-age stands). Indeed, the results suggest that the *absolute* wood NPP response to external N inputs, and interactive effects with temperature and precipitation (Fig. 4), depend on the current production of a stand, which may serve as an index of production capacity. Thus, we searched for interactive effects on wood NPP between external N inputs and the two temporal climate variables of the two higher productivity stands combined *versus* the lower productivity stand. We note that our three stands, regardless of age and site quality, represent production rates ranging from moderately low observed in poorer sites to moderately high in more fertile sites (Fig. 2). Our scope of inference, however, does not include highly productive stands below 100 years of age because such productive stands are not common in this region (Nilsson et al. 2010). We also note that soil N mineralization rates were not incorporated into the investigation of the response of wood NPP. Many studies have shown that available soil N for plant-use in these forests is dominated by organic rather than inorganic N (Näsholm et al. 1998, Inselsbacher and Näsholm 2012). Further, an earlier study of *Ps*8 demonstrated the dominance of organic N in these forests (Inselsbacher et al. 2014). Thus, data on N mineralization rates would not be helpful because such data would only provide information on a small fraction of the soil N supply to trees.

In order to generalize the outcome, we synthesized data from three studies using different approaches to estimating wood NPP; in *Ps*8 wood NPP was estimated based on site-specific derived allometric equations (Lim et al. 2015), whereas in *Ps*3 and *Ps*16, wood NPP was based on national allometric equations (Marklund 1988, cf. Vestgarden et al. 2004). We examined a potential bias between the two approaches by comparing biomass estimates from the two methods using the same mensuration measurements of DBH and H obtained in the nine plots of *Ps*8 (three replicated plots in each of N0.2, N2.2, and N9). The estimated woody biomass was not different between the two methods (Appendix S1: Fig. S2, 10.46 kg dry mass m^{-2} for the national *vs*. 10.50 for the site-specific equations, paired t-test, $p = 0.386$) and the relative difference (mean = 0.19 ± 0.97%, $n = 9$) was unrelated to mean diameter at plot level ($p = 0.094$). These results suggest that estimates of wood NPP across the sites were not biased by the methodologies used.

Age-related wood NPP dynamics

Stand age and site quality may affect productivity, making it difficult to synthesize data across stands (Fig. 2). From the modeled age-related wood NPP dynamics, we confirmed that two stands (*Ps*3 and *Ps*8) were of similar productivity due to a combination of age and site index, while older stands (here, *Ps*16) are less productive, regardless of site index.

Stem growth (and wood NPP) of managed even-aged stands follows a pattern whereby current annual increment rises after stand establishment, peaks when maximum leaf area is attained, and then declines (Assmann 1970). The age-related dynamics of wood NPP, modeled based on the Heureka Forestry Decision Support System (Wikström et al. 2011; Fig. 2), peaked at about one-third of the maximum age of *P. sylvestris,* similar to other expressions of productivity (Vitousek and Reiners 1975, Goulden et al. 2011). Maximum wood NPP is reached earlier and attains higher rates at sites of better quality (Assmann 1970), and differences in wood NPP among sites become very small as stands age.

The estimated wood NPP of *Ps*8 and *Ps*16 (located only 8 km apart) fell on the simulated line describing the age-dependent dynamics of wood NPP for a site of similar quality. The age-related decline in production observed was ~80 g C m^{-2} yr^{-1}, with the older stand producing ~50% of the younger forest (Fig. 2), a reduction similar to previously reported in coniferous boreal forests (Ryan et al. 1997, Luyssaert et al. 2008). The decreased production with age has been variably attributed to declining soil nutrient availability as a result of nutrient immobilization, changing forest structures associated with decreasing leaf area and its efficiency, increased competition among individuals, and hydraulic resistance of vertical growth (Gower et al. 1996, Ryan et al. 1997, Smith and Resh 1999, Binkley et al. 2002, Martínez-Vilalta et al. 2007).

