

# Nutrient Relations in Coniferous Forests

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### Abstract

The environment controls physiological processes in plants and thus their growth. The question how forests will respond to global environmental changes is addressed with different approaches and using two coniferous tree species: Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.).

I have used the relationship (nitrogen productivity) between a plant's growth rate and the amount of nitrogen in the plant to analyse the growth response to temperature. Data on needle dry matter, production, and nitrogen content in needles from a wide range of climatic conditions were collected and needle nitrogen productivities were calculated. The result is that the nitrogen productivity (net carbon gain of a canopy) of conifers is not sensitive to temperature. Growth responses to temperature in conifers are therefore mediated by changes in nitrogen availability.

I have used three Swedish forest experiments to study the long-term fate of N addition. The fertilisation increased tree biomass, more strongly for spruce than pine. Once fertilisation had ceased, the growth rates in all treatments in pine stands at Lisselbo and spruce stands at Stråsan converged towards similar levels, in contrast to pine stands at Jädraås where the production of stem volume remained higher than in fertilised plots. Nitrogen budgets established 12 years (pine) and 7 years (spruce) after the last N addition show that the increases in N stocks in the pine stands were mainly in the soil. In contrast, in the spruce ecosystem trees accumulated most of the added N and the increase in the soil was restricted to the humus layer. In the pine ecosystem, large losses of added N (between 254 and 738 kg ha<sup>-1</sup> out of 1040 kg ha<sup>-1</sup> added as fertilizer) occurred, whereas in the spruce ecosystem more N was recovered than could be accounted for by inputs (between 250 and 591 kg ha<sup>-1</sup>).

I have used humus and needle nutrients and site characteristic from 37 pine and 50 spruce stands from all over Sweden to analyze forest nutrient relations. Biologically controlled nutrients (C, N, P, S) are less variable and more correlated, but the biological control is not limited to only the covalently bound elements. Stoichiometric relations are not entirely rigid but are more constrained in needles than in humus. The use of nitrogen as a basis in stoichiometric relations may give stronger relations than the use of carbon.

*Keywords:* tree growth, environmental change, soil nitrogen, nitrogen productivity, conifers, nitrogen budget, long-term fertilisation, stoichiometry, humus, needles.

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## Dedication

*“Where the tree of knowledge stands is always Paradise”: thus speak the oldest and youngest serpenters.*

Friedrich Nietzsche

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## List of Publications

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

- I Ladanai, S. and Ågren, G.I. 2004. Temperature sensitivity of nitrogen productivity for Scots pine and Norway spruce. *Trees - Structure and Functions* 18, 312-319.
- II Ladanai, S., Ågren, G.I., Hyvönen, R. and Lundkvist, H. 2007. Nitrogen budgets for Scots pine and Norway spruce ecosystems 12 and 7 years after ending of long-term fertilization. *Forest Ecology and Management* 238, 130-140.
- III Hyvönen, R., Ladanai, S., Andersson, B., Persson, T., Linder, S. and Ågren, G. 2008. Is site productivity permanently changed by fertilization? (Manuscript).
- IV Ladanai, S., Ågren, G.I. and Olsson, B.A. 2008. Relationships between tree nutrition, soil properties and site condition in *Picea abies* and *Pinus sylvestris* forests in Sweden (Manuskript).

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# 1 Introduction

Mankind could not live without granting as true the fictions of logic, without measuring reality against the purely invented world of the unconditional and self-identical, without a continual falsification of the world by means of numbers (Nietzsche, 1886).

## 1.1 Background

Forests cover nearly 30 % (3,500 Mha) of the world's land area (excluding Greenland and Antarctica) and provide many goods and services that society depends upon, among them serving as an important sink of carbon dioxide. Environmental change, which is expected to accelerate during the next decades (e.g., IPCC, 2001a,b,c; Steffen et al., 2001), will have a large influence on forests, but the consequences of this change for forestry are still unresolved (e. g., Asner et al., 2001). Forestry is a well established branch of business, particularly in Sweden, where forests are the principal natural resources and sixty percent of the territory (about 23 million ha) is covered by forests (SVO, 2007). For the successful development of forest economy one must understand by "forest" not only the trees but the whole of their environment. A major challenge for sustaining or recovering forest service functions is to provide a valuable yield while being kind to the environment. In Sweden, all forests, according to the Forestry Act, should be managed with environmental consideration (SVO, 2007) Insights into the relationships between environmental conditions and patterns of changes in forest processes are essential for understanding the consequences of global change on forests. A key task in forest ecology is to investigate the changes in forests resulting from environmental changes.

Sustainable forest management, becoming a dominant concept for forestry worldwide, is today no longer related only to timber production, but embraces functions of the entire ecosystem (e. g., Lämås & Eriksson, 2003) and there is a rapidly growing demand for measurements and monitoring of pattern and processes at the ecosystem level in forests. But what is an ecosystem (a similar concept, biogeocoenosis, was coined by Sukachev in 1959 (Sukachev & Dylis, 1964)? Figure 1 visualize a typical terrestrial ecosystem (forest) made up of biotic factors (plants, animals, and microorganisms) and abiotic factors (air, water, rocks), i.e., an integrated system of living organisms and inorganic, non-living, environment. Like all systems ecosystems are a combination of interacting, interrelated parts that form a unitary whole or functional unit which can be made the object of scientific studies.

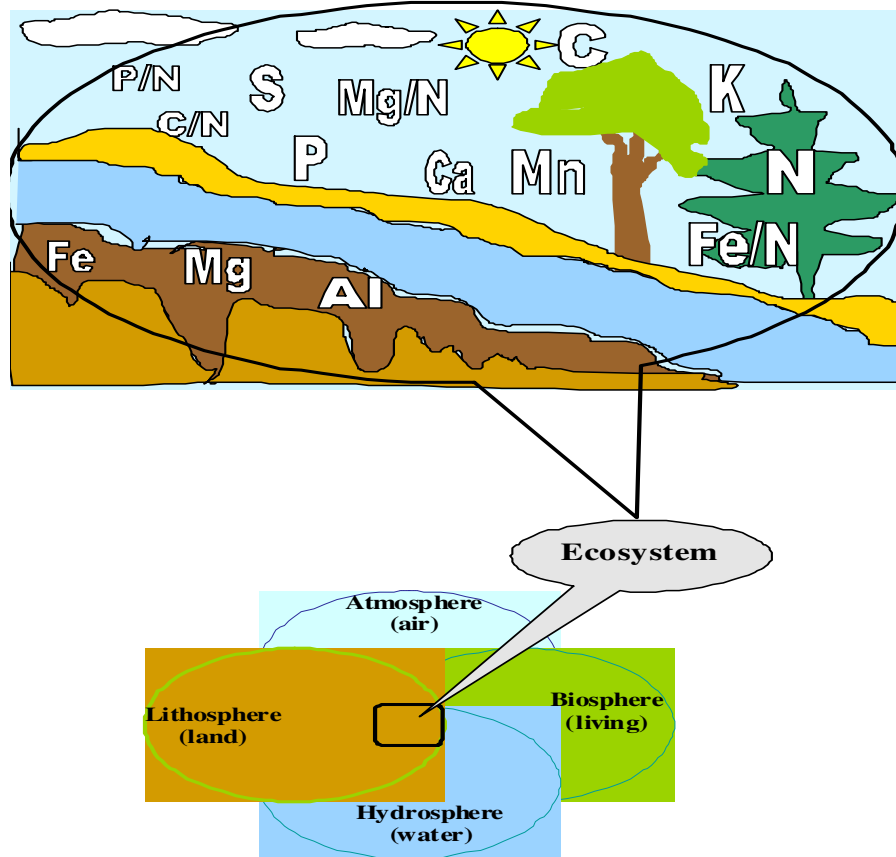


Figure 1. Visualization of an ecosystem consisting of atmosphere (air), hydrosphere (water), lithosphere (land) and biosphere (living material).



Cycling of nutrients is one of the major aspects of the interrelationship between plants and the soil, the components of an ecosystem that most clearly define ecosystems limits and express ecosystems nature (Rodin & Basilevich, 1967). These components are not separate entities but rather a unified system constantly in association with each other. An ecosystem perspective is fundamental in predicting the response of forest to environmental conditions (e. g., Loreau, 1998, 2000).

However, substantial uncertainty still exists about many aspects of forest ecosystems. In natural ecosystems the multiple dimensions of environmental variables, interactions among the variables, their temporal and spatial variability impose uncertainty in examining relationships between productivity and environment (Monserud & Rehfeldt, 1990; Monserud et al., 1990; Reich et al., 1997; Raich et al., 1997; Wang, 1997). The aggregated form of this uncertainty appeared already during the 1980s, when scientist, politicians and the public were very concerned about environmental pollutions and forest decline; Europe's forests were written to death and effects of air pollution, particularly acid rain, was one of the main issues of environmental research in the Nordic countries (Abrahamsen, 1996). At the same time, the overall growth of forests of Europe was increasing at unprecedented rates (Spiecker et al., 1996; Fisher & Binkley, 2000). That is, rather paradoxically the period of decline was also found to be one of accelerating growth. Beside the sociological contribution to the mismatch between perception of forest decline and reality was the uncertainties about the role of forest soils (e. g., Fisher & Binkley, 2000). Overall, the unpredicted changes of growth in European forests have illustrated our incomplete understanding of processes and principles governing forest ecosystems. Moreover, an enhanced tree growth can be a sign of ongoing changes in the system, with unknown end.

In the context of the above mentioned uncertainties there is the need for an ecosystem perspective in plant-environment issues. Plants growing in a particular environment will be influenced directly and indirectly by a whole complex of environmental factors and their interactions and one of the possible ways of studying forest response to global environmental changes is through plant responses. The annual accumulation of matter and energy in the living mass of trees is one of the most important characteristics of forest ecosystems. The perspective I have applied is one where forest ecosystem processes such as nutrients cycles, plant growth and stand development are expressed and interpreted in terms of nitrogen and other elements.

