Interactive effects on biomass production between nitrogen and water availabilities in boreal forests

Hyungwoo Lim

Faculty of Forest Science
Department of Forest Ecology and Management
Umeå

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Cover: Interactive effect on annual biomass production between nitrogen addition (N) and precipitation (P).

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Abstract

Biomass production in boreal forests is mainly nitrogen (N) limited, so alleviating this limitation can improve productivity. As the climate warms, N limitation is expected to be reduced, which, in turn, could result in enhanced biomass productivity. However, empirical evidence from long-term studies is scarce. In addition, although water availability may constrain biomass production once N limitation has been partly or fully alleviated, little is known about the effect of the interaction between N and water availabilities on biomass production.

In this research, I first examined the interactive effect on biomass production between N and water availabilities, based on field experiments in a Norway spruce forest and a Scots pine forest, supplementing these results with additional data from a literature survey. Nitrogen additions enhanced biomass production in both types of forest, while water availability only affected production in the pine forests in which N limitation had been partly or fully alleviated. In Scots pine forests, biomass production increased with increasing precipitation as the rate of N addition also increased. These forests are N limited, but the sigmoidal response to N additions indicates that even under moderate N supply, N availability meets their demand if precipitation is near average, and N limitation increases with increasing precipitation.

Second, I examined the effect of soil warming on biomass production in the Norway spruce forest. The treatments comprised fertilization and soil warming (+5°C) at a plot scale of 100 m^2 for 18 years. Increased biomass production in association with soil warming was only observed in the unfertilized plots, suggesting that the enhanced biomass production was mediated by increased N availability. However, the enhancement was ephemeral and, therefore, not of sufficiently long duration to significantly enhance biomass accumulation. Foliar nutrient analyses together with the findings from earlier studies of the same plots, suggest that soil warming shifted N uptake to deeper soil and may increase C stock in the mineral soil.

Synthesizing the above results, I conclude that 1) biomass production of N limited boreal forests is strongly responsive to N additions following a sigmoidal curve, but the magnitude of response may depend on soil water availability, and 2) a warmer climate may not alleviate N limitation and thus will not increase biomass accumulation.

Author's address: Hyungwoo Lim, SLU, Department of Forest Ecology and Management, SE-901 83 Umeå, Sweden, Email: Hyungwoo.Lim@slu.se

Dedication

To my father

In order to seek truth, it is necessary once in the course of our life, to doubt, as far as possible, of all things.
    René Descartes

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I   Lim, H., Oren, R., Palmroth, S., Tor-ngern, P., Mörling, T., Näsholm, T., Lundmark, T., Helmisaari, H., Leppälammi-Kujansuu, J. and Linder, S. (2015). Inter-annual variability of precipitation constrains the production response of boreal *Pinus sylvestris* to nitrogen fertilization. *Forest Ecology and Management*, 348, pp. 31–45.

II   Lim, H., Oren, R., Linder, S., From, F., Nordin, A., Fahlvik, N., Lundmark, T. and Näsholm, T. (2017). Annual climate variation modifies nitrogen induced carbon accumulation of *Pinus sylvestris* forests. *Ecological Applications*, 27(6), pp. 1838–1851.

III Lim, H., Oren, R., Näsholm, T., Strömgren, M., Lundmark, T. and Linder, S. Transient effect of soil warming on boreal forest productivity leads to negligible biomass accumulation (submitted).

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The contribution of Hyungwoo Lim to the papers included in this thesis was as follows:

I   Performed field- and lab work, in addition to data collected from the Svartberget field station. Analyzed data and wrote the manuscript under guidance of Prof. Oren and Prof. Näsholm, and with input from co-authors.

II   Performed field- and lab work, in addition to data collected from the Svartberget field station and modeling by Dr. Fahlvik. Analyzed data and wrote the manuscript under guidance of Prof. Oren and Prof. Näsholm, and with input from co-authors.

III Performed field- and lab work together with staff of the Svartberget field station, in addition to data collected from the field station. Analyzed data and wrote the manuscript under guidance of Prof. Näsholm and Prof. Oren, and with inputs from co-authors.

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1 Introduction

Production of tree biomass functions as an active C sink (Myneni, et al., 1997); this is the outcome of CO_2-utilization by the canopy using captured light (Monteith and Moss, 1977; Linder, 1985; Landsberg and Waring, 1997; Waring, Landsberg and Linder, 2016). Light capture is determined by the amount of incident light during the growing season, leaf area (Waring, 1983; Gower, et al., 1999), and its spatial distribution in the canopy (Stenberg, 1996; Kim, et al., 2011). Biomass production is the product of captured light and the efficiency with which it is used to convert CO_2 into carbohydrates and further into biomass (Binkley, Stape and Ryan, et al., 2004). Increasing the supply of a limiting resource increases the productivity through various mechanisms, such as increased photosynthetic rates and/or improved light capture as a result of increased leaf area (Waring, 1983). Increasing the supply of a limiting resource can also alter C partitioning from below- to aboveground, thereby increasing aboveground production (Linder and Axelsson, 1982; Hynes and Gower, 1995; Maier, et al., 2004; Ryan, et al., 2010). In boreal forests, alleviating nitrogen (N) limitation considerably enhances the biomass production of boreal trees (Tamm, 1991; Bergh, et al., 1999).

When more of the most limiting resource becomes available, trees will grow until another resource becomes deficient, as described by the "law of the minimum" (Liebig, 1840). Indeed, when fertilization has been used to alleviate N limitation, even greater productivity enhancement has been achieved in response to improved water availability (Albaugh, et al., 2004; Axelsson and Axelsson, 1986). Nitrogen addition commonly leads to increasing leaf area but decreasing belowground C allocation relative to aboveground allocation (Linder and Axelsson, 1982; Albaugh, et al., 2004), potentially increasing the demand for water because of greater transpiration (Ewers, et al., 2001). For some tree species, fertilization may also induce drought stress (Ewers, Oren and Sperry, 2000; Betson, et al., 2007), leading to defoliation to avoid excessive water-loss through transpiration (Linder, et al., 1987), and thus

causing reduction in the capacity for capturing light (Bergh, et al., 1999). In a current climate of boreal forests, water availability is not considered to limit biomass production because precipitation generally exceeds evaporation and adequate water is supplied from the snowmelt (Bergh, et al., 1999). In addition, N limitation is so severe that other climate factors are not considered to limit production (Sigurdsson, et al., 2013). Nevertheless, this could change if N limitation is alleviated as a result of increasing N deposition (Solberg, et al., 2009) and greater N mineralization in a warmer climate (Melillo, et al., 2002). Under such circumstances, water availability may constrain biomass production because increased canopy photosynthesis as a result of reduced N limitation may increase water demand (Ewers, et al., 2001). Moreover, N uptake may also be restricted by low soil water availability because root N uptake depends on both diffusive- and mass flow fluxes in the soil solution (Oyewole, et al. 2014). Currently, little is known about the interactive effects between water and N on the biomass production of boreal forests (cf. Betson, et al., 2007).