Although the native productivity over the T20 site index declined from intermediate-age (*Ps*8) to the older stand (*Ps*16), both relative and absolute enhancements of wood NPP by external N inputs were marginally different (p = 0.074 for absolute and 0.052 for relative). Nevertheless, as the maximum external N input was less in *Ps*16 than that in *Ps*8, it is possible that, had a higher external N input been administered in that stand, a greater wood NPP might have been observed. However, considering (*i*) the lack of response of *Ps*3 and *Ps*8 – bracketing the age of peak production – to higher external N inputs, (*ii*) lack of evidence for growth limitation by other nutrients (Lim et al. 2015), and (*iii*) the convergence of age-related wood NPP curves with age across all site indices, the age-induced growth limitations in *Ps*16 appear unrelated to nutrition, but rather imposed by other age-related changes.

Response of wood NPP to external N inputs

We note that response of wood NPP to external N inputs vary considerably among studies, due not only to stand age (de Vries et al. 2009), but also to the fact that the shape of the response relates to the range of external N inputs. For example, a more linear response was shown in a *Picea abies* stand where external N inputs ranged from 0.2 to 5.2 g N m^{-2} yr^{-1} (Gundale et al. 2014), consistent with a less defined sigmoidal pattern that would have emerged in our study, had we focused on the same external N input range (Fig. 3a). Considering the full range of external N inputs in the present study, and consistent with the first hypothesis, wood NPP responded to external N input rates following a sigmoidal fit, with a point of inflection at ~3 g N m^{-2} yr^{-2} (Fig. 3a). A negligible response of wood NPP was observed at rates below ~1 g N m^{-2} yr^{-1} and a more continuous wood NPP response up to a maximum at 4 – 5 g N m^{-2} yr^{-1}. The response pattern was similar in the three stands regardless of stand productivity, but displaced downwards in the lower productivity stand (Fig. 3a). Such a response is implied in de Vries et al. (2014), although in that analysis, the lack of response over the broader range of external N inputs was attributed to growth limitation by the availability of other nutrients (e.g., Oren et al. 1988). However, having no limitation from other nutrients in *Ps*3 (Nilsen and Abrahamsen 2003) and *Ps*8 (Lim et al. 2015) suggests that the absence of growth enhancement observed beyond a threshold of external N inputs is related to factors other than nutrition (Fig. 3a).

Soil microbes and, in particular, ectomycorrhizal fungi might access and immobilize N entering forest floor efficiently, restricting the uptake of N into trees (Näsholm et al. 2013, Hasselquist et al. 2016). This effect would be expected to hamper the response of wood NPP at low N input rates. A restricted wood NPP response to external N input at low rates is consistent with the “bryophyte effect”, whereby components of the understory attenuate anthropogenic N input in boreal forests (Gundale et al. 2011). In similar forests, the bryophyte effect is saturated at about the rate at which our forests begin to respond (~0.5 g N m^{-2} yr^{-1}, see Gundale et al. 2011), below the maximum response efficiency (RE$_N$, increase in wood NPP per external N input), suggesting additional understory and soil processes competing with trees for N. It is also plausible that the lack of response of wood NPP to low N input rates is caused by N utilization in a greater belowground production of fine-roots and mycorrhizal fungi (Hasselquist et al. 2012). As the capacity of these processes and components is progressively met, N availability to trees would increase with increasing N input, allowing an increase in wood NPP.