## 1.2 This thesis is about interactions between trees and controls on their growth

### 1.2.1 Trees and the climatic environment

The IPCC (Intergovernmental Panel on Climate Change) report (IPCC 2007) leaves no doubt that human activities cause global warming. Although trees have responded to global warming in the past - to temperatures higher than they are now - the rate of change predicted in the 21st century is likely to be unprecedented (Saxe et al., 2001). There are no processes that are not affected by temperature conditions and global warming is expected to affect growth of trees.

There is a huge literature dealing with analyses of climate impact on tree growth from very different perspectives. Most of this research has been directed towards deriving statistical and empirical relations between tree growth and climatic variables. However, these correlations have shown no logical geographical or temporal patterns (Mäkinen, 2003) and reflect the current growth of trees, but not how trees will respond in the future. Our incomplete understanding of growth process identified by the unpredicted changes of growth in European forests and acceptance of global warming has reinforced forest growth modelling towards causal explanation.

The knowledge of the causes is crucial for the sustainable management of forests and causal reasoning plays an essential role in human decision-making. In order to consider causes or to explain a process by unravelling the hidden mechanisms underlying its regular behaviour, process-based models are needed. These models are challenged to simulate growth of structurally and physiologically complex organisms using explicit mathematical expressions to capture growth response to environmental conditions.

In order to analyse climate effect on forest growth a modeling approach was applied. In view of the concern about climatic changes, it is important to test temperature sensitivity of parameters of biological productivity with the potential to improve the utility of models for predicting forest growth in response to a changing climate.

### 1.2.2 Trees and the soil environment

Plants need nutrients from the soil to grow. Soils play a major role in sustaining stand productivity and forest value by regulating nutrient cycles. Soil fertility is maintained when nutrients are efficiently recycled through the soil food web and the soil-plant system. An understanding of controls on soil nutrients remains a vitally important question for determining the stock of nutrients available for plant uptake. The variability in soil nitrogen availability with climate can be a more important growth factor than the variability in tree physiology with climate (e. g., Salih et al., 2005).

Understanding the fate of nutrients deposited to terrestrial ecosystems is a key to predicting their impact, but literature concerning the long-term fate of applied nutrients in forest ecosystems is still rather limited. Continuous addition of nutrients is assumed to gradually saturate the ecosystem with nutrients and a progressively increasing proportion of applied nutrients have been assumed to circulate within the ecosystem (Aronsson & Elowsson, 1980). Thus, besides the climate changes, a fertilization effect of nitrogen deposition can be responsible for the observed increases in growth of European forests (Kahle et al., 2008). Several experiments show that nutrient content in trees and soil can increase. Thus, increased tree growth was observed rapidly after the start of nutrient additions (Tamm et al., 1999). Consequently, more C is sequestered in the forests through significantly improved tree growth (Tamm et al., 1999; Berg et al., 1999; Högberg et al., 2006; Ladanai et al., 2007; Hyvönen et al., 2008). The sequestration of C and N in forests is an important issue in the global change debate (e.g. Tamm et al., 1999; Janzen, 2004) and there is the strong coupling between C and N (e.g., Rastetter et al., 1992, 1997). The question is whether the increased growth rate will also be sustained in the future if the nitrogen deposition declines. Forest ecosystems where nitrogen cycling has been accelerated may be able to maintain an elevated level of biomass production even when the external forcing in terms of N influx is decreased (Ingestad et al., 1981; Ingestad, 1987, 1991). However, this aspect has not been tested.

Moreover, forests are likely to be heterogeneous in their response to N (Wilson & Emmett, 1999). Thus, not all of the added nutrients contribute to C sequestration and N-use efficiency varies between experimental stands.

N-use efficiency for C sequestration in trees is strongly depended on soil N status, application rates, tree species, stand age and forms and combinations of added nutrients (e.g., Hyvönen et al., 2008). Furthermore, short-term studies can give a completely misleading picture of the long-term development (e.g., Ågren & Hyvönen, 2003) and short-term and long-term results may differ not only in degree but also in direction, but the literature concerning the long-term fate of N applied to forest ecosystems is still rather limited (Aber et al., 1989; Mälkönen et al., 1990; Mälkönen & Kukkola, 1991; Aber & Magill, 2004).

In order to answer to what extent the addition of nutrients can improve the long-term site productivity I explore the consequences of nutrient additions (their fate and redistribution) as well as the long-term effects of the interruption in the nutrient and water additions on (i) soil C and N pools, (ii) nutrient content in needles and (iii) tree growth. The effects of simultaneous acidification and liming were also investigated.

### 1.2.3 Relationships between indicators of plant productivity and environmental conditions

Plants and their environments are intimately connected by exchange of chemical elements and there exists reciprocal control of elemental composition (e.g., Redfield 1958; Odum 1971). Plants and other living organisms must control their internal chemical balance within certain ranges that normally differ from the chemical composition of the external environment (Ågren & Bosatta, 1998), which can vary greatly in space and time. The cycling of nutrients is one of the major aspects of the interrelationship between plants and the soil. Plant-soil interactions are major drivers of plant growth (Bonkowski et al., 2000). Overall, growth of organisms and cycling of nutrients are linked (e.g., Augustine & McNaughton, 2004).

However, inherent complexity among ecosystem components often limits our ability to resolve plant-soil interrelations (e. g., Johnson-Maynard, 2005). Investigations of the effects of soil properties on plants are often focused on growth without enough emphasis given to the mineral composition of plants. Moreover, information about soil-plant interaction are usually limited to few elements, often only one (Reimann et al., 1998), and multi-element plant chemistry data sets collected from several species

under the same conditions over a large area are rare (Reimann et al., 2001). Furthermore, the biogeochemistries of the nutrients differ greatly due to the degree of biological control, chemical bond properties and the origin of the elements. Those elements that are covalently bound and coupled to biological processes for transformations, e.g., biologically controlled (such as N and C), might show different spatial properties than elements cycled through both biological and geological processes (such as P, S and K) or elements under more geological control (Ca, Mg, Mn, Fe, Al). There may also be a difference between macro- and micronutrients (e. g., Wood et al., 2006; Wanatabe et al., 2007), but the reason why micronutrients should be more variable than macronutrients is unknown. A further problem with soil-plant interaction is that plant and soil properties vary spatially and spatial variability influences structure and function of forest ecosystems (e.g., Legendre & Fortin, 1989).

The different scale of impact of elements and the different nature of their biogeochemical cycles imply large variations of their ratios in space and time and thus divergent impact on biota. This issue can be addressed by examining concentration ratios (stoichiometry) rather than variations in tissue nutrient amounts (Sturner & Elser, 2002). Despite the growing interest in ecological stoichiometry (Sturner & Elser, 2002) - an area in which mass-balance constraints for different chemical elements and their interactions with environmental constraints play an important role, this theory has been relatively limited, in particular at the whole ecosystem. Many of the ways in which elemental interactions are affected still poorly understood and there are no simple rules for how stoichiometric ratios will change (e. g., Ågren, 2004). It is suggested that by examining multiple elements in ecosystem compartments and the ratio between them, we can obtain additional insight in how these compartments are linked.

The relationship between element composition of organisms (plants) and their environment (soils) has many practical applications. Thus, many fertilization experiments suggest that element level in plants should be dictated by site properties. Thus, foliar nutrient concentrations have been related to site index (Kayahara et al., 1995; Wang, 1995). Altitude, latitude and longitude have been used as indirect measures of regional climate (e.g., Monserud et al., 1990; Klinka et al., 1996), and available soil nutrients (e.g., Fralish, 1994; Klinka et al., 1994; Wang, 1995; Wang & Klinka, 1996) in order to obtain measures of overall site quality.

In order to arrive at a better understanding of the elemental interactions in forest ecosystems, I examine how plant and soil nutrients are related in Swedish coniferous forests. One aim has been to analyze how needle nutrients and site index are related to geographic coordinates and humus properties. This objective has been accomplished by analyzing needle, humus and site characteristics sampled in 37 and 50 naturally established Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) stands.

### 1.3 Why I use different approaches

Firstly, the question how forests will respond to changed environmental conditions is currently addressed with a number of different approaches, but they are not combined in most studies. An empirical or statistical approach can produce accurate predictions, but cannot provide managers with information on how to manipulate the system; the mechanistic or reductionistic approach is a powerful tool that provides information on how complex interactions affect ecosystem dynamics, but may not provide the same degree of precision as the empirical approach. Empirical models are driven by statistical assumptions that speak to the underlying process being modeled: whether or not they can be accepted is a process-based question not an empirical question (Robinson & Ek, 2000). As each approach provides a valid way to analyse forests, I suggest that using both of them may be an efficient method for achieving a more complete understanding of forest ecosystem dynamic.

Secondly, fundamental questions remain about the separate and interactive effects of climatic and edaphic variables on terrestrial ecosystems (e. g., Breshears et al., 2005). Model simulations relying on a process-based methodology reveal that the impact of temperature on net carbon gain may be by the effect of soil organic matter decomposition and mineralization of soil nutrients. However, there are no clear mechanisms explaining the response of nutrient uptake to soil temperature. Moreover, there is a lot of contradiction in empirically derived relationships between net assimilation and soil temperature (e.g., DeLucia, 1986; Day et al., 1990; Man & Lieffers, 1997; Landhausser et al, 2001). Furthermore, there is lack of a general analytical theory of nutrient uptake in soil and there is no good agreement on how to simulate nutrient uptake (Verburg et al., 2001). However, the major issue is probably how to obtain a correct estimate of the rate of nitrogen mineralization and thus the supply of nitrogen to the trees.

Overall, our mechanistic understanding of the key processes in nutrient cycles and experimental data for the model parameters will have to be improved before the process-based simulation models, that have been developed to overcome the limitations set by empirical models, can become fully operative. Instead, nutrient budgeting, indicating trends in resources at the ecosystem level (Ranger & Turpault, 1999), has been widely used to generate quantitative ecological data on ecosystem functions (Ranger et al., 2002) and as an accounting method to elucidate complex nutrient cycles (Duvigneaud & Denaeyer-De Smet, 1970; Bonito et al., 2003). Element balances have a well-established basis in natural science and rely on the underlying principle of "conservation of matter" that elements cannot be created or destroyed, but have a tendency to dissipate in the wider environment (Öborn et al., 2003).