The large amount of soil organic matter in boreal forests (Dixon, et al., 1993; Schimel, et al., 2001) is considered to result from cold temperatures (Berg, 1986; Coûteaux, Bottner and Berg, 1995), and it is expected that the soils of boreal forests will release a considerable amount of C (Jenkinson, Adams and Wild, 1991; Goulden, et al., 1998; Melillo, et al., 2011; 2017) and mineral N (Melillo, et al., 2002; 2011) under a warmer climate. Increasing soil temperatures would, therefore, logically promote biomass productivity through stimulating N mineralization (Melillo, et al., 1993; Savage, et al., 2013). Indeed, studies involving experimental soil warming have shown 50 – 100% greater biomass productivity relative to reference conditions within a decade (Strömgren and Linder, 2002; Melillo, et al., 2011; Dawes, et al., 2015). Although these studies argued that the positive response was mediated through the stimulation of N mineralization (Melillo, et al., 2011), it is not, in fact, clear whether the enhancement was due to the increased N mineralization or to other factors unrelated to N (e.g., effects on seasonal stomatal conductance and photosynthesis, length of the plant growing season). In addition, a short study period (≤ 10 years) relative to a very long forest management rotation (≥ 100 years) may be unable to confirm whether the effect is transient (cf. Melillo, et al., 2017). The key question is whether such a strong increase in production persists over extended periods or is temporary due to acclimated microbial activity and/or to depletion of the labile pool of organic matter (Kirschbaum, 2004; Bradford, et al., 2008; Melillo, et al., 2017).

This thesis aims to increase our understanding of the mechanisms involved in the responsiveness of boreal forests, mainly focusing on the interactive

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effects on boreal biomass production between N limitation and climate factors. Synthesizing the above aspects, I investigate what other factors limit production when N limitation is relaxed (chapter I, II) and ask if an increase in soil temperature reduces N limitation (chapter III). To evaluate these questions, I analyzed the interactive effect on biomass production between N additions and climate variables (precipitation, temperature, light), and between an addition of optimal nutrients and an increase in soil temperature, hypothesizing that 1) alleviating N limitation enhances biomass production by improved light-utilization and by shifting C partitioning, but 2) that production becomes more susceptible to water availability, and 3) an increase in soil temperature enhances production by reducing N limitation. Soil temperature was increased (+5 °C) by means of heating cables buried under organic layers. Large variations in climate factors allowed investigation of the interactive effects on biomass production.

2 Approaches

The response of tree nutrition to the treatments was examined using foliar N content (Ingestad, 1979; Linder, 1995) and ^{15}N natural abundance (Högberg, 1997) as indicators. The main response variable, biomass production, was estimated based on allometric functions derived from harvested trees, and annual measurements of tree variables and optical openness of canopy from mensuration plots. Moreover, additional data were provided by modeling (4CA, Kim, et al., 2011; the Heureka Forestry Planning System, Wikström, et al., 2011) and a literature survey (Nilsen and Abrahamsen, 2003; Vestgarden, Nilsen and Abrahamsen, 2004; From, et al., 2016). For details of the methods, see Appendix and the methods section in chapter I.

Over an extended period of time, structure-related spatial variations, such as stand density and tree size (Reineke, 1933; Yoda, 1963; Westoby, 1984), and size distribution (Binkley, et al., 2010) also affect stand production (difference in biomass between measurement times) and relative production rate (production per biomass at a given time; Pommerening and Muszta, 2016) or growth efficiency (production per leaf area; Waring, 1983). This can often produce increasingly biased results towards the end of long-term treatment studies as initial tree size and production become progressively decoupled from later production behavior, thus possibly co-varying with treatment effects. Therefore, I evaluated stand dynamics-related spatial variation and incorporated the variation into models when an effect was detected. The basis of modeling in this research was to explain the spatial and temporal variations. In each step of the analyses, extracted information was used to generate statistical models synthesizing all variables (Figure 1).

The Rosinedal experimental site was established with pseudo-replicated plots (1000 m^2, n = 3) within eddy-covariance footprints, resulting in a somewhat different standing biomass and production between control and treatment plots in the pre-treatment period. Hence, foremost, I separated the effect of treatment on biomass production from the potential effects of stand
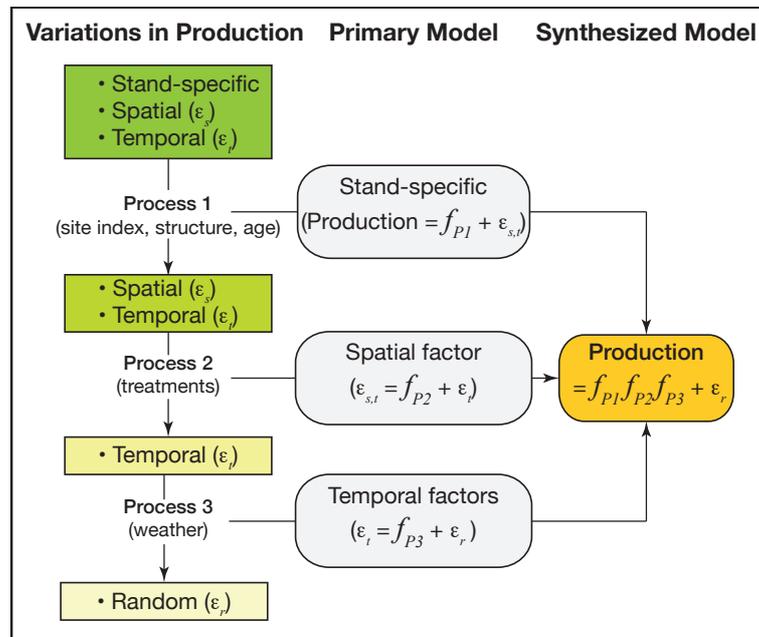
Figure 1. A flow diagram of the data analyses; rectangles indicate variations in biomass production and rounded rectangles indicate models explaining the variations. Three types of variation in biomass production were separated into (1) variation associated with stand-specific factors (f_{P1}; stand density, age, site index, etc.), (2) variation associated with spatial factors (f_{P2}; treatment: N addition, irrigation, or soil warming), and (3) variation associated with temporal factors (f_{P3}; weather: light, temperature, precipitation, VPD, etc.). The ε indicates variation. Redrawn from chapter II.

dynamics (relative growth rate, size distribution, and size-density relation; see Fig. 2 of chapter I). This meant that even if stand structure prior to treatment application was somewhat different, it did not bias the treatment effect.