At the other end of the N input scale, exceeding a certain level of N addition may not result in a greater biomass production (Aber et al. 1995, de Vries et al. 2014). Indeed, as external N inputs reached 4 – 5 g N m^{-2} yr^{-1} (Fig. 3a), the increase in wood NPP saturated. The lack of response of wood NPP to external N inputs above this rate is consistent with findings showing no growth response in *P. sylvestris* stands to fertilization increasing from 3.4 to 6.8 g N m^{-2} yr^{-1} (Tamm et al. 1995, Högberg et al. 2006). In a previous study (Lim et al. 2015), 67 g C m^{-2} y^{-1} increased wood production at the highest external N input (N9) was almost entirely achieved through a 104 g C m^{-2} y^{-1} reduction in C partitioning to fine-root and mycorrhizal fungi. This mechanism, however, must reach a limit at lower external N inputs (say, 4 – 5 g N m^{-2} yr^{-1}) because a minimum amount of C, depending on site and species, must be invested in fine-root and mycorrhizal fungi. Further increase of N supply would not result in a higher wood production, suggesting that trees accumulate excess N as amino acids, mainly in the form of arginine (Näsholm and Ericsson 1990). As external N inputs increased above the point at which production responds, N leaching may have increased as well (Dise and Wright 1995, Andersson et al. 2002).

Interactive effect of external N inputs and climate variations on wood NPP

Although wood NPP did not respond to external N inputs at low and high external N inputs (< ~1 and > ~4.5 g N m^{-2} yr^{-1}), we found that the temporal variations (cf. error bars, Fig. 3a) mask a more complex response to external N inputs driven by inter-annual variation of climatic variables. As expected based on a previous analysis of *Ps*8 (Lim et al. 2015, using only the reference and the high N addition treatment), both *Ps*3 and *Ps*8 showed a similar sensitivity of wood NPP to temperature during the growing season (*T*, Fig. 4b), with the response simply shifted in parallel upwards to higher values with increasing external N inputs. However, a lesser *T* sensitivity of wood NPP was observed in *Ps*16 (Fig. 4a), consistent with Kellomäki et al. (1982), who investigated the response of growth to temperature in slow-growing, nutrient limited forests. Alternatively, the less sensitivity to *T* in *Ps*16 may simply reflect a difficulty in detecting effects of inter-annual variation in *T* when production rates are low (Castagneri et al. 2012).

Although wood NPP of both low and high productivity stands responded positively to increasing *T*, the inter-annual variability was much greater under higher than under lower external N inputs (Table 3, Figs. 4a, b). The reason is that the variation in precipitation during the growing season (*P*) infused an additional inter-annual variation to wood NPP where N limitation to growth was reduced or eliminated, and wood NPP was high. Thus, after accounting for *T*-induced variation of wood NPP, *P* explained about half of the remaining variation, but only when and where water availability was generally low (*P* < ~400 mm in *Ps*8 and *Ps*16), and where growth potential increased with external N inputs (Figs. 4b, d). Even in *Ps*16, where *T* marginally explained the inter-annual variation of wood NPP, *P* contributed significantly to reduction in the remaining variation in plots where growth potential was enhanced by external N input (Figs. 4a, c).

In *Ps*8, the sensitivity of wood NPP to *P* increased with increased external N inputs (Table 2, Figs. 4c, d). It is interesting to note that in *Ps*16, N5.2 produced a similar wood NPP sensitivity to *P* as in N2.2 of *Ps*8 (0.36 *vs.* 0.50 g C m^{-2} mm^{-1}, p = 0.686). Trees relieved from nutrient limitation by N addition may be subjected to a greater water limitation (Betson et al. 2007, Lim et al. 2015) because N addition reduces C partitioning to fine roots and mycorrhizal fungi while increasing leaf area index and foliage biomass (Linder 1987, Linder et al. 1987, Ewers et al. 2000, Palmroth et al. 2006). Thus, increased N addition may result in a greater sensitivity of trees to soil water availability.

Not only will wet years allow trees to meet their growth potential more easily, but also in such years the potential for growth may increase as well because water uptake greatly affect nutrient uptake (Cramer et al. 2008, Matimati et al. 2014, Oyewole et al. 2014). In *Ps*8, this resulted in a positive relation between foliage N contents and P ($R^2 = 0.36$, $p = 0.004$, data not shown), with potential enhancements of photosynthesis and growth processes (Linder 1987). However, as previously stated, the enhancement of wood NPP by N addition in *Ps*8 resulted mainly from shifting C allocation rather than increasing photosynthesis (Lim et al. 2015, Tarvainen et al. 2016). The interactive effect of water and N on wood NPP observed here corroborates the notion that only when water and N are in abundant supply will trees shift allocation from preferential growth of fine roots and mycorrhizal fungi, to preferential growth of woody components.

