



## Inter-annual variability of precipitation constrains the production response of boreal *Pinus sylvestris* to nitrogen fertilization



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### ABSTRACT

Tree growth resources and the efficiency of resource-use for biomass production determine the productivity of forest ecosystems. In nutrient-limited forests, nitrogen (N)-fertilization increases foliage [N], which may increase photosynthetic rates, leaf area index ( $L$ ), and thus light interception ( $I_C$ ). The product of such changes is a higher gross primary production and higher net primary production (NPP). However, fertilization may also alter carbohydrate partitioning from below- to aboveground, increasing aboveground NPP (ANPP). We analyzed effects of long-term N-fertilization on NPP, and that of long-term carbon storing organs (NPP<sub>S</sub>) in a *Pinus sylvestris* forest on sandy soil, a wide-ranging forest type in the boreal region. We based our analyses on a combination of destructive harvesting, consecutive mensuration, and optical measurements of canopy openness. After eight-year fertilization with a total of 70 g N m<sup>-2</sup>, ANPP was 27 ± 7% higher in the fertilized (F) relative to the reference (R) stand, but although  $L$  increased relative to its pre-fertilization values,  $I_C$  was not greater than in R. On the seventh year after the treatment initiation, the increase of ANPP was matched by the decrease of belowground NPP (78 vs. 92 g C m<sup>-2</sup> yr<sup>-1</sup>; ~17% of NPP) and, given the similarity of  $I_C$ , suggests that the main effect of N-fertilization was changed carbon partitioning rather than increased canopy photosynthesis. Annual NPP<sub>S</sub> increased linearly with growing season temperature ( $T$ ) in both treatments, with an upward shift of 70.2 g C m<sup>-2</sup> yr<sup>-1</sup> by fertilization, which also caused greater amount of unexplained variation ( $r^2 = 0.53$  in R, 0.21 in F). Residuals of the NPP<sub>S</sub>- $T$  relationship of F were related to growing season precipitation ( $P$ ,  $r^2 = 0.48$ ), indicating that  $T$  constrains productivity at this site regardless of fertility, while  $P$  is important in determining productivity where N-limitation is alleviated. We estimated that, in a growing season average  $T$  (11.5 ± 1.0 °C; 33-year-mean), NPP<sub>S</sub> response to N-fertilization will be nullified with  $P$  31 mm less than the mean (325 ± 85 mm), and would double with  $P$  109 mm greater than the mean. These results suggest that inter-annual variation in climate, particularly in  $P$ , may help explaining the reported large variability in growth responses to fertilization of pine stands on sandy soils. Furthermore, forest management of long-rotation systems, such as those of boreal and northern temperate forests, must consider the efficiency of fertilization in terms of wood production in the context of changes in climate predicted for the region.

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### 1. Introduction

The production of biomass in forest ecosystems at a particular regime of incoming solar radiation is the outcome of the amount of radiation absorbed by the canopy and its utilization in the production of carbohydrates and further of biomass. The amount of photosynthetically active radiation intercepted by the canopy ( $I_C$ ) depends on both the canopy leaf area index ( $L$ ) and its spatial

## Nomenclature

ANPP	aboveground NPP ( $\text{g C m}^{-2}$ )	NEE	net ecosystem C exchange
BA	basal area ( $\text{m}^2$ )	NPP	total net primary production ( $\text{g C m}^{-2}$ )
$\Delta$ BA	annual basal area increment ( $\text{m}^2$ )	NPP'	NPP excluding fine-roots and ectomycorrhizae ( $\text{g C m}^{-2}$ )
BNPP	belowground NPP ( $\text{g C m}^{-2}$ )	NPP <sub>CR</sub>	NPP of coarse-roots ( $\text{g C m}^{-2}$ )
C	carbon	NPP <sub>EM</sub>	NPP of ectomycorrhizae ( $\text{g C m}^{-2}$ )
DBH	diameter at 1.3 m (m)	NPP <sub>FR</sub>	NPP of fine-roots ( $\text{g C m}^{-2}$ )
F	fertilized stand	NPP <sub>S</sub>	NPP of long-term carbon storing organs ( $\text{g C m}^{-2}$ )
GPP	gross primary production ( $\text{g C m}^{-2}$ )	P	growing season precipitation (mm)
H	tree height (m)	R	reference stand
$\Delta$ H	total height increment (mm)	RC	live-crown ratio
I	photosynthetically active radiation ( $\text{MJ m}^{-2}$ )	RSD	relative stand density
$I_c$	light interception ( $\text{MJ m}^{-2}$ )	SD	stand density (trees $\text{ha}^{-1}$ )
L	leaf area index ( $\text{m}^2 \text{m}^{-2}$ )	SNA	specific (projected) needle area ( $\text{cm}^2 \text{g}^{-1} \text{dw}$ )
LC	length of the green crown (m)	T	mean daily temperature during growing season ( $^{\circ}\text{C}$ )

organization (Stenberg, 1996; Nilson, 1999; Stenberg et al., 2001; Kim et al., 2011). Converting  $I_c$  to biomass depends on processes sensitive to temperature, soil moisture and nutrient availability (Monteith, 1977; Linder, 1987; Runyon et al., 1994; Haxeltine and Prentice, 1996).