For the soil warming experiment, two replicated sub-plots of each treatment were established within each of two main treatment plots (irrigated or irrigated + fertilized; a treatment plot scale of 2500 m^2 with net evaluation scale of 1000 m^2) at the Flakaliden experimental site (cf. Linder, 1995; Bergh and Linder, 1999; Strömgren and Linder, 2002). Although the experimental design allowed an investigation of whether soil warming enhances biomass production via increased N availability, the statistical power was weak (n = 2 for the soil warming treatment) and there was no opportunity to test the interaction between fertilization and soil warming (n = 1 for the fertilization treatment). Moreover, pre-treatment values of standing biomass and production differed between plots.

In order to separate the effect of soil warming from factors potentially affecting biomass production, I developed a growth model (involving

normalized relative growth rate) using individual trees in each plot. This allowed me to test the treatment effect with stronger statistical power (n = the number of trees per plot rather than n = 2). To scale up the size of the effect to the stand level, I used individual trees from the main stand (n = 4) as an input variable in the growth model. The computed normalized sum of squares was 0.069 between modeled and observed biomass, and thus the small error allowed assessment of the potential soil warming effect on biomass accumulation. For detailed information on the analyses, see chapter III.

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3 Effects of nitrogen additions and water availability on biomass production

Experiments examining the response of biomass production to nitrogen (N) additions were conducted on a Norway spruce forest within the Flakaliden experiment and on a Scots pine forest within the Rosinedal experiment. At Flakaliden, a combination of irrigation and fertilization had been applied with an optimal level for nutrients (average N addition rate of 6.5 g N m^{-2} y^{-1}, cf. Linder, 1995) since 1987. At Rosinedal, there was no irrigation treatment, and fertilizer was applied at the rate of 10 g N m^{-2} y^{-1} for the first five years, and thereafter 5 g N m^{-2} y^{-1} using Skog-Can fertilizer [NH_4 (13.5%), NO_3 (13.5%), Ca (5%), Mg (2.4%), and B (0.2%); Yara, Sweden]. At the time of the investigation, the Norway spruce forest (55-year-old) had been fertilized for 30 years, and the Scots pine forest (90-year-old) had been fertilized for eight years. The soil type is sandy loamy till at Flakaliden, and fine sand at Rosinedal. The thickness of the organic layer was similar in the two forests, ranging between 2 and 6 cm. An irrigation treatment was used for testing the effect of water availability on growth of the Norway spruce forest, while in the Scots pine forest, annual precipitation during the growing season was used. In the analyses, the biomass production represents stem biomass (stem and bark) for the spruce forest, while for the pine forest it represents woody biomass (stem wood, branches, and coarse-roots).

Nitrogen fertilization increased foliar N content, leaf area index (LAI), and biomass production in both the Norway spruce and Scots pine forests (Figure 2). In the spruce forest, irrigation did not affect the LAI or biomass production of either the control or fertilized plots and hence no interaction between water and N was detected. As LAI responded only to fertilization, biomass production was also only responsive to the fertilization, exhibiting no interaction with irrigation. From the 20th year, the irrigated plot was also fertilized, resulting in similar production to that in the fertilized plot. In the

Scots pine forest, fertilization doubled foliar N content throughout the study period (p < 0.001). While LAI of the control plot was unchanged over time, LAI of the fertilized plot increased gradually. These responses to fertilization were similar to those documented in the "Optimum nutrition experiments" (Tamm, 1991; Tamm, et al., 1999), showing no effect of P or K on biomass production, and thus demonstrating that the production is primarily limited by low soil N availability. I, therefore, considered these stands to be N limited, and the response to fertilization to reflect alleviation of N limitation.

In the Norway spruce forest, fertilization was shown to augment foliar N content, and annual LAI dynamics were similar to annual biomass production. This corroborates the general mechanism of the response to fertilization: fertilization alleviated N limitation, which resulted in increased LAI and possibly photosynthesis rates, leading to enhanced biomass production. Indeed,
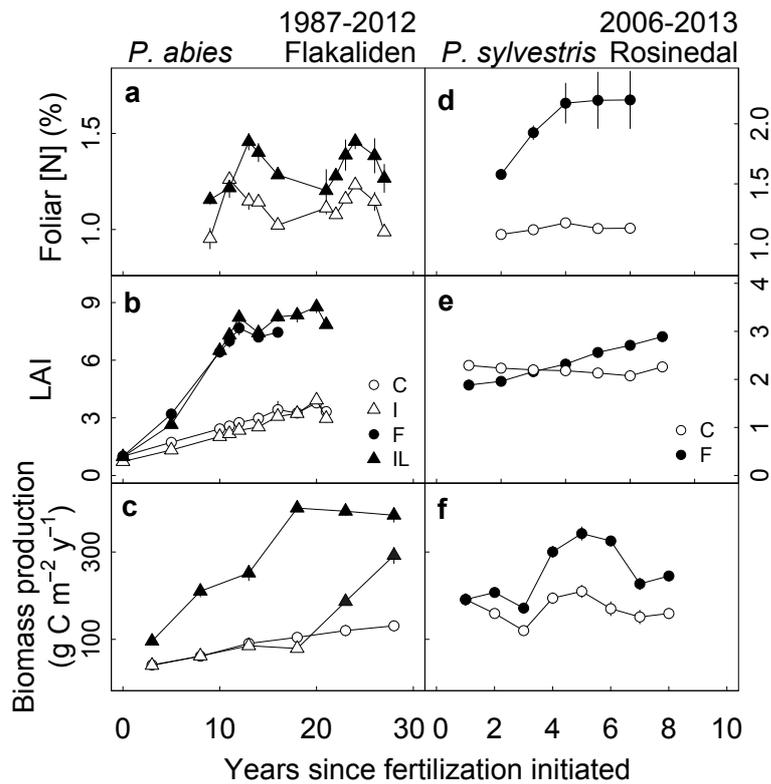

Figure 2. (a, d) Nitrogen content of 1-year-old foliage, (b, e) leaf area index (LAI), and (c, f) biomass production in the Flakaliden Norway spruce forest and in the Rosinedal Scots pine forest. C, I, F, and IL represent control, irrigated, fertilized, and irrigated + fertilized plots, respectively. In panel c, the irrigated plot was fertilized from the 20th year. Note that scales on the x- and y-axes are different between the spruce and the pine forests.