Thirdly, because of the complexity of the interactions between plants and soil an alternative approach is to use field data to fit the relationship between element composition of plants and soils empirically and information obtained from such observations can be used to tell us, directly, about the interactions driving a plant-soil system.

#### 1.4 Aims of thesis

The purpose of this thesis is to improve our understanding of the controls over trees growth and production by focusing on climatic and edaphic factors (Fig. 2). Additionally, this thesis attempts an integration of model and experimental research to analyze responses to environmental changes of the various forest ecosystem components that operate on multiple time and space scales.

#### 1.5 Hypotheses

(1) I hypothesized that the responses of coniferous forests to environmental changes is time-dependent and modifies forest properties in an ecosystem-specific, e.g., soil-, species- and site-specific way.

(2) Additionally, I hypothesized that there is generality in the relations between plants and soil. Although plant-soil interactions regulate ecosystem processes and are major drivers of plant growth, the nature of soil influence on forest production has not been consistently explained.

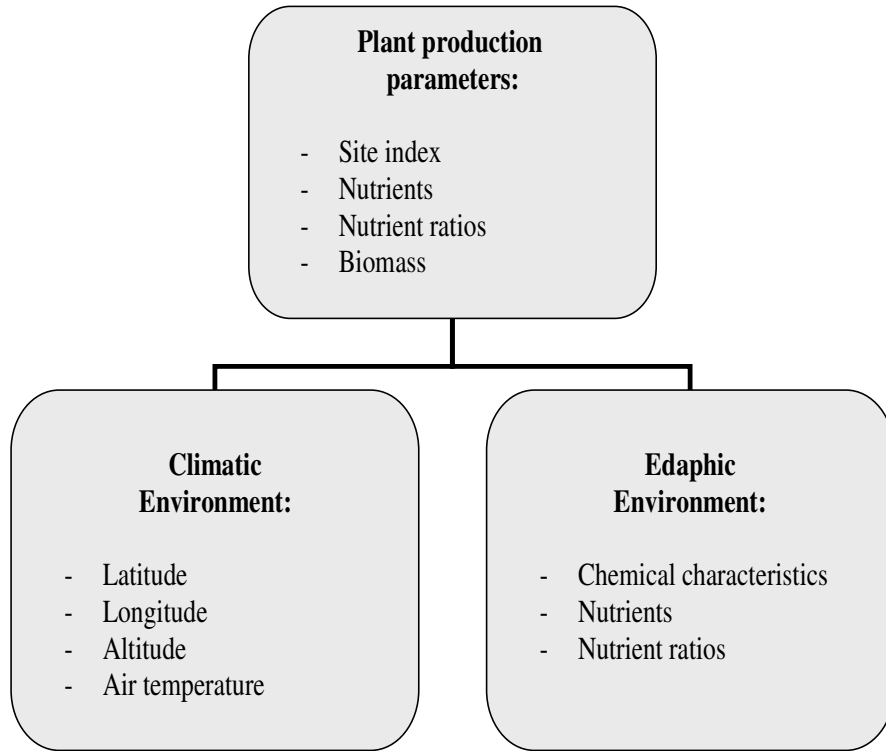


Figure 2. Diagrammatic representation of interactions among indicators of plant productivity and environmental conditions.



## 2 Materials and methods

### 2.1 Tree species

I will focus my analysis on the coniferous tree species Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) because they are the most widespread tree species in Scandinavia and belong to the most commonly-used high-production forest species in Sweden.

### 2.2 Data bases

The first database used in modeling approach (paper I) includes stand level data of dry matter, production, and nitrogen content in needles of pine and spruce trees was collected from literature (Appendix 1, 2 in Paper I). It encompasses a wide range of temperature conditions and covers most of the natural geographic distribution of these species.

The second database, used in empirical approach (paper II and III) are from “Ekologen data base” (Gay et al. 1994) and from the database from fertilisation experiments at Unit for Field-based forest research, SLU. These databases includes data on stem diameters at breast height (DBH), tree heights, nutrient concentrations in biomass components, and soil nitrogen data from three different experimental sites. All studied sites are located in Central Sweden (Figure 3). I have also obtained information from published and unpublished data sets for a Scots pine stand in the Swedish Coniferous Forest Project (SWECON) at Jädraås (Persson, 1980) and for two long-term Swedish Forest Optimum Nutrition Experiments: Scots pine at Lisselbo (Tamm et al., 1974b) and Norway spruce at Stråsan (Tamm et al., 1974a). The data have been supplemented by own measurements of soil

data and tree diameter at Lisselbo and Jädraås. A brief summary of the general characteristics of experimental sites is given in Table 1.

Table 1. Site characteristics and overview of treatments in the experiments.

Site	Lisselbo	Stråsan	Jädraås
Latitude, Longitude,	60°28'N; 16°57'E;	60°55'N; 16°01'E;	60°49'N; 16°30'E;
Altitude	80 m <sup>b</sup>	350 m <sup>b</sup>	185 m <sup>c</sup>
Experiment #	E42 <sup>a</sup>	E26A <sup>a</sup>	E75 (IhII) <sup>c</sup>
Tree species	Scots pine <sup>b</sup>	Norway spruce <sup>b</sup>	Scots pine <sup>c</sup>
Treatment period	1969–1985 <sup>a</sup>	1967–1990 <sup>a</sup>	1974–1992 <sup>c</sup>
Soil material	Sediment <sup>b</sup>	Till <sup>b</sup>	Sedimentary gneiss <sup>c</sup>
Soil profile	Sandy, iron podzol <sup>b</sup>	Glacial till, iron podzol <sup>b</sup>	Sandy, iron podzol <sup>c</sup>
Mean annual temperature, °C	4.8 <sup>b</sup>	3.1 <sup>b</sup>	3.8 <sup>c</sup>
Mean annual precipitation, mm	593 <sup>b</sup>	745 <sup>b</sup>	600 <sup>c</sup>
Stand age at start of treatment	14 <sup>b</sup>	9 <sup>b</sup>	15 <sup>c</sup>
Form of N added	Ammonium nitrate <sup>b</sup> (NH <sub>4</sub> NO <sub>3</sub> )	Ammonium nitrate <sup>b</sup> (NH <sub>4</sub> NO <sub>3</sub> )	Ammonium nitrate <sup>c</sup> (NH <sub>4</sub> NO <sub>3</sub> )
Amount of fertiliser N (kg ha <sup>-1</sup> ) added	240 during 1969–1970 <sup>a</sup> 800 during 1971–1985 <sup>a</sup>	520 during 1967–1971 <sup>a</sup> 1240 during 1972–1990 <sup>a</sup>	1790–1030 during 1974–1992 <sup>c</sup>
Additional treatments	Lime (Ca) Acidification with sulphur (Ac1, Ac2)	Lime (Ca)	

<sup>a</sup>Tamm and Popovic (1995)

<sup>b</sup>Gay et al., (1994)

<sup>c</sup>Axelsson and Bråkenhielm (1980).

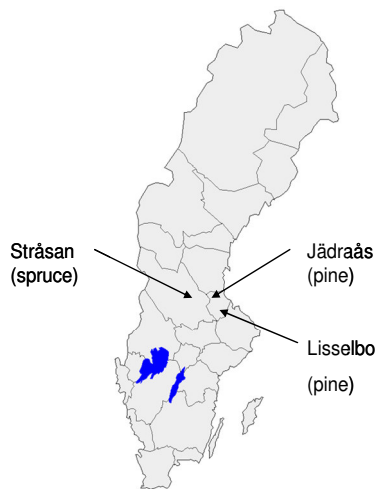


Figure 3. Location of the experimental sites in Sweden.

Monitoring data from forest stands in the Swedish database for ICP Forest (International Co-operative Program on Assessment and Monitoring of Air Pollutions Effects on Forests) Level II constitutes the third database (paper IV). This database, used in an empirical approach, is a large set of data on nutrient concentrations in needles as well as site and soil characteristics and covers a wide range of Scots pine and Norway spruce stands conditions found in Sweden. In this analysis, 87 monitoring plots were used. The plots are located with increasing density from northern to southern Sweden (Figure 4). Sampling of data was performed by The Swedish Forest Agency in accordance with recommendations described by the ICP Forests program.

The tree and environmental variables with which I will work in the thesis are given in Table 2 and the following methods will be used to analyse plant-environmental interactions:

- Modelling plant growth (Sector 2.3)
- Budgeting nutrients (Sector 2.4)
- Correlations between ecosystem variables (Sector 2.5)

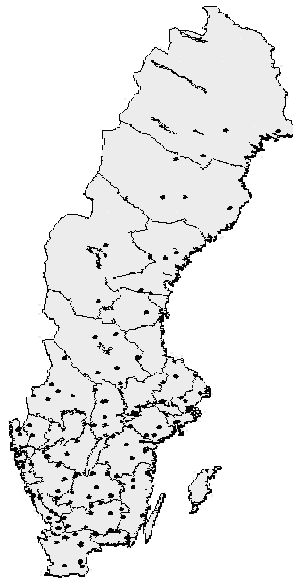


Figure 4. Approximate locations of the sample plots.

Table 2. Tree and environmental variables that will be used in the thesis.