Given the complexity of the interactions, we synthesized the results described above into a simple representation of the relative response of wood NPP to variations in external N inputs and P in the higher productivity stands (Fig. 5), quantifying the impact of external N inputs on C accumulation in tree wood biomass over a range of P. The response is relativized to wood NPP of reference stands (N0.2), in which wood NPP did not respond to P (Figs. 4c, d). In the higher productivity stands, the temperature-induced changes in wood NPP reflect the same *absolute* sensitivity to T at all external N inputs and P conditions (Fig. 4b), showing a similar increase with T. The *relative* changes in wood NPP may, however, reflect a decreased N-induced drought stress in cooler years and increased N-induced drought stress in warmer years, perhaps owing to the effect of temperature variation on vapor pressure deficit (Katul et al. 2009). Under improved N supply, stands may be particularly sensitive to increased vapor pressure deficit with temperature, because a lower fine root-to-leaf area ratio (Linder et al. 1987; Ewers et al. 2000) reduces water uptake capacity relative to the transpiration needs, resulting in lower conductance and photosynthesis.

N-induced drought stress may affect production not only during the drought, but also in the following years when trees may experience a large increase in litterfall, reducing stand leaf area index and, thus, potentially canopy photosynthesis (Linder et al. 1987, Bergh et al. 1999). In this study, however, the reduction of canopy leaf area with drought was small with no effect on the amount of light captured, transpiration, and canopy conductance (Lim et al. 2015, Tor-ngern et al. 2016). It is therefore not surprising that neither *P* nor *T* in previous years explain the variation in current wood NPP in any of the sites.

Our values of RE_N to external N inputs were within the range shown in previous studies and maximized between external N inputs of ~2 and 4 g N m^{-2} yr^{-1} (Fig. 3b), reaching in the higher productivity stands near the maximum RE_N reported for studies in boreal forests (Hyvönen et al. 2008, Gundale et al. 2014). Previous studies, however, have reported linear relations between annual growth and external N inputs (Gundale et al. 2014, From 2014), but in our study wood NPP responded in a sigmoidal fashion to increasing external N inputs. Therefore, our RE_N values reflect the negligible response of wood NPP to external N input below and above the sensitive range. In addition to the spatial variation of RE_N, associated with stand developmental stage and external N inputs (Fig. 3b), the temporal variation of wood NPP, produced by the variation of *P*, is likely to infuse additional variation in RE_N. Using the results shown in Fig. 5a, we produced estimates of the temporal (inter-annual) variation of RE_N, showing a high sensitivity to *P* (Fig. 5b). Thus, accounting for both sources of systematic variation, the spatial variation of RE_N in relation to external N inputs (Fig. 3b), and temporal variations in relation to *P* and *T,* results in better estimates of wood NPP than using a temporally fixed RE_N in conjunction with spatially varying external N inputs (de Vries et al. 2014). The results of these analyses highlight the fact that there is no simple way to account for the effect of N deposition on forest growth, and that it is necessary to develop and test models that couple C and N cycling with ecosystem physiology, thus explicitly incorporating the effects of climatic and environmental factors (Thornton et al. 2007).

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Table 1. Summary of the characteristics of the three stands used in the study.