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Indeed, captured photosynthetically active radiation (PAR) explained most of the variation in biomass production in the Norway spruce forest (Figure 3a; R^2 = 0.986, p < 0.001); fertilization doubled light capture and caused a more than six-fold increase in light-use efficiency (0.64 g C MJ^{-1} for fertilized with irrigation and 0.10 g C MJ^{-1} for both irrigation and control plots). As biomass production of the Norway spruce forest was defined on the basis of stem biomass, the increased light-use efficiency indicates a shift in biomass allocation from below- to aboveground. Thus, the mechanisms behind the fertilization-enhanced biomass production included an increase in captured light and a relative shift in biomass allocation to aboveground.
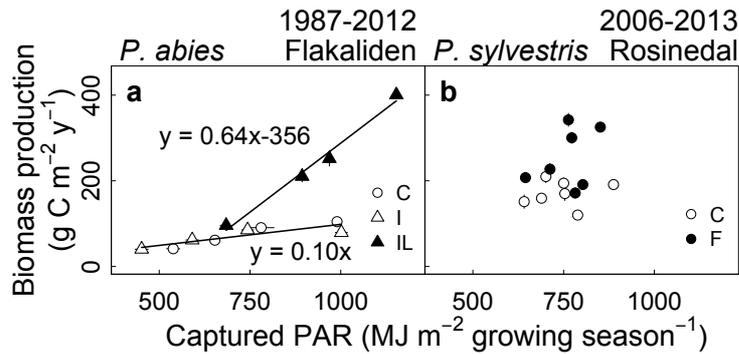

Figure 3. Biomass production in relation to captured photosynthetically active radiation (PAR) (a) in the Flakaliden Norway spruce forest and (b) in the Rosinedal Scots pine forest.

In the Scots pine forest, fertilization also increased foliar N content, LAI, and biomass production. The LAI of the control plot did not change during the study period, while a 53% increase in LAI was recorded in the fertilized plot (2.29 in the first year, 2.26 in the seventh year in the control; 1.88 in the first year, 2.89 in the seventh year in the fertilized plot). However, captured PAR by this leaf area was unrelated to the production of woody biomass (Figure 3b; minimum p = 0.136 for fertilized). This led me to examine further the annual variation in biomass production based on differences in resource availability related to a climate variation, specifically temperature and precipitation, during the growing season.
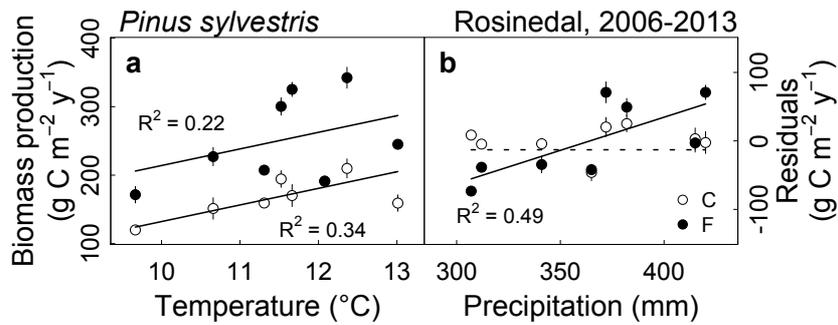
Figure 4. Relationships between biomass production and climate variables in the control and fertilized plots in the Rosinedal Scots pine forest. In (a) the relationship is with growing season mean daily temperature; in (b) residuals from the linear regression with temperature are related to growing season precipitation. Redrawn from chapter I.

Production of biomass was related to air temperature during the growing season in both treatments, with a similar sensitivity (24.3 g C m^{-2} per 1 °C for both treatments, p = 0.419 for the interaction between the temperature and fertilization), with an offset of 81.3 g C m^{-2} y^{-1}. Large residuals remained from the relationship (Figure 4a), and for the fertilized plots (but not for the control plots) these residuals were largely explained by the precipitation (p = 0.800 for the control and < 0.001 for the fertilized plot; Figure 4b). No interaction was observed between temperature and precipitation during the growing season (p = 0.964).

Thus, although biomass production in both Norway spruce and Scots pine forests was highly responsive to fertilization, the forests differed in their response to variation in water availability. Water availability only explained variation in biomass production of the Scots pine forest where the N limitation had been alleviated. Notably, the responsiveness to N was lost when precipitation was < ~300 mm (Figure 4b). It is thus plausible that N limited biomass production in interaction with water availabilities in the Scots pine forest, whereas in the Norway spruce forest only N limited biomass production.

Such different responsiveness to water between the Norway spruce and the Scots pine forests could be attributed to differences in the site-specific soil water holding capacities and species-specific water-use efficiency (Ewers, et al., 2001). A higher soil water holding capacity may have alleviated water limitation of the Norway spruce trees, suggesting that the temporal variation in biomass production was imposed by incident light only (Figure 3a). Indeed, a Norway spruce forest in southern Sweden (the Asa experimental forest), where the soil texture is fine sand and potential evaporation is greater than at Flakaliden, northern Sweden (Bergh, Linder and Bergström, 2005), showed a

Table 1. *Captured light during the growing season (APAR), carbon partitioning (g C m^{-2} y^{-1}), and relative component net primary production (NPP) to total NPP in the control and the fertilized plots (8.8 g N m^{-2} y^{-1}) in the seventh year of the treatment (2012) in the Scots pine stand at the Rosinedal experimental site. The p-values relate to the difference in NPP between control and fertilized plots based on a two-sample t-test (n = 3).*

Components	Control	% NPP	Fertilized	% NPP	p-value
APAR (MJ m^{-2})	642 (83)		713 (121)		0.489
ANPP (g C m^{-2} y^{-1})	262 (29)	0.50	340 (23)	0.67	**0.024**
Stem	114 (13)	0.22	156 (10)	0.31	**0.012**
Branch	39 (25)	0.08	47 (20)	0.09	0.691
Foliage	99 (22)	0.19	118 (39)	0.23	0.195
Cone	5.2 (0.02)	0.01	9.0 (0.08)	0.02	**< 0.001**
Miscellaneous	4.9 (0.02)	0.01	9.4 (0.08)	0.02	0.186
BNPP (g C m^{-2} y^{-1})	257 (9)	0.50	165 (8)	0.33	**0.006**
NPP$_{CR}$	21 (3)	0.04	34 (2)	0.07	**0.004**
NPP$_{FR}$	138 (6)	0.27	92 (7)	0.18	**0.005**
[a]NPP$_{EM}$	98 (5)	0.19	40 (3)	0.08	**0.003**
NPP (g C m^{-2} y^{-1})	519 (30)	1.00	505 (24)	1.00	0.603

ANPP: aboveground NPP; BNPP: belowground NPP; NPP$_{CR}$: NPP of coarse-roots; NPP$_{FR}$: NPP of fine-roots; NPP$_{EM}$: NPP of ectomycorrhizae.