Plant variables	Environmental variables	
	<i>Climatic</i>	<i>Edaphic (soil)</i>
Site index	Latitude	Chemical characteristic
Needle nutrients concentration	Longitude	Nutrients concentrations
Nitrogen pool in tree components	Altitude	N pool
Nitrogen productivity	Mean annual temperature	C pool
Needle biomass		Nutrient ratios
Basal area		
Nutrient ratios		

### 2.3 Method I: Modelling plant growth

The growth response of a tree is a complex function of several processes with both direct and indirect effects and operating at different time scales. A way to circumvent this problem is to operate at a high level of integration, thus avoiding having to look at a large number of detailed processes (Ågren, 1996; Ågren & Bosatta, 1998). It is well established that nutrients, notably

nitrogen exert a strict control on growth (Ingestad, 1979, 1980, 1981). An important criterion when choosing a representation of a system is that it can be done with as few qualitatively different processes as possible (Ågren, 1984). Thus, the growth response to nitrogen was formalized in the nitrogen productivity concept (Ågren, 1983ab, 1985; Ågren & Bosatta, 1998), which states that the relation between the plant's absolute growth rate and its content of nitrogen is linear. The nitrogen productivity concept (Fig. 5) integrates a large number of complicated processes and reduces them into one single linear relationship between growth and nitrogen, where the simple basic equation has the following form

$$\frac{dW}{dt} = P_N(N - c_{N,min}W) \quad (1)$$

where  $W$  is plant biomass (dry weight),  $N$  amount of nitrogen in the plant,  $t$  time,  $c_{N,min}$  a certain minimum concentration of nitrogen in plant that is not active in growth and thus discounted, and  $P_N$  the nitrogen productivity. Thus, the nitrogen productivity expresses the amount of plant mass produced per unit of time and nitrogen.

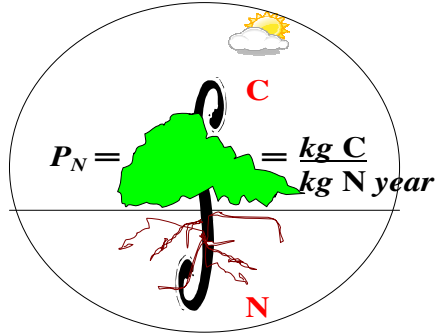


Figure 5. Visualization of the nitrogen productivity concept, where a large number of complicated plant processes that are involved in growth are integrated and reduced into one single linear relationship between growth and nitrogen. The production of plant biomass is in this way placed in the context of carbon and nitrogen cycling between plants and soil in an ecosystem.

In process-based growth model (Eq. 1) based on the nitrogen productivity concept the production of plant biomass couples the carbon and nitrogen cycling between plant and soil in an ecosystem. However, the usefulness of the relation (Eq. 1) depends on its ability to perform under a varied set of climatic conditions. The nitrogen productivity is constant over a wide range of nitrogen concentrations, but the parameter should in

principle depend upon external variables such as weather, which limits growth independently of the mineral nutrients (Ågren, 1983ab).

For simplicity, the nitrogen productivity has been applied to the production of new foliage. On the other hand, foliage drives the production of other tree components and knowledge of foliage biomass should therefore suffice to predict total tree growth. Nitrogen productivity (for foliage production) for a given stand, defined as the amount of foliage produced per amount of nitrogen in the canopy per unit of time (Ågren, 1983a), was calculated as biomass of current-year needles/total nitrogen in needle biomass. This calculation uses the idea that growth of needles can be equated with current-year needle biomass and that the determining resource is nitrogen in the needle biomass.

Mechanistic (modelling) approach requires a strict relationship between causes and consequences (Kryazhimskii et al., 2001). Nitrogen productivity for production of new foliage, where canopy size and architecture influence light interception and self-shading becomes important and causes the nitrogen productivity to decrease with the size of the canopy, which can be expressed as

$$P_N = a - bW_c \quad (2)$$

where  $W_c$  is the total needle biomass, and  $a$  and  $b$  are species-specific parameters (Ågren, 1983a). Using this model we tested the temperature sensitivity of nitrogen productivity by analysing the temperature sensitivity of the parameters  $a$  and  $b$ .

## 2.4 Method II: Budgeting nutrients in forest ecosystems experiments

Various terms in the ecosystem nitrogen budget have been quantified by estimating the total content of N in the three important compartments in the ecosystem [i.e. whole tree biomass, humus layer, and mineral soil 0–20 cm (pine stand) and 0–30 cm (spruce stand)]. The nitrogen storage in the pine stand at Lisselbo was estimated for 1971 and 1997, when the first and last soil samplings, respectively, were made. The spruce stand at Stråsan was monitored from 1972, when the first basal area measurement was made, until 2003, when the last diameter measurement was made. The inputs of nitrogen that we included were inorganic fertiliser, wet plus dry deposition, and biological N-fixation. The changes in nitrogen pools were calculated as

the differences in nitrogen amounts in trees, humus layer, and mineral soil between the beginning and the end of the investigation period. However, soil N pool changes over time in the spruce stand were based on comparisons between control and treated plots in 1997 because initial data were lacking. I have also examined long-term effects of interruption of annual nutrient loading on tree growth and soil C and N stores by analyzing data from an experiment in the pine stand at Jädraås.

Biomasses of tree components (needles, branches, stems and roots) have been estimated from average tree diameter at breast height using species-specific regression functions (Marklund, 1988). The N stocks in the tree components have been calculated by multiplying the biomass of each component by published nitrogen concentrations.

## 2.5 Method III: Correlations between ecosystem variables

I have used observations sampled in 1995, 1996 and 1997 for 50 Norway spruce and 37 Scots pine stands. General site variables, needle variables and soil variables were selected. The general site variables includes the Swedish site index H100 (the height of dominant trees at age 100 years, Hägglund & Lundmark, 1977), latitude, longitude and altitude. The soil variables included only the humus layer and contains concentrations by dry mass of C, N and P (total content by dry oxidation method), extractable hydrogen ions and salt extractable cations (0.1 M BaCl followed by ICP analysis). The needle variables were plant essential nutrients (macronutrients: N, P, K, S, Ca, Mg; micronutrients Mn and Fe) along with nonessential nutrients (Na and Al) in one-year old needles. Nutrient concentrations have been expressed both relative to C and N in order to investigate different stoichiometric variables.

Coefficients of variation ( $CV = \text{standard deviation}/\text{mean}$ ) has used to express variability in soil and needle variables. Pearson's rank correlation coefficients have been calculated for a range of combination of variables to find factors relevant in soil-plant interrelations. The obtained data matrix contained 830 analyses of 22 needles and 25 soil variables. For our evaluation, the evidence of trends as well as the strength of the connection was important. Correlations coefficients larger than 0.32 and 0.27 for pine and spruce, respectively, are considered significant ( $P < 0.05$ ).





## 3 Results and discussions

### 3.1 Climate impact on tree growth (Paper I)

From the mechanistic (modelling) approach it is clear that nitrogen productivity and needle biomass is negatively related (Fig. 6, 7). While temperature has no effect on nitrogen productivity for Norway spruce (Fig. 7), nitrogen productivity for Scots pine is sensitive, although weakly, to temperature and the sensitivity affects both the magnitude at low needle biomass and self-shading (Fig. 6). Nitrogen productivity decreases with temperature except at the large needle biomasses. I see two possible explanations. First of all, it should be observed that nitrogen productivity represents the net carbon gain of a canopy and is therefore a balance between photosynthesis and respiration (Ågren, 1996). In natural environments changes in temperature are often accompanied by changes in light intensity and our observations suggest in consistency with other observations (Ziska & Bunce, 1997; Ellsworth, 2000, Hennessey & Field, 1991) that pronounced impact of light availability on net assimilation exceeds the impact of temperature. Secondly, increasing temperature may also be accompanied by water stress, which could lead to decreasing production with increasing temperature as a result of increasing evaporative demands. Climatic changes, where the pattern of precipitation is altered, may therefore require a revision of our analyses. The observed decrease of sensitivity towards the large needle biomass could be a shift from a juvenile to an adult growth phase. Unfortunately, there is a lack of knowledge about the response of mature trees to climate change (Källomäki et al., 2000). Finally, much of the difference at low needle biomasses depends on a few data points and over large ranges of needle biomasses the difference between high and low temperature is small.

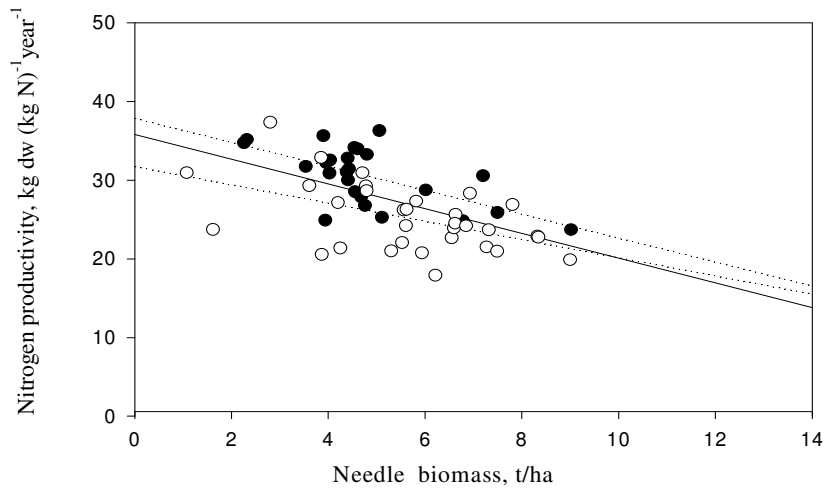


Figure 6. The relation between nitrogen productivity and needle biomass for *P. sylvestris* stands. Regressions: broken line and filled circles ( $T < 5$ )  $P_N = 37.82 - 1.52W$ ,  $r^2 = 0.38$ ; broken line and open circles ( $T > 5$ )  $P_N = 31.70 - 1.16W$ ,  $r^2 = 0.26$ ; solid line and all circles (all  $T$ )  $P_N = 35.8 - 1.57W$ ;  $r^2 = 0.33$

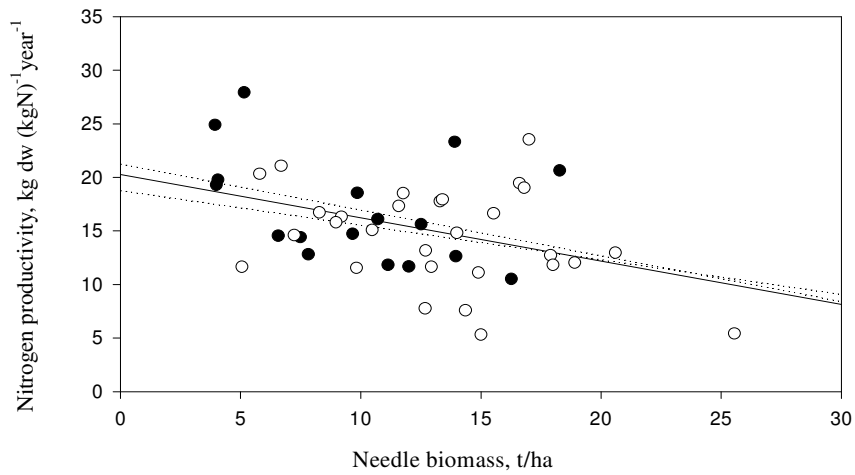


Figure 7. The relation between nitrogen productivity and needle biomass for *P. abies*. Regressions: broken line and filled circles ( $T < 5$ )  $P_N = 21.22 - 0.43W$ ,  $r^2 = 0.14$ ; broken line and open circles ( $T > 5$ )  $P_N = 17.59 - 0.23W$ ,  $r^2 = 0.11$ ; solid line and all circles (all  $T$ )  $P_N = 19.80 - 0.37W$ ;  $r^2 = 0.16$

Overall, as the two investigated coniferous species have rather different physiologies, it is possible that other conifers could show a similar

insensitivity in nitrogen productivity. However, temperature also influences tree growth indirectly by its effect on decomposition of soil organic matter and mineralization of soil nutrients (Eberhardt et al., 2000); this might be the mechanism through which long-term temperature effects operate.