Stand	Åmli (*Ps*3) (Nilsen et al. 2003)	Rosinedal (*Ps*8) (Lim et al. 2015)	Åheden (*Ps*16) (Gundale et al. 2011)
Location	58°54'N, 08°34'E	64°10'N, 19°45'E	64°14'N, 19°46'E
Growing season temperature (°C) (Annual temperature)	12.2 (5.6)	11.5 (1.2)	11.5 (1.2)
Growing season precipitation (mm) (Annual precipitation)	592 (1225)	325 (600)	325 (600)
Soil	Medium sandy and fluvial deposit Haplic Arenosol	Fine sandy and silty glacial outwash sediments Typic Haplocryods	Fine sandy and silty glacial outwash sediments Typic Haplocryods
Understory vegetation	*Vaccinium myrtillus* *Vaccinium vitis-idaea* *Calluna vulgaris* *Cladonia* spp.	*Vaccinium myrtillus* *Vaccinium vitis-idaea* *Pleurozium schreberi* *Hylocomium splendens* *Cladonia* spp.	*Vaccinium vitis-idaea* *Calluna vulgaris* *Pleurozium schreberi* *Dicranum sp.* *Cladina rangiferina* *Cladina arbuscula* *Cladonia* spp.
Initial age (year)	~30	~80	~160

Stand density (trees ha^{-1})	1470	888 ± 136	494 ± 187
Site index	[1]T23 ([2]F15)	T20	T20
Mean diameter at 1.3 m (cm, min – max)	11.2	16.6 (4.8 – 27.5)	22.2 (4.7 – 45.2)
Mean tree height (m, min – max)	9.8	14.9 (8.1 – 19.0)	17.4 (7.2 – 27.2)
Expressed productivity	Stem volume (m^{3} ha^{-1} yr^{-1})	Wood NPP (g C m^{-2} yr^{-1})	Basal area at 1.3 m (m^{2} ha^{-1} yr^{-1})
Method to estimate wood NPP	[3]National allometric equations (Vestgarden et al. 2004)	Site specific allometric equations (Lim et al. 2015)	National allometric equations (Marklund 1988)
Background N deposition (g N m^{-2} yr^{-1})	0.8	0.2	0.2
N addition levels (External N inputs) (g N m^{-2} yr^{-1})	0, 3, 9 (N0.8, N3.8, N9.8)	0, 2, 8.8 (N0.2, N2.2, N9)	0, 0.3, 0.6, 1.25, 5 (N0.2, N0.5, N0.8, N1.45, N5.2)
Study period (year)	8 (1991 – 1998)	8 (2006 – 2013)	7 (2005 – 2011)
Number of replicates	4	3	6 (7 for N0.5 and N5.2)

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[1] Dominant height in meters at total age of 100 years (H100)

[2] Dominant height in meters at age of 40 years (H_{40}); this can be converted to H_{100} by a relation ($H_{100} = 1.351 \times H_{40} + 2.61$, Tveite 1980).

[3] Authors estimated biomass expansion factors using the national allometric equations (Marklund 1988)

Table. 2. Coefficient of determinants and estimated parameters for the multiple linear regressions (Eq. 4 – 6) for the higher productivity and lower productivity stand.

Stand	External N inputs (g N m^{-2} yr^{-1})	^{2}Intercept (SE)	^{2}*T* (SE)	^{2}RMSE	^{2}p-value	^{3}*P* (SE)	^{3}p-value
Higher productivity	0.2	-128.90 (40.94) a	25.86 (3.47)	26.21	< **.001**	.036 (.141)	.799
(*Ps*3 and *Ps*8)	0.8	-138.30 (11.73) a	25.86 (3.47)	33.72	< **.001**	.129 (.086)	.142
	2.2	-92.42 (12.28) b	25.86 (3.47)	27.77	< **.001**	.499 (.105)	< **.001**
^{1}R^2 of Eq. 4 = 0.917	3.8	-76.69 (11.73) b	25.86 (3.47)	36.33	< **.001**	.091 (.094)	.344
	9.0	-47.06 (12.28) c	25.86 (3.47)	54.87	< **.001**	.969 (.210)	< **.001**
	9.8	-42.40 (11.73) c	25.86 (3.47)	57.46	< **.001**	-.063 (.151)	.679
Lower productivity	0.2	35.12 (37.12) d	4.73 (2.25)	3.19	**.044**	.004 (.037)	.923
(*Ps*16)	0.5	29.50 (43.99) d	4.73 (2.25)	7.45	**.044**	-.017 (.086)	.852
^{1}R^2 of Eq. 4 = 0.617	0.8	47.21 (43.99) d	4.73 (2.25)	9.31	**.044**	-.018 (.107)	.875
	1.45	78.11 (43.99) d	4.73 (2.25)	6.84	**.044**	-.102 (.064)	.172
	5.2	-29.11 (43.99) e	4.73 (2.25)	16.62	**.044**	.346 (.114)	**.029**