[a]NPP$_{EM}$ was estimated by NPP$_{FR}$ multiplying the ratio of ectomycorrhiza-respiration to root-respiration measured at the experimental site (0.71 in the control and 0.43 in the fertilized plot; Hasselquist, Högberg and Metcalfe, 2012).

considerable reduction in both LAI and production in fertilized plots during dry years, while no reduction in those variables was observed in the fertilized plots with irrigation (Bergh, et al., 1999). Such differences may, therefore, explain why the Norway spruce trees appear to be more responsive to the amount of captured light and Scots pine to water availability in the current study. However, because the most limiting resource, N, affects production until other resources become limiting, the Flakaliden spruce forest may also encounter water limitation in the future due to increased LAI and thus water losses via transpiration (Bergh, et al., 2005; Ewers, et al., 2001).

Based on the relationship between captured PAR and stem biomass production (Figure 3a), alleviating N limitation in the Norway spruce forest was shown to increase stem biomass production indicated by both increasing gross primary production and shifting C partitioning. In the Scots pine forest, however, gross primary production explained only a third of increased biomass production in the fertilized plot based on 11% higher captured PAR (Table 1) and had no effect on leaf area-based net photosynthetic rates (Tarvainen, et al. 2016), suggesting that other mechanisms were also responsible for the growth response. Indeed, comparing biomass production of each compartment

between control and fertilized plots, aboveground C partitioning increased at the expense of belowground, indicating that a shift in C partitioning was mainly involved in the enhancement of aboveground biomass production. Furthermore, the high sensitivity to water availability suggests that the shift in biomass allocation may only happen when supplying both N and water.

The difference in the responsible mechanism could be attributed to the different stage of stand development in the two forests. The Norway spruce stand was at an earlier stage of development at which time the canopy is expanding, thus leading to enhancement in the gross primary production potential (Landsberg and Waring, 1997). On the other hand, the canopy of the Scots pine forest was closed, thus leading to a small change in gross primary production potential.

To extend the scope of inference from the case study in the Scots pine forest, I further assessed the interactive effect between rates of N addition and precipitation on biomass production of other Scots pine forests on sandy soils. Additional data were obtained from a plot with a low N addition rate (2 g N m^{-2} y^{-1}) at the Rosinedal experimental forest, and a 160-year-old Scots pine forest at the Åheden experimental forest with five levels of N addition (0, 3, 6, 12.5, and 5 g N m^{-2} y^{-1}; cf. Gundale, Deluca and Nordin, 2011; From, et al., 2016) for seven years, and also from published data from a 30-year-old pine forest in Åmli, Norway with three N addition levels (0, 3, and 9 g N m^{-2} y^{-1}) for eight years (Nilsen and Abrahamsen, 2003). In order to evaluate the sensitivity of biomass production to precipitation along a gradient of N additions, I had to account for variation unrelated to temporal variation; the native site productivity as a function of age and the native site fertility, and responsiveness of biomass production to N additions (Figure 5).

First, native site productivity was compared among stands using age, site index, and annual production of control plots in each stand (Figure 5a). Biomass production under native conditions was similar between Åmli and Rosinedal; each of the two stands was positioned before or after peak productivity, but production was greater than that of the much older stand, Åheden. Moreover, the three stands were positioned as projected based on the generic age-related dynamics. Therefore, the two higher productivity stands were pooled into a single population, considered as an example of moderately high productivity stands, and the lower productivity stand was considered as an example of moderately low productivity stands, with the reduction probably caused by advanced age.

Next, I assessed the response of biomass production to N additions for each of the stands. Biomass production increased along N addition gradients following a sigmoidal fit for both stands, but was displaced downwards for the
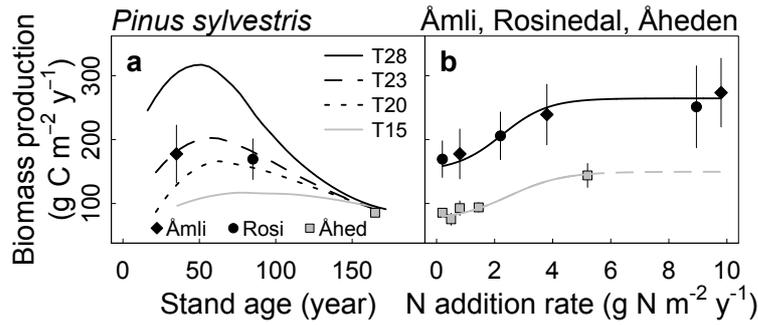
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Figure 5. (a) Biomass production in relation to age for different site fertilities. T indicates *Pinus sylvestris*, and the subsequent numbers indicate dominant height in meters. To decouple stand-specific variation among the three stands, age-related production was generated for site indices of T20 and 23, and representing low (T15) and high (T28) site fertilities, using the Heureka Forestry Decision Support System (Wikström, et al., 2011, Fahlvik, Elfving and Wikström, 2014). (b) Biomass production along a gradient of N additions for each stand productivity. The solid line is for a pooled population of Åmli and Rosinedal (moderately high productivity), the grey line is for Åheden (moderately low productivity), and the dotted grey line is an extrapolation for the low productivity stand.

lower productivity stand, with an offset of ~100 g C m^{-2} y^{-1} (Figure 5b); the response for each of the higher productivity stands was not different from that for their pooled data (p = 0.501). Irrespective of the baseline productivity, extra biomass production in response to N addition started from < 2 g N m^{-2} y^{-1} and was saturated at ~5 g N m^{-2} y^{-1}. Large variations remained from the response curves, suggesting that variability unrelated to N additions may have caused the variation in biomass production. Based on the magnitude of responsiveness among N addition rates using analysis of variance with Tukey's post-hoc test, the N additions were separated into three populations, control (only background N deposition), low (0.3 – 3 g N m^{-2} y^{-1}), and high N additions (over 5 g N m^{-2} y^{-1}) (minimum p = 0.187 for the difference within a population, p < 0.001 for the difference among populations).