### 3.2 Nutrients factor of tree growth (Papers II, III)

The concentrations of N in current needles in the Jädraås experiment are shown in Figure 8. The basal area development for the three stands and different treatments are shown in Figure 9. In all stands and treatments investigated, the fertilisation increased basal area, more strongly, however, for spruce than pine. In the spruce stand, the growth stimulation was so strong in all fertilised plots that by the end of the fertilisation period, the basal area in the fertilised plots was about three times that in the unfertilised plots. However, once fertilisation had ceased, all treatments in all stands had similar rates of basal area growth except the NPK treatment at Lisselbo, which had a somewhat more rapid development, and Ca and Ac1 treatments, which fell behind. Moreover, needle nitrogen concentrations decreased to the same levels as in the unfertilised plots after the interruption.

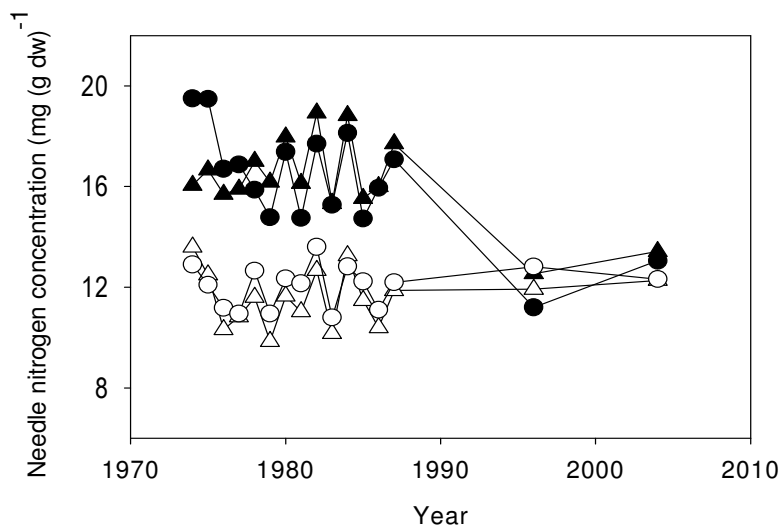


Figure 8. Changes over time in concentrations of N in current (C+0) needles in the four treatments in the Jädraås experiment. Control: O. Irrigation: Δ. Fertilization: ●. Irrigation+fertilization: ▲.

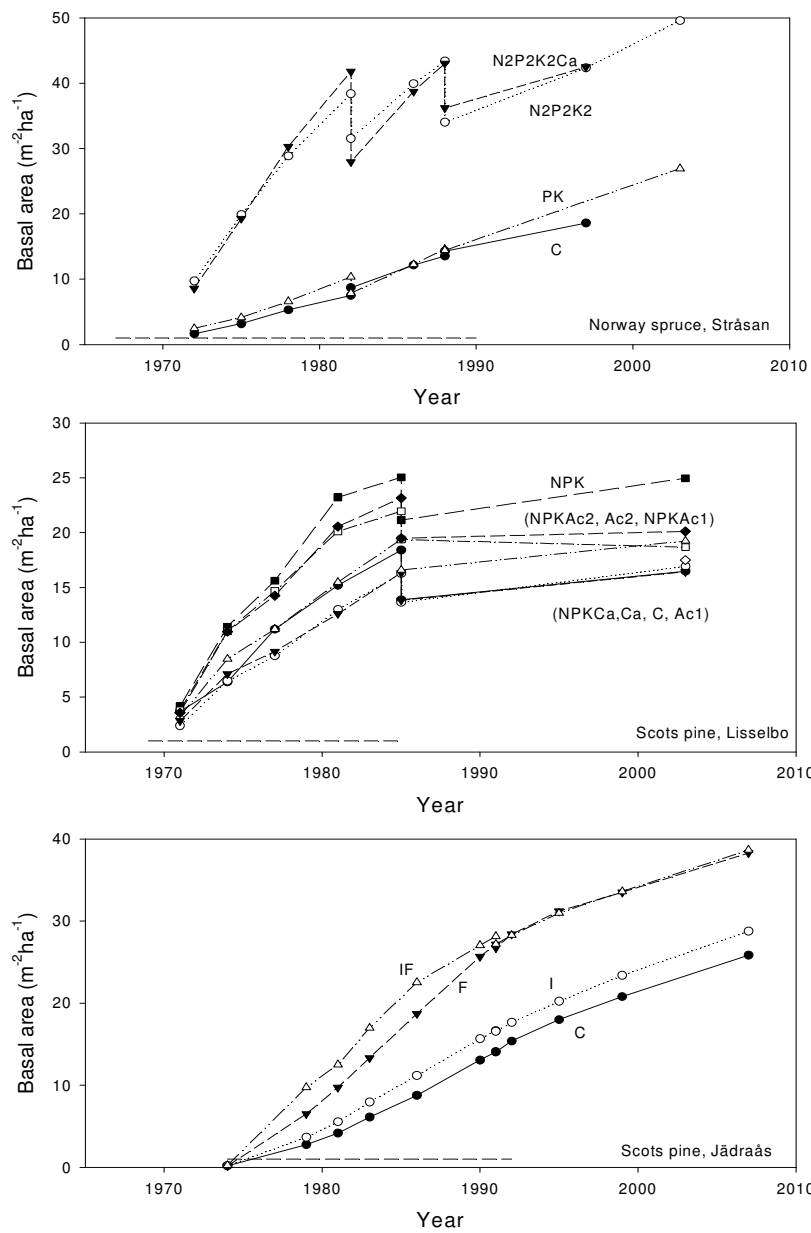


Figure 9. Basal area development for pine and spruce stands and different treatments. Pine at Lisselbo: C (●), Ca (○), Ac1 (▼), Ac2 (Δ), NPK (■), NPKAc1 (□), NPKAc2 (◆), NPKCa (◇), only one data point. Spruce at Stråsan: C (●), NPK (○), NPKCa (▼). Pine at Jädraås: C (●), I (○), F (▼), IF (Δ).

The distribution of N between ecosystem compartments in the Lisselbo pine and the Stråsan spruce stands 12 and 7 years after the end of long-term fertilisation is shown in Figure 10. In both stands, the effects of the N additions could still be observed after the N addition had ceased. However, there are differences in response between the pine and spruce stands. In both stands fertilization increased biomass and this biomass increase was sustained in all spruce plots but only in the NPK-fertilized pine plots. However, there are differences between the experiments at Lisselbo and Stråsan and the complete nutrient experiment at Jädraås, where the fertilization resulted in a long-term increase in the forest production and probably also caused a shift in N uptake from organic towards inorganic forms (Figure 10).

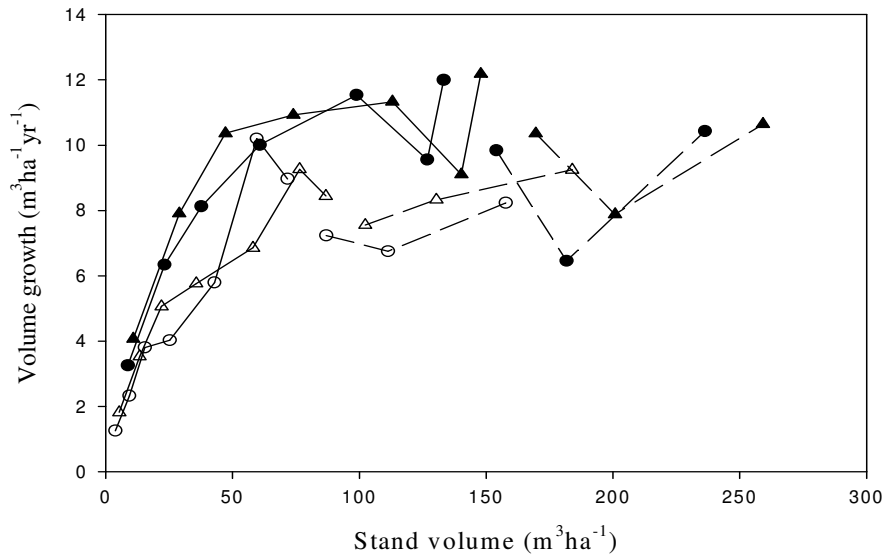


Figure 10. Volume growth versus volume in the experiment. Control (0) is denoted with O, irrigation (I) with  $\Delta$ , fertilization (F) with  $\bullet$ , and irrigation+fertilization (IF) with  $\blacktriangle$ . Solid lines connect periods with fertilization. Dashed lines connect periods without fertilization.