[1] Eq. 4: wood NPP response to the growing season temperature (*T*) and precipitation (*P*) over rates of external N input.

[2] Eq. 5: wood NPP response to *T*.

[3] Eq. 6: response of residuals produced from the Eq.5 to *P*.

The RMSE is root mean square error.

Different letters in the intercept column indicate intercepts are different among external N inputs in each productivity stand ($p < 0.05$).

Figure Legends

Fig. 1. A flow diagram of data analyses; rectangles indicate variations in net primary production (NPP) of woody mass and rounded rectangles indicate models explaining the variations. Three types of variation of wood NPP were discriminated into *i*) variation induced by site-specific factors – age-site index related wood NPP; process 1, *ii*) variation by spatial factors – ε_s, external N inputs; process 2, and *iii*) variation by temporal factors – ε_t, temperature and precipitation; process 3. Results of each process are presented in Fig. 2 – 4, and explained variations were synthesized for modeling wood NPP (Fig. 5). Further details on each of the three stands are given in Table 1, equations are given in the Material and Methods section, and estimated parameters in Eq. 3 are given in Table 2.

Fig. 2. Dynamics of net primary production (NPP) of woody mass in response to stand age for reference plots in each of the three study stands. Using the Heureka Forestry Decision Support System (Wikström et al. 2011), dynamics were generated based on site indices (SI); the letter 'T' denotes *P. sylvestris* and the following number indicates a dominant height in meter at 100 years of age. Thus, T15 is sites of very low productivity and T28 of very high productivity for this species. Error bars are combined spatiotemporal standard deviation.

Fig. 3. (a) Net primary production (NPP) of woody mass in response to external N inputs (the sum of N fertilization and background deposition) for a combination of moderately-high productivity stands (*Ps*3 and *Ps*8), and a moderately-low productivity stand (*Ps*16). Lines are fits from a logistic function (Eq. 1); dotted lines indicate the individual responses for *Ps*3 and *Ps*8, and the dashed extension indicates projected values for *Ps*16; the standard deviation of the annual values (error bars), representing temporal variability of wood NPP, increased within a population with external N inputs. (b) The response efficiency of wood NPP ($\mathrm{RE_N}$, increase in wood NPP per external N input) in response to external N inputs, produced based on the fits in (a).

Fig. 4. Net primary production (NPP) of woody mass in response to temperature during the growing season (T) for (a) moderately-low productivity stand (*Ps*16), and (b) a combination of

the both moderately-high productivity stands (*Ps*3 and *Ps*8) (diamonds for *Ps*3; circles for *Ps*8; values for external N input rates are in g N m^{-2} yr^{-1}. Statistically, populations in moderately-low productivity stand were N5.2 and rest of external N inputs, and in moderately-high productivity stands were N0.2 with N0.8, N2.2 with N3.8, and N9 with N9.8. Wood NPP, at mean *T* (averages over 33-year record), in response to precipitation during the growing season (*P*) in (c) moderately-low productivity stand and (d) moderately-high productivity stands. Wood NPP was similar in N0.2 of *Ps*8 and N0.8 of *Ps*3, and higher than that of *Ps*16, and did not respond to *P*. Where N was added, plots responded to *P* only below ~400 mm (with N2.2 and N5.2 sharing a similar response). Error bars are spatial standard deviation (among replicates).