In the nutrient-limited boreal forests, many studies on conifers have shown that nitrogen (N)-fertilization enhances productivity and resource-use efficiency (e.g. Kukkola and Saramäki, 1983; Axelsson and Axelsson, 1986; Mälkönen et al., 1990; Mälkönen and Kukkola, 1991; Tamm, 1991; Valinger, 1993; Bergh et al., 2005; Jacobson and Pettersson, 2010). Depending on initial conditions, reducing or eliminating N-limitation through N-fertilization could increase aboveground biomass production in three ways: (1) by increasing L and thus  $I_c$ , (2) by increasing photosynthetic rates of foliage (per unit area), both of which contribute to increases of gross primary production (GPP, or whole canopy photosynthesis), and (3) by shifting carbohydrate partitioning from belowground production of fine-roots and mycorrhizae to favor aboveground production of foliage and wood (Linder and Axelsson, 1982; Vose and Allen, 1988; Colbert et al., 1990; Cromer and Jarvis, 1990; Haynes and Gower, 1995; Albaugh et al., 1998; Nilsson and Wallander, 2003).

Inter-annual and geographical variation of temperature and precipitation exert large influence on NPP (Melillo et al., 1998; Knapp and Smith, 2001) by affecting GPP and carbohydrate partitioning to belowground (Litton and Giardina, 2008). At a macro scale, spatial variation in temperature is known to affect site productivity (Fries et al., 1998), but even small topographic gradients at a decameter scale introduce spatial variability of moisture and soil water holding capacity, which can influence local productivity (Sampson and Allen, 1999; McCarthy et al., 2007; Noormets et al., 2010). However, the effect of inter-annual variation of weather conditions on NPP response to fertilization was seldom assessed (Oren et al., 2001; Nilsen and Abrahamsen, 2003; Jacobson and Pettersson, 2010), especially over periods sufficiently long to allow functional responses to emerge (Samuelson et al., 2014). Such responses are essential for performing cost-benefit analysis on fertilization, as the benefit is entirely dependent on the response to fertilization (Jacobson and Pettersson, 2010). If the response to fertilizing depends on inter-annual variation in weather, the mean and extremes of which may change with global climate, forest managers may need to employ functional responses together with climate prediction to obtain estimates of future responses, especially in long-rotation systems. Indeed, recent work on adaptive forest

management suggests periodic reassessment of silvicultural treatments in the context of environmental and climatic changes (Spittlehouse and Stewart, 2003; Seppälä et al., 2009; Lindner et al., 2010; Janowiak et al., 2014).

Among the diverse goals of forest management, the primary goal of fertilization is to increase the production of wood fiber. Another can be to increase carbon (C) sequestration in long-lasting woody biomass (stem wood, branches, coarse-roots, and cones). Belowground C flux in forest ecosystems often accounts for a considerable fraction of GPP (Ryan, 1991), and may even exceed NPP (Law et al., 1999). In *Pinus sylvestris* forests, NPP belowground (BNPP) may range widely, between one and two-thirds of NPP (Linder and Axelsson, 1982; Helmisaari et al., 2002; Xiao et al., 2003) decreasing with soil nutrient availability. Yet, generally N-fertilization studies show inconsistent effects on total belowground C flux, ranging from no change in over three-year long experiment in tropical *Eucalyptus saligna* plantations (Giardina et al., 2003), to a decrease in temperate pine stands (Haynes and Gower, 1995; Palmroth et al., 2006). The majority of studies from boreal and temperate forests showed that N-fertilization reduces soil respiration and/or microbial biomass, indicating a reduction of C flux to belowground (Franklin et al., 2003; Lee and Jose, 2003; Olsson et al., 2005; Oishi et al., 2014).

The objectives of this study were to examine the effect of N-fertilization on biomass production of a boreal mature *P. sylvestris* stand and its interaction with inter-annual variation of climate conditions using a combination of destructive harvesting, consecutive standard mensuration measurements, and optical measurements of canopy openness over eight years. The study was conducted in the footprints of eddy-covariance flux measurement towers, meaning control and fertilized plots were not randomly located, representing pseudo-replication. Thus, although the site in which the two towers are located is very uniform, we included stand characteristics as co-variables to account for differences in preexisting conditions, the major concern with pseudo-replicated studies. Our hypotheses were that N-fertilization enhances production by (H1) enhancing light capture (Giardina et al., 2003; Bergh et al., 2005) and (H2) enhancing C investment aboveground at the expense of belowground partitioning (Linder and Axelsson, 1982; Ingestad and Ågren, 1991; Haynes and Gower, 1995; Ericsson et al., 1996; Palmroth et al., 2006). We also expected that (H3) the inter-annual variability of (a) temperature and (b) precipitation interacts with fertilization resulting in variable NPP responses (Linder, 1987; Linder et al., 1987; Tamm et al., 1999; Bergh et al., 2005; Choi et al., 2005).

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