As a result of a significant increase in humus N, the N applications caused significant changes in ecosystem N content and total soil N in the pine experiment at Lisselbo. There was also a significant increase in mineral soil N in the NPK and NPKAc2 treatments (Fig. 11). In the spruce stand, the increase in the soil was restricted to the humus layer, whereas the mineral soil N pool might rather have decreased. The differences in response between the pine and spruce stands are probably attributable to

species difference. The potential of spruce to increase its needle biomass is much larger than that of pine; Ågren (1983a) estimated the maximum needle biomasses for pine and spruce to be 20000 and 49000kg DW ha<sup>-1</sup>, respectively. Another aspect is the differences in soil texture (Tab. 1) and hence soil nutrient retention capacity. The effects of acidification or liming in addition to the fertilisation had no consistent pattern. Without fertiliser, acidification and liming seem to be almost without long-term effects, although it is possible that high acid dosage increased N stocks somewhat more.

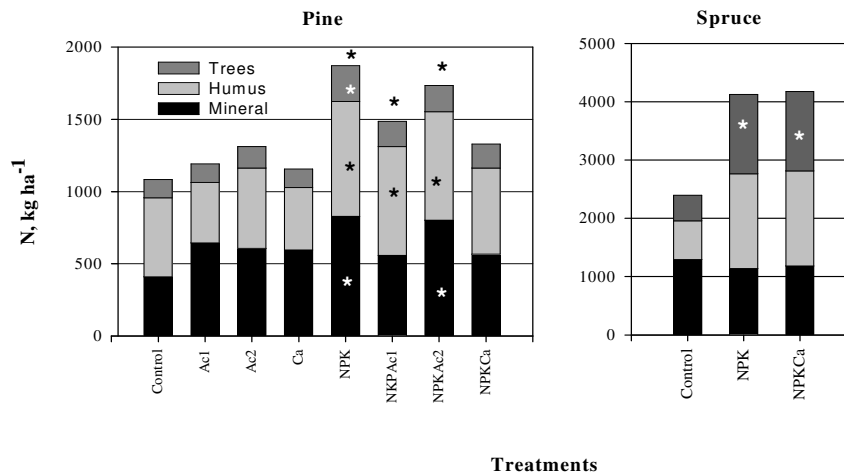


Figure 11. Nitrogen pools in 1997 in the Lisselbo pine and Stråsan spruce ecosystems compartments. Significant differences ( $P < 0.05$ ) between control and treatments are marked with (\*).

The nitrogen economy of the pine ecosystem, averaged for fertilized and unfertilized plots is shown in Figure 12. Pool changes of nitrogen in pine ecosystem compartments are shown in Figures 13. The N budgets are not closed. The losses of N in the fertilized pine plots are most likely leaching losses. There are two potential sources for the extra N in the unfertilized plots. First of all, it is likely that some nitrogen is derived from mineralization in deeper soil horizons than those included in the budgets. Another possible explanation for the N deficit is the uncertainty in the total input. Nitrogen fixation is one uncertain component in the total input. If an ecosystem responds to N deposition as the trees in fertilization experiments, the nitrogen pools of ecosystem compartments and hence C sequestration, is expected to increase with N deposition in N-limited forest. However, it is evident that trees and soils differ in response to N addition.

Thus, deposition of N increases N in trees and decreases the N stock in mineral soil layers. Moreover, the risk of nitrogen leaching cannot be assessed only on the basis of nitrogen addition; the ability of an ecosystem to retain N, particularly in deep mineral soil horizons, has to be taken into account.

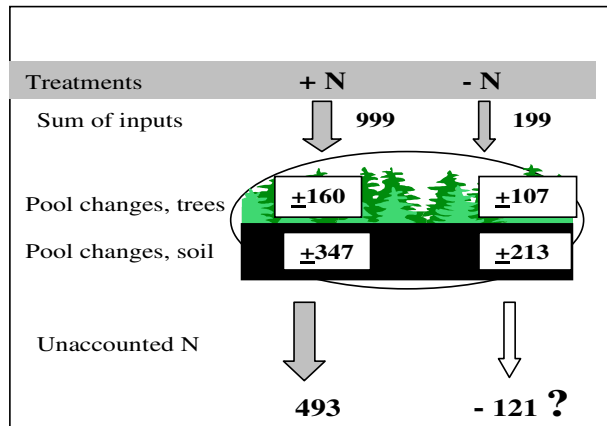


Figure 12. An overview of the nitrogen economy of the pine forest ecosystems at Lisselbo, expressed as averages for fertilized (+N) and unfertilized (-N) plots, respectively. For details of treatments, see Table 2 in Paper II. Values are kg N ha<sup>-1</sup> per 26 years and show the sum of inputs, net increments in trees and soil (pool changes over 26 years) and amount of N not unaccounted for.

On average, 56 % of the applied N in the Lisselbo pine stand, added alone or in combination with acid in high doses, still remained in the soil (Fig. 13). This is considerably more than the average 35% for all fertilized plots (Fig. 12) and the 30% reported previously (Tamm *et al.*, 1999). On the other hand, when N was added in combination with low acid or lime, only 13 % remained in the soil. Even if the increased growth of forests can be linked to increased nitrogen availability, the differences in growth responses across fertilizer combinations (Fig. 11) indicate that factors other than nitrogen are of significance. A larger increases in soil nitrogen in the NPK and NPKAc2 plots compared to NPKAc1 and NPKCa plots (Fig. 11) as well as higher retention capacity of these plots compared to other fertilized plots (Fig. 13) indicate that the interaction between N deposition and acidification remains a controversial issue.

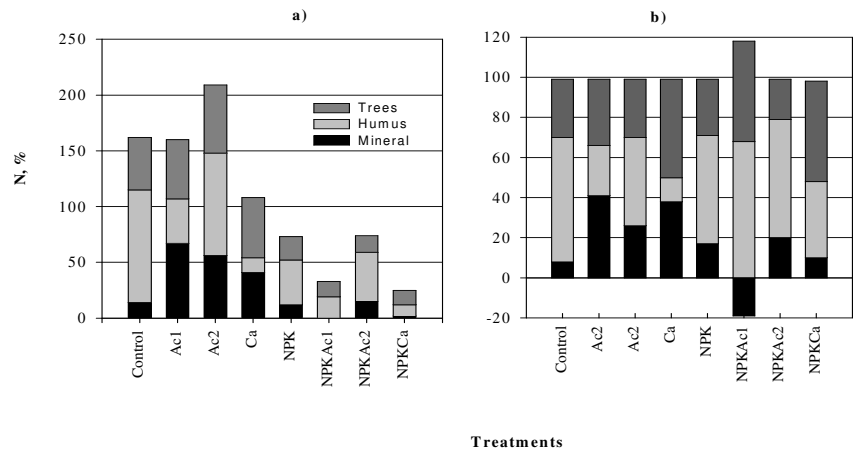


Figure 13. Pool changes of N in pine ecosystem compartments: a) Relative to total inputs; b) Relative to change in ecosystem.

### 3.3 Relations between ecosystem variables (Paper IV)

I will in this section focus on the relative strengths of the controls of different element cycles in forest ecosystems. Elements that are under biological or geological control should show low variability and those that are related should have high correlations.

#### 3.3.1 Variability in needle and soil properties

Table 3 and Figure 14 give a compilation of CV's in 22 needle and 25 humus variables. The variability in humus properties is considerably larger than in needle properties; this should be a result of humus properties being determined by both litter (needle) properties and soil processes. There is a coupling between variability in needles and humus (Figure 15) such that variables that vary much in needles also vary much in the humus; this is most clearly seen in spruce. Together this suggests that negative feedbacks stabilizing the interactions between elements are exerted by the trees and not in the soil (humus).



Table 3. List of variables with abbreviations used in figures and tables and their coefficients of variation (CV) for humus and needle variables in pine and spruce stands. CV's for element/carbon ratios in needles are by definition equivalent to element concentrations in needles but are included in the table for easy comparison with element/carbon ratios in humus.

		CV, %			
		Pine		Spruce	
		Needle	Humus	Needle	Humus
<b>Needles and humus variables</b>	<b>Abbreviation</b>				
<i>Basic variables</i>					
Hydrogen ions extractable	H		41		49
Aluminium	Al		44		87
Sodium	Na		61		69
Organic carbon (total)	C-tot		33		29
Organic nitrogen (total)	N-tot	14	38	11	29
Phosphorous (total)	P-tot	13	20	18	26
Potassium	K	31	49	23	45
Sulphur	S	10		11	
Calcium	Ca	38	45	25	54
Magnesium	Mg	12	55	13	42
Iron	Fe	18	92	24	124
Manganese	Mn	32	85	31	106
<i>Nitrogen scaled variables</i>					
Carbon nitrogen ratio	C/N		17		13
Phosphorus nitrogen ratio	P/N	10	62	22	42
Potassium nitrogen ratio	K/N	33	59	28	46
Sulphur nitrogen ratio	S/N	10		12	
Calcium nitrogen ratio	Ca/N	42	64	27	60
Magnesium nitrogen ratio	Mg/N	18	72	19	33
Iron nitrogen ratio	Fe/N	15	82	26	122
Manganese nitrogen ratio	Mn/N	35	108	30	132
<i>Carbon scaled variables</i>					
Nitrogen carbon ratio	N/C	14	17	11	13
Phosphorous carbon ratio	P/C	13	80	18	43
Potassium carbon ratio	K/C	31	49	23	41
Calcium carbon ratio	Ca/C	38	75	25	56
Magnesium carbon ratio	Mg/C	12	95	13	34
Iron carbon ratio	Fe/C	18	86	24	133
Manganese carbon ratio	Mn/C	32	109	31	137

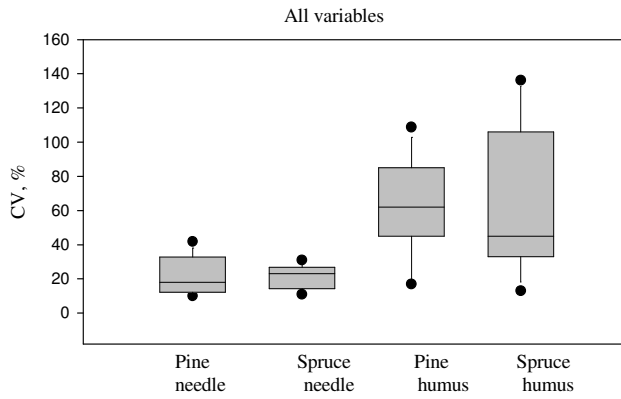


Figure 14. Box plots of coefficients of variation (CV, %) of needle and humus variables in pine and spruce stands. The box plot shows the median (line), 75th and 25th percentiles (box), the 5th and 95th percentiles.