Fig. 5. Estimated (a) net primary production (NPP) of woody mass relative to reference condition (N0.2) and (b) the response efficiency of wood NPP (RE_N, increase in wood NPP per external N input), in response to a combination between external N inputs (the sum of N fertilization and background deposition) and growing season precipitation (*P*) for a combination of two moderately-high productivity stands (*Ps*3 and *Ps*8). The response was simulated based on results shown in Fig. 4, and limited to the range in which *P* affected the response to N supply.

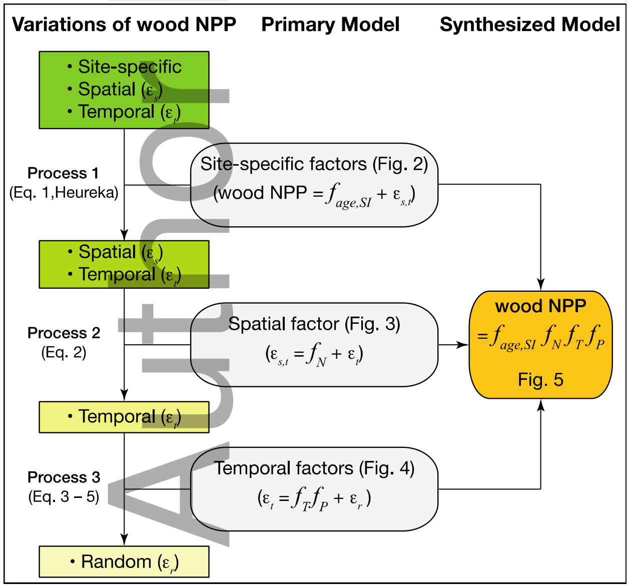


Fig. 1.

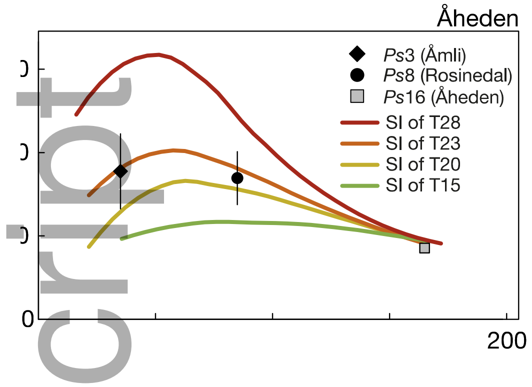

Åheden
Ps3 (Åmli)
Ps8 (Rosinedal)
Ps16 (Åheden)
SI of T28
SI of T23
SI of T20
SI of T15
0
200

Fig. 2.