After removing the spatial variations from native productivity and N additions (Figure 5), annual variation in temperature and precipitation explained 91.7% of the remaining variation in the higher productivity stands (Figure 6) and 61.7% in the lower productivity stand (Figure 7). As observed
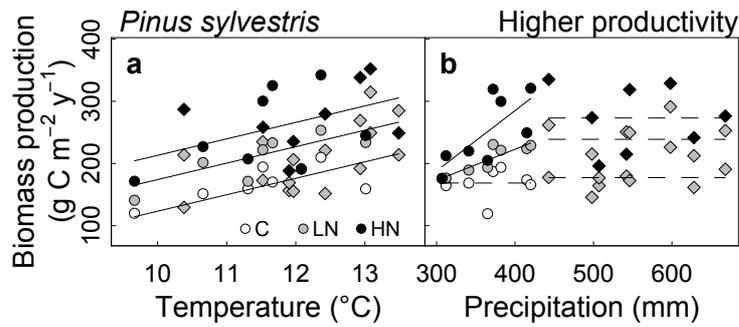
Figure 6. (a) Biomass production in response to temperature during the growing season, and (b) predicted biomass production using the mean temperature of the last 30-year-record related to precipitation during the growing season, in the higher productivity stands, Åmli and Rosinedal. C, LN, and HN represent the control, low rates of N addition (2 and 3 g N m^{-2} y^{-1}), and high rates of N addition (8.8 and 9 g N m^{-2} y^{-1}), respectively. For detailed information on statistical analyses and results, see chapter II.
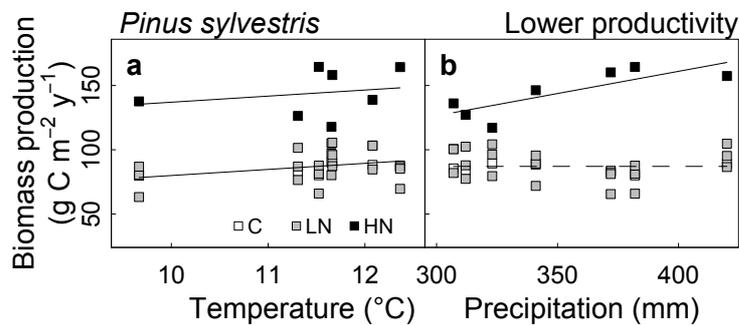

Figure 7. (a) Biomass production in response to temperature during the growing season, and (b) predicted biomass production using the mean temperature of the last 30-year-record related to precipitation during the growing season, in the lower productivity stand, Åheden. C, LN, and HN represent the control, low rates of N addition (0.3, 0.6, and 1.25 g N m^{-2} y^{-1}), and high rates of N addition (5 g N m^{-2} y^{-1}), respectively. For detailed information on statistical analyses and results, see chapter II.

in the Rosinedal case study, biomass production was related to temperature, with the same sensitivity among N additions (Figure 6a, 7a), whereas the sensitivity to precipitation was increased with increasing N addition rates, but only up to a precipitation rate of ~400 mm (Figure 6b, 7b), suggesting that N limitation increases with increasing precipitation. The relative biomass response to N additions decreased with increasing air temperature. This may reflect decreased N-induced water stress in cooler years and increased N-

induced water stress in warmer years, perhaps due to the effect of temperature variation on vapor pressure deficit (Katul, et al. 2009).

In Scots pine forests on sandy soils, a significant effect of water availability on production was observed in plots where N limitation was fully or partially alleviated, whereas water availability had no effect on biomass production in the N limited plots. The question is, then, what is the mechanism responsible for this interaction? The findings can be interpreted as altered biomass allocation being the primary cause of the increased aboveground biomass increase. If biomass allocation shifts in relation to the rate of N addition following the sigmoidal response curve (Figure 5b), plots with higher N addition could be more sensitive to water availability because a greater water demand from increased leaf area may not match the capacity of roots to take up water, due to reduced root biomass (Figure 6b, 7b). This could also be interpreted as water limitation restricting canopy photosynthesis in N fertilized plots, and/or restricting root uptake of added N. From the view of the restricted canopy photosynthesis, fertilization would increase foliar N contents and LAI, leading to enhancement of canopy photosynthesis and transpiration. An earlier study from Rosinedal suggested that long-term mean canopy-scale photosynthesis rates had increased due to fertilization-induced increased canopy leaf area (Tarvainen, et al., 2016). It, however, explained only up to a third of the increased aboveground biomass. In addition, increased LAI causes an increase in self-shading (a 27.8 % greater LAI resulted in only a 11.1% greater captured light in year 7, Table 1), thereby restricting the magnitude of enhanced photosynthesis and transpiration (Tor-ngern, et al., 2015). Another explanation may be a restriction of N uptake imposed by water limitation. Models of plant N acquisition suggest that movement of N from bulk soil to roots is the limiting process for plant N gain (Tinker and Nye, 2000). Notably, N addition was applied as mineral N with a significant proportion of nitrate, one of the most mobile N forms, whereas in native soils in these forests, N is mostly present in organic forms, which are much less mobile (Oyewole, et al., 2016; 2017). Thus, adequate water supply may greatly promote uptake of the added mineral N. This explanation is also supported by a positive relationship between foliar N content and precipitation in the fertilized plot at Rosinedal (R^2 = 0.36, p = 0.004, data not shown). Based only on the current field observations without a direct test on the effect of N mobility, it is not possible to distinguish the processes between water demand of leaves and N uptake by roots. For a better understanding of N acquisition and tree functioning, therefore, a study on biomass growth and allocation with respect to N mobility should be considered (cf. Tarvainen and Näsholm, 2017).

4 Effects of soil warming on biomass production

Biomass production in boreal forests is very responsive to N additions, as discussed above. Hence, an increase in soil temperature would logically lead to enhanced biomass production due to an increase in the rate of soil N turnover by stimulating decomposition of soil organic matter. Experimental soil warming was applied for 18 years at a plot-scale of 100 m^2 to test the hypotheses that 1) soil warming enhances biomass production, 2) the enhancement persists for a long period, and 3) the effect is mediated through N availability. Experimental plots were established as sub-plots within a fertilized (IL; fertilized + irrigated) and an unfertilized (I; irrigated) plot at the Flakaliden site, thus allowing the evaluation of the effect of soil warming in relation to N availability. If biomass production of the IL plots increases in response to soil warming, then the effect of soil warming should be unrelated to N availability. The set-up further allowed eliminating the potential bias resulting from an interaction between soil temperature and moisture. In addition to annual biomass production and its accumulation, foliar N content and ^{15}N natural abundance were also examined for tree N uptake and its sources.