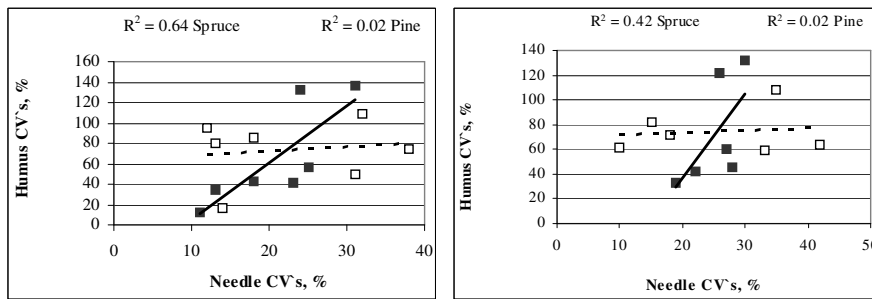


Figure 15. Correlations between humus CV and needle CV for: a) nutrient to carbon ratios (N/C, P/C, K/C, Ca/C, Mg/C, Fe/C, Mn/C); b) nutrient to nitrogen ratios (P/N, K/N, Ca/N, Mg/N, Fe/N, Mn/N). Pine: broken line and open symbols. Spruce: solid line and filled symbols.

It is difficult to clearly distinguish groups of elements with clear differences in variability. The differences in variability between species are small. The similarity between tree species might be a result of overall similarities in physiology whereas the lack of differences between humus properties might reflect the small, in global perspective, variability in bedrock properties.

### 3.3.2 Correlations between variables

Variables that have at least one significant correlation coefficient with another variable are given in Tables 2-8 in paper IV. The fractions of significant correlations between variables are shown in Figure 16.

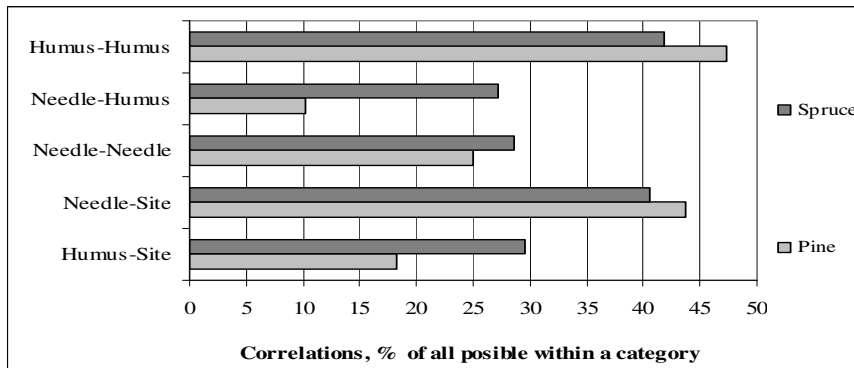


Figure 16. Proportion of significant correlations between ecosystem variables in pine and spruce stands in percent of all possible within a category.

### Correlations with site variables

Climate, as reflected by geographical location, has an overall effect on productivity (site index), Figure 17. Latitude, which correlates with temperature, shows the strongest effect followed by longitude, which correlates with precipitation. For both variables the correlations are strongest for spruce, which may be a result of pine having a wider niche and thus its production will be more strongly affected by other variables than those captured in physical climate. Altitude correlates, but weakly, with site index probably because the effects of latitude and longitude override altitude as a factor.

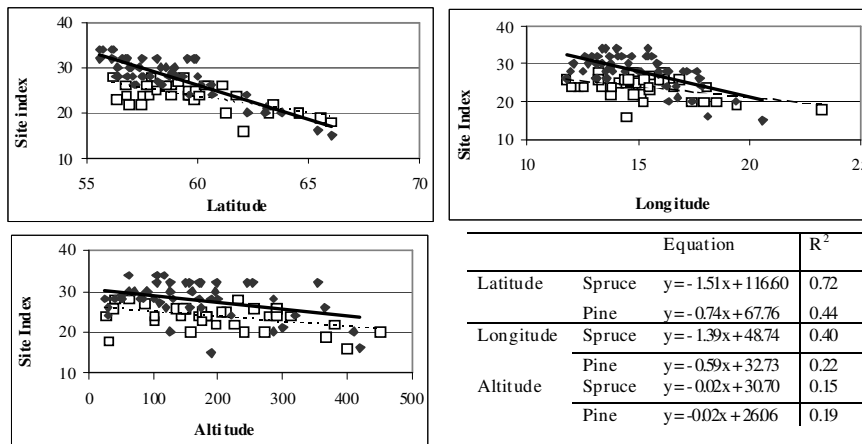


Figure 17. Correlations between site index and geographic variables in pine and spruce stands. Pine: broken line and open symbols. Spruce: solid line and filled symbols.

The few correlations between site properties and humus are probably spurious (Figure 18). Needle variables are more strongly related to geographical variables than humus variables (Figure 19). The strong positive relation between SI (and negative for latitude and longitude) and needle N concentration reflects the larger requirements for N at higher growth rates (Figure 18). From general stoichiometric theory (Sternner & Elser 2002; Ågren, 2008) positive relations between growth rates and element concentration are expected as observed for pine. A possible explanation for the negative correlations in spruce is that nitrogen is growth limiting and that the availability of the other, non-limiting, elements increases slower than growth with a resulting dilution effect.

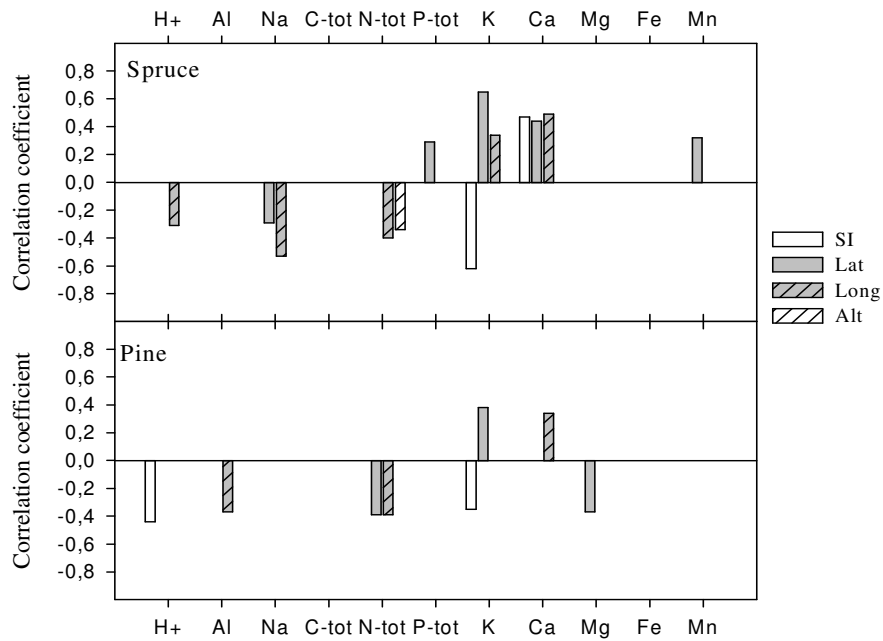


Figure 18. Significant correlations between humus and site variables in spruce and pine stands.

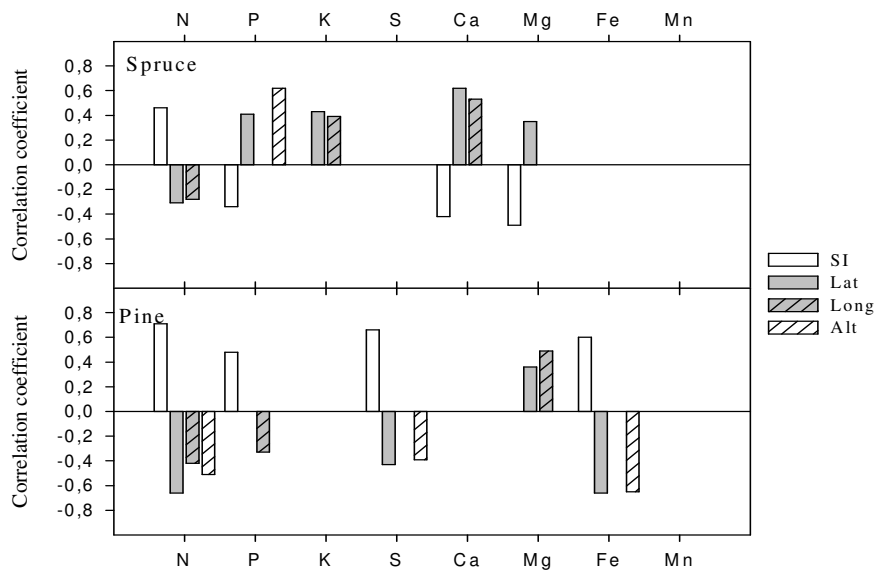


Figure 19. Significant correlations between needle and site variables in spruce and pine stands.

#### Correlations between needle variables

All of the correlations between element concentrations in the needles are positive except K versus Ca in pine (Figure 20) which is the only sign of antagonistic relations between elements (e. g., Lamppu & Huttunen, 2003). The correlations are dominated by those where organically bound elements are involved. In pine, but not spruce, N and P are the most strongly coupled elements, which agrees with the suggestion by Knecht and Göransson (2004) that the uptake of these two elements should be the most strongly regulated. Overall, there is a stronger control of macronutrients in trees.