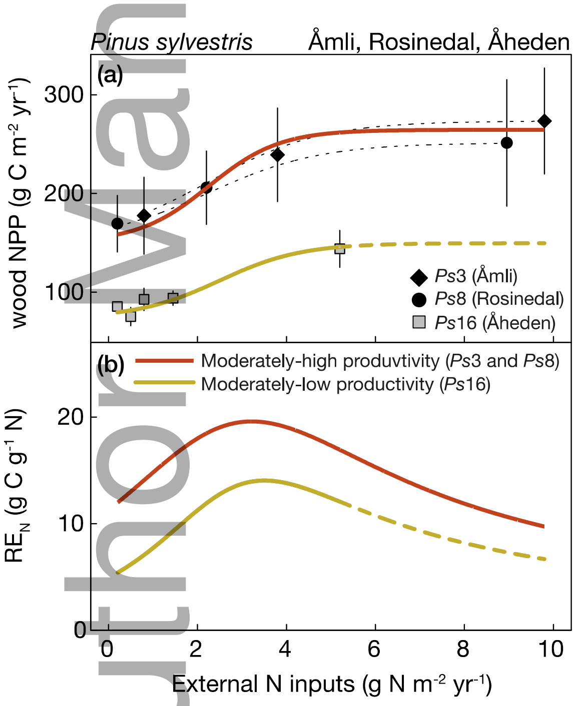
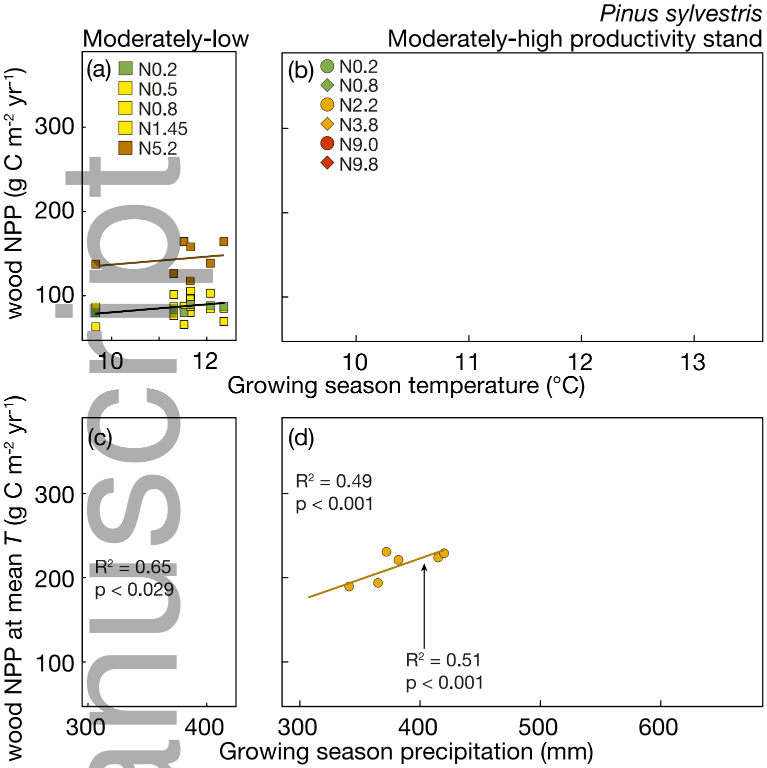

Pinus sylvestris
Åmli, Rosinedal, Åheden
(a)
wood NPP (g C m-2 yr-1)
300
200
100
Ps3 (Åmli)
Ps8 (Rosinedal)
Ps16 (Åheden)
(b)
Moderately-high produvtivity (Ps3 and Ps8)
Moderately-low productivity (Ps16)
REN (g C g-1 N)
20
10
0
0
2
4
6
8
10
External N inputs (g N m-2 yr-1)

Fig. 3.



816

817 Fig. 4.

818

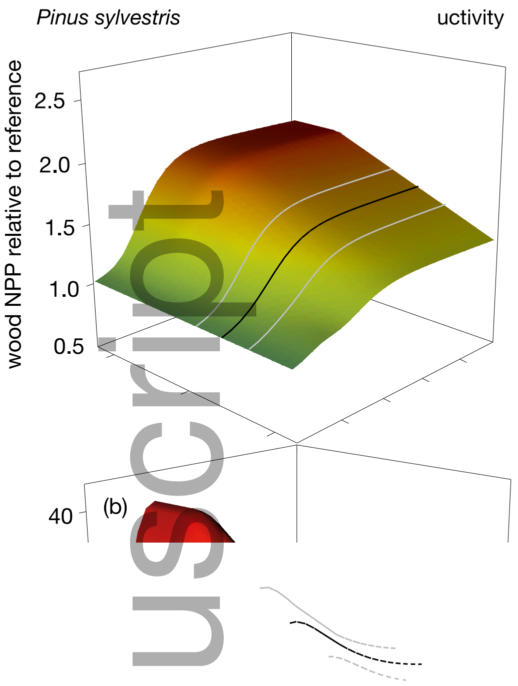

Pinus sylvestris
uctivity
wood NPP relative to reference
2.5
2.0
1.5
1.0
0.5
(b)
40

Fig. 5.