Throughout the 18 years of the soil warming treatment, foliar N content decreased in response to soil warming in both fertilization treatments, interacting with observed years in the unfertilized treatment (Table 2. and chapter III). Foliar $\delta^{15}N$ increased in response to soil warming in both treatments ($p < 0.001$). At the end of the experiment, LAI had increased with fertilization (Figure 2b), but was not affected by soil warming (minimum p = 0.279 for fertilized plots). Increased soil N turnover should, theoretically, lead to a transient upward shift in $\delta^{15}N$ in needles (Högberg, et al., 2011) and such a shift was indeed noted. However, the difference in needle $\delta^{15}N$ was not transient but remained throughout the study period (Table 2). As soil warming doubled root biomass in the deeper soil (Leppälammi-Kujansuu, et al., 2013), I

Table 2. Effect of soil warming on foliar N content, $\delta^{15}N$, and leaf area index (LAI) in unfertilized (I) and fertilized plots (IL). Foliar N content and $\delta^{15}N$ were tested using a mixed model, and LAI in 2012 was tested using a two-sample t-test. For detailed information on statistical analyses and results, see the chapter III.

Variables	Fertilization	Effect	DF	p-value
Foliar N content	I	Soil warming	1	0.827
		Year	9	**<0.001**
		Soil warming·Year	10	**0.033**
	IL	Soil warming	1	**0.003**
		Year	9	**<0.001**
		Soil warming·Year	10	0.603
Foliar $\delta^{15}N$	I	Soil warming	1	**<0.001**
		Year	6	0.236
		Soil warming·Year	5	0.351
	IL	Soil warming	1	**<0.001**
		Year	6	**<0.001**
		Soil warming·Year	6	0.395
LAI in 2012	I	Soil warming	1.45	0.356
	IL	Soil warming	1.01	0.279

speculate that this continued shift occurred because trees exposed to soil warming depended to a larger extent on N uptake from deeper soil, more ^{15}N-enriched than the upper (organic) soil (Högberg, et al., 2011; Nadelhoffer and Fry, 1988). It is, therefore, conceivable that the warming-induced higher foliar $\delta^{15}N$ under native soil conditions was due to stimulated N mineralization at the early stage of the experiment, and following depletion of the labile N pool in the shallow horizon, roots proliferated and acquired ^{15}N enriched N from deeper in the soil (Leppälammi-Kujansuu, et al., 2013). Thus, the forest behaved as if it were N limited, constructing roots rather than increasing leaf area and aboveground biomass production, in contrast to the expected response to N addition.

In the unfertilized plots, soil warming increased biomass production by up to 44 g C m^{-2} y^{-1} in the fifth year, and decreased thereafter, whereas in the fertilized plots, soil warming did not affect biomass production (Figure 8a). The absence of any effect of soil warming in the fertilized plots corroborates the notion that the effect of soil warming was mediated by increased N availability. In the unfertilized plots, however, the enhancement of biomass production by soil warming was short-lived, and thus not sufficiently long to build up a significant amount of extra biomass (Figure 8b). Even when considering the very long rotation time of these forests and even longer forest succession periods, the current observation does not support the idea of

compensatory enhanced biomass production replacing the soil C loss resulting from soil warming.
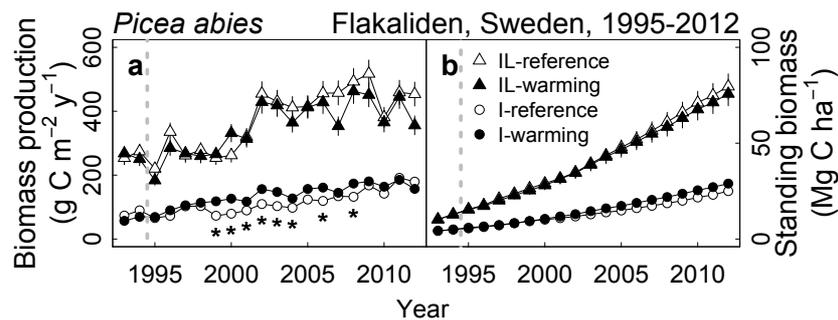

Figure 8. (a) Biomass production and (b) standing biomass in response to soil warming in unfertilized (I) and fertilized (IL) plots. The two quantities were estimated using initial aboveground wood biomass from the main plots (n = 4 plots of 1000 m^2) as input to the size-relative production model (Eq. 2 in chapter III). The dashed vertical line indicates the initiation of soil warming (April 1995), and error bars are standard errors (n = 4). Asterisks indicate difference of biomass production between reference and soil warming plots (two sample t-test, $p < 0.05$).

According to the above section, increased N availability led to significantly higher biomass production, accompanied by increased LAI and foliar N content. However, it is surprising to note that soil warming was not associated with an increase in any of these variables, thus challenging the idea that soil warming increased N availability. If it happened at all, however, the effect was ephemeral, manifesting as a short-lived extra production associated with soil warming. Therefore, the transient increase in tree growth with soil warming was conceivably driven by short-lived enhancement of N availability.

Synthesizing earlier results reported from the same plots, I analyzed the likely effect of soil warming on soil C pools and fluxes. Fertilization greatly increased the C and N contents of the organic layer of these plots, consistent with the increase in needle litterfall (Fröberg, et al. 2013), whereas soil warming failed to produce an observable effect on any of these variables. However, soil warming increased soil CO_2 efflux (Strömgren, 2001), heterotrophic respiration (Eliasson, et al. 2005), and the biomass, production, and mortality of fine roots in unfertilized plots (Majdi and Öhrvik, 2004; Leppälammi-Kujansuu, et al. 2013; 2014). In addition, lower foliar N content, no change in LAI (Table 2), and only a minor effect of earlier soil thaw on photosynthetic recovery in the spring (Bergh and Linder, 1999), combine to suggest a small reduction or no effect on photosynthesis by soil warming, hence not supporting the suggestion of increased N availability. Furthermore,

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an appreciably higher decomposition rate in warming plots should, over time, have resulted in a smaller steady-state pool of C in the O horizons and potentially in the mineral soil of these plots. Based on the response of biomass and decomposition to soil warming, I conclude that a warmer climate may not alleviate N limitation, perhaps due to thermal acclimatization of soil microbes to higher temperatures and/or depletion of labile soil organic matter (Kirschbaum, 2004; Bradford, et al. 2008; Melillo, et al. 2017) and, thus, that soil warming will not result in either enhanced biomass production or increased soil C loss.