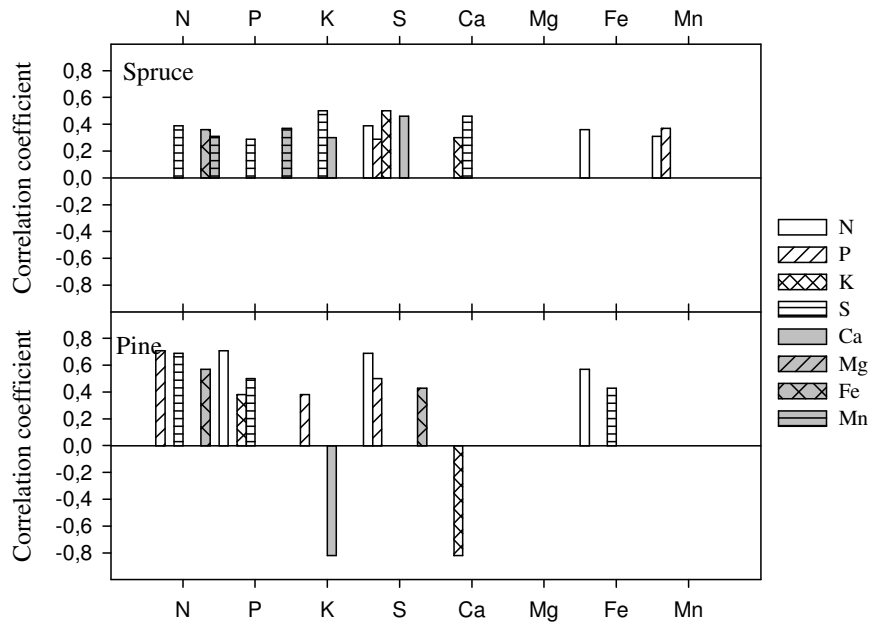


Figure 20. Significant correlations between needle variables in spruce and pine stands.

The choice of basis for expressing needle element content is important (Figure 21). Using N as a basis rather than dry mass or C increases the number of correlations. This indicates that from a stoichiometric perspective N is a more important reference than C. The reason is probably that C compounds make the structure as well as serve as storage compounds (e.g. starch) and expressing element concentrations relative to N capture more of functions.

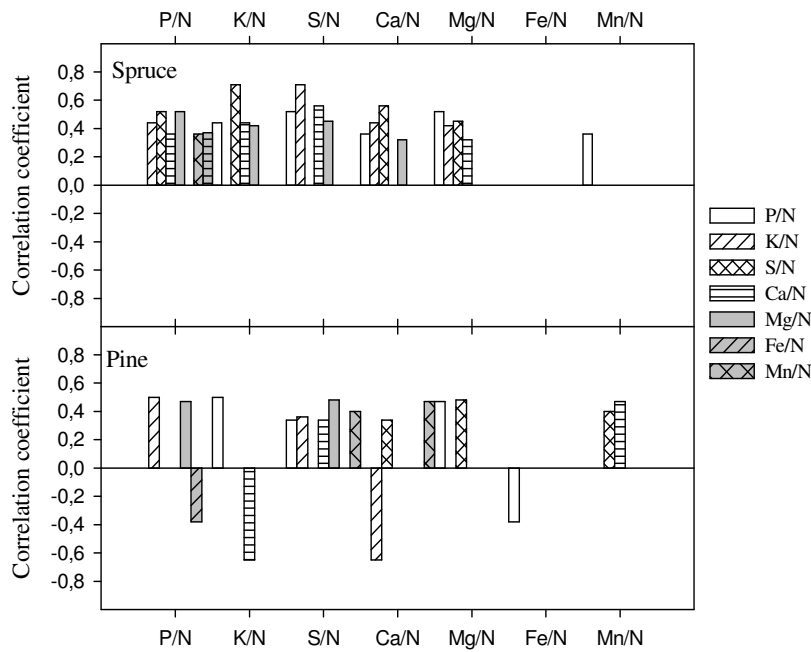


Figure 21. Significant correlations between needle nutrient ratios in spruce and pine stands.

#### Correlations between humus variables

Humus variables turn out to be those that are most strongly correlated among themselves (Figure 16). In contrast to needles, the biologically controlled elements (C, N, P) do not dominate the number of correlations but correlations between the other elements are frequent as well (Tables 5, 6 in paper IV). This could be a sign of the importance of purely chemical exchange reactions in maintaining element balances in humus. A reason for the tight correlation could be that fresh litter is less variable with respect to element concentration than live tissue as a result of retranslocation during senescence. As a consequence of the tight correlations between C and N in humus, it makes in contrast to needle variables little difference if correlations between elements in humus are calculated with C or N as basis.

#### Needle variables versus humus variables

There are almost no correlations to be found between needle and humus basic variables for pine and only a quarter of the possible ones are significant for spruce (Figures 16, 22). This lack of strong coupling between vegetation and soil is not unique to our investigation. For example, Wood *et al.* (2006)

found in their study in Costa Rican rain forests that relations between soil element stocks and leaf nutrient concentrations existed for only two (P, Mn), and possibly Ca, out of seven investigated elements. This lack of correlations is partly explained by the noise created by the variable content (minerals in the humus samples). However, even when I get around this problem by normalizing relative to C and N, there are still few correlations in pine stands. The decoupling between living needles and their dead remains in the humus should in part result from retranslocation of nutrients in needles at senescence. The existence of several correlations of this kind in spruce forests (Figure 22) may be an indication that pine forests in general are rather open with important contributions to humus formation from ground vegetation in contrast to dense spruce forests with in some cases no ground vegetation at all.

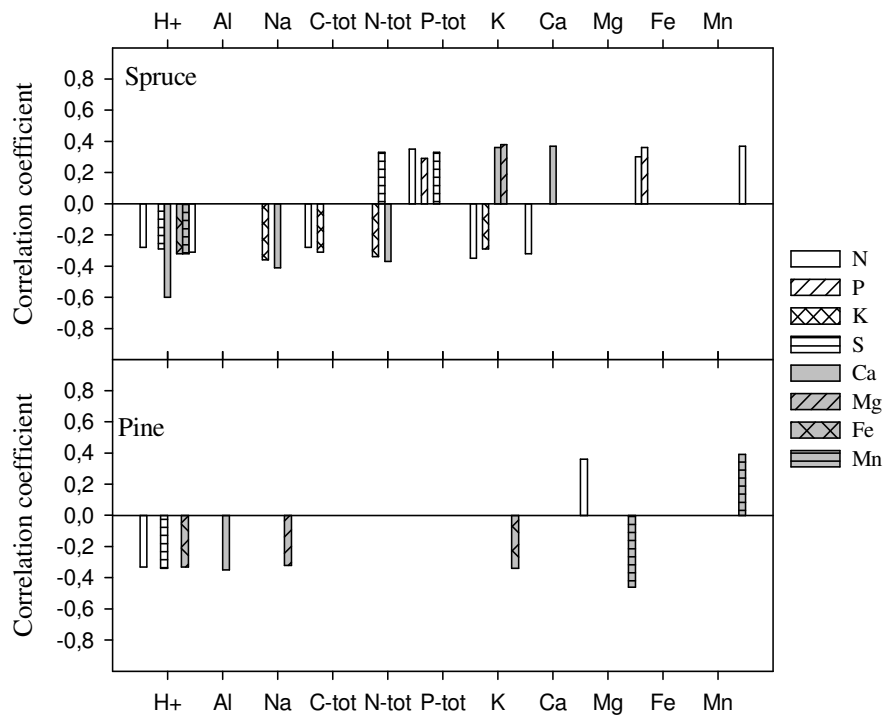


Figure 22. Significant correlations between humus and needle variables in spruce and pine stands.



## 4 Conclusions

One main result is that the nitrogen productivity or net carbon gain of conifer canopy is not sensitive to temperature. This emphasizes the importance of indirect effects of climatic change through effects on nutrient availability.

Another striking observation is that the response of boreal coniferous forest ecosystems to long-term nitrogen addition is time-, species- and site-specific. Thus, when N additions decline or are terminated, some ecosystems are likely to revert to pre-treatment N stocks. Moreover, tree species differ in their partitioning of added N; in pine ecosystem the soil is the major sink for N, whereas trees conserve a large proportion of added N in the spruce ecosystem. Furthermore, the accelerated growth of European forests is probably linked to increased nitrogen availability, but the differences in growth responses across fertiliser combinations indicate that factors other than nitrogen are of significance. The interaction between N deposition and acidification, which remains a controversial issue, the ability of the ecosystem to retain nitrogen and the mineral soil, which is likely to participate actively in N cycling, are all important to include when quantifying the long-term capacity of forest ecosystems to retain and redistribute nitrogen. Mode of nutrient addition matters. Chronic addition of complete nutrient solution resulted in long-term production increase, while the result of high annual doses of macronutrients was that production converged towards similar level. Overall, the hypothesis (1) that the responses of coniferous forests to environmental changes is time-dependent and modifies forest properties in an ecosystem-specific way is supported.

There is a difference in the relative strengths of the control of element cycles in forest ecosystems both between different tree species and between

ecosystem components (plant and soil). As a consequence, the hypothesis (2) that there is generality in the relations between plant and soil must include that the links in element cycling between trees and the humus formed under them is stronger in spruce forest than in pine forests. Spruce production is also more strongly affected than pine production by variables captured in physical climate. This suggests a tighter biogeochemical cycling of nutrients in spruce ecosystems. Humus is formed by biological processes but it is also a substrate for chemical exchange reactions. Because plants and decomposers have different stoichiometries, this mixture (humus) will be less well defined than its end members the fresh litter and the decomposers. On the other hand, humus as a substrate for exchange reactions seems less variable, which can explain why relations between cations are similar independently of site.

The biogeochemistries of the nutrients differ greatly, but the biological control is not limited to only the organically bound elements that require biological processes for transformations. Moreover, the basis for investigating stoichiometric relations is important. The use of N as a basis in stoichiometric relations rather than C or dry weight points to more relations between elements. However, stoichiometric relations are not entirely rigid. The hypothesis (2) that there is generality in the relations between plant and soil is not supported must include that there are differences between elements.

There is a strict control of the relations between N and C in both needles and humus. There is also control, although less so, in the relations between several other elements but some elements that seem also to be under no biological control (e.g. Mn). One might therefore travesty Odum (1971) "The ecosystem is less than the sum of its part".

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