In the context that low N availability hampers biomass production in boreal forests, this study focused on the effect of increased soil temperature, which may alleviate N limitation by increasing soil N turnover rate. Although the findings from a very long-term treatment period indicate to us the most probable response of C storage in woody biomass to N availability induced by an increase in soil temperature, it can mislead us in our understanding of a systematic climate change consequence in relation to atmospheric $[CO_2]$ – air temperature – soil temperature relationships, unless all interactions are considered (Hyvönen, et al., 2007). Because a warmer climate is accompanied by elevated atmospheric $[CO_2]$, the interactions among the factors are more complex. For example, a warmer climate may not improve N availability, but it could affect photosynthesis in response to temperature and vapor pressure deficit. In addition, the positive effect of elevated CO_2 has been attributed to increased water-use efficiency (Keenan, et al., 2013), but it may or may not be compensated for by the higher vapor pressure deficit caused by increased temperature (Katul, et al., 2009), or increased self-shading as a result of increased leaf area (Tor-ngern, et al., 2015). Thus, the findings of this study should be applied in the context of the above limitations.

5   Synthesis of the chapters

The chapters that form the foundation of this thesis aim at increasing our understanding of how biomass production responds to relaxation of N limitation in the boreal forest ecosystem, where N availability is generally limiting. The N limitation is caused by a slow soil N turnover rate at cold temperatures and/or by a slow N delivery in the soil solution. Nevertheless, adding N can alter the quantity and quality of N in the system, reducing N limitation. On the other hand, increasing soil temperature may stimulate soil N turnover, thus leading to increased soil N availability. The chapters in this thesis focus on these two manipulations that potentially lead to alleviation of N limitation, thereby assessing how biomass production will respond to the altered N availabilities.

The first and second chapters describe experiments that were conducted in a *Pinus sylvestris* forest subject to the footprints of eddy-covariance flux measurement towers under a reference treatment (no N addition) and two rates of N application (2 and 8.8 g N m^{-2} y^{-1}), mimicking N deposition and fertilization. The area where the three towers were located was uniform, and treatment plots were pseudo-replicated (1000 m^2, n = 3) due to the difficulty in establishing replicates for eddy-covariance flux measurements. Hence, relative stand density from the size-density baseline was used as a covariate and an initial condition among the three stands was examined, in order to facilitate evaluations of the intended spatial and temporal variations.

The first chapter focuses on both reference and high N addition (8.8 g N m^{-2} y^{-1}) plots, comparing production in response to precipitation and temperature variability. The high N addition resulted in great sensitivity to drought, nullifying the effect of N addition on production in drought years, but in wet years the effect was double that under the reference conditions. Further, estimating growth of each biomass compartment demonstrated that shifting C partitioning from below- to aboveground was mainly responsible for the enhanced biomass production caused by the N addition.

Some of the questions raised in the first chapter are addressed in the second chapter; namely, what is the rate of N addition that leads to a significant increase in production and what is the rate that leads to a saturated response? Depending on the conditions under which N limitation is partly or fully alleviated, does the sensitivity to climatic and edaphic factors change? In order to answer these questions, the data were supplemented with results from the low N addition stand (2 g N m^{-2} y^{-1}), another forest exposed to six levels of N addition rate for seven years, and data from a published paper with three N addition levels applied for eight years. Due to the dissimilar site properties among the three forests (site fertility, age, and thus productivity), I used site indices and age as covariates in the Heureka Forestry Planning System, dividing the sites into two productivity classes (moderately high and moderately low stands), facilitating further analyses. Results from this chapter showed that the response of production to N additions followed a sigmoidal curve, saturating at $4 - 5$ g N m^{-2} y^{-1} and that the response efficiency (produced C per added N) was maximized at ~3 g N m^{-2} y^{-1}, regardless of site productivity. Further, the response of biomass production to precipitation increased with increasing rate of N addition, while the response to temperature was similar among the different N rates. These forests are N limited but the sigmoidal response to N indicates that even under moderate N supply, the N availability meets its demand if precipitation is near average, and N limitation increases with increasing precipitation.

Besides external N additions, a warmer climate could increase soil N turnover rate, thus leading to enhanced biomass production. The research described in the third chapter was conducted in sub-plots within the Flakaliden experimental forest, exposed to soil warming for 18 years in nutrient-optimized and native fertility plots. The aim was to test the idea that an increase in decomposition of soil organic matter resulting from soil warming augments N availability, leading to greater long-term C storage in woody biomass, and thus compensating for C loss from the decomposition. Assembling published results from the same plots, the chapter provides rough estimates of how decomposition was affected by soil warming. Based on the long-term effects of soil warming on C storage, together with the decomposition estimates, as well as foliar nutrient responses, this study concluded that the effect of soil warming on an enhancement in tree C storage is mediated by N availability, but is short-lived. This does not support the idea that soil warming causes a significant biomass accumulation. However, soil warming could lead to an increase in C stock in the mineral soil.

Synthesizing the results from all chapters, I suggest three conclusions. First, biomass production of N limited boreal forests is strongly responsive to N

additions, but the response may only occur when and where precipitation is not limiting. In the study, vapor pressure deficit was not responsible for the annual variation in biomass production, and thus soil water availability may represent the factor that interacts with N availability. This suggests that interactions between soil water status and added N may affect N availability.

Second, in the mature Scots pine forest at Rosinedal, where the canopy was closed, a shift in C partitioning was mainly responsible for N-induced increased aboveground biomass production. Although the method used to estimate belowground C partitioning could be biased, due to the assumption of the same carbon-use efficiency between roots and mycorrhizal fungi, provided that the enhanced aboveground biomass entirely resulted from increased gross primary production, the required LAI in the fertilized plot would have been unrealistically greater than that in the control (thus, LAI of 5.3 in the fertilized *vs.* 2.3). Based on the first and the second conclusions, I further speculate that N addition altered quantity and composition of N, and biomass allocation rather than total production. Therefore, in the forests, where stand development continued, a shift in allocation is an important factor in response to increased N availability caused by interaction between N forms and water status in the soil.

Finally, a warmer climate may not alleviate N limitation perhaps due to a change in the quality of organic matter and composition of microbial communities, thus not leading to increased biomass accumulation in boreal stands. In addition, synthesizing findings from earlier studies relating to the same experiment, the study suggests that soil warming may increase C stock in the mineral soil due to greater biomass, production, and turnover of fine roots in that layer combined with reduced extra soil respiration. Although no data are presented supporting the suggestion that irrigation removed any effect of soil drying, or that there was any interaction between soil temperature and water content, a drier soil may still not have favored soil N turnover.

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