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Growth and Nutrition of Coniferous Forests on Acidic Mineral Soils – Status and Effects of Liming and Fertilization

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SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

Growth and nutrition of coniferous forests on acidic mineral soils – status and effects of liming and fertilization

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Abstract

Deposited air-borne S- and N -containing pollutants acidify forest soils in southern Sweden. It has been suggested that this may severely affect forest yield. Liming and/or application of specific nutrients, e.g. phosphorus (P) and potassium (K), have been proposed as countermeasures. The influence of such measures, and of nitrogen (N) addition, was investigated in two experimental series over 5–10 years. Stem growth and needle element concentrations were assessed, predominantly in high-yielding Norway spruce [*Picea abies* (L.) Karst.] and Scots pine (*Pinus sylvestris* L.) stands, 30–60 years old, growing on acidic mineral soils in southern Sweden. The effect on crown transparency was also evaluated in some of the Norway spruce stands. The treatments included liming (500–6,000 kg ha^{-1}), and N addition at low annual doses (2×10 kg N ha^{-1}) and in single shots (150 kg N ha^{-1}). Combinations of lime+N, lime+PK and lime+PKN were also tested. The effects were generally weak or negligible, except that growth was significantly increased by N fertilization in the Scots pine stands, and by lime+PKN in some of the Norway spruce stands. In another study, the survival and growth of Norway spruce seedlings were found to be more or less unaffected when planted in pre-harvest acidified, limed or N fertilized soil, although the Ca and Zn concentrations in their needles rose after liming, while those of Mn and Al declined. In closed-canopy stands of Norway spruce and Scots pine with N concentrations of more than 15–16 mg (g DM)$^{-1}$ in current-year needles, N fertilization was indicated to not necessarily stimulate increased growth. Other indicators of highly N-rich forests (e.g. elevated arginine levels) also start to appear above this level. The closed-canopy stands growing on the most acidic soils showed no signs of severe damage or nutrient deficiencies. These findings, together with the small or negligible effects of the tested countermeasures against soil acidification, suggest that as regards stem growth, needle-element concentrations or crown transparency, there seems to be no acute need for liming and/or PK addition in SW Sweden in Norway spruce stands on sites similar to those examined.

Key words: acidification, ammonium nitrate, calcite, crown transparency, defoliation, dolomite, forest production, needle chemistry, Norway spruce, phosphorous, *Picea abies*, *Pinus sylvestris*, potassium, regeneration, Scots pine.

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Deposited air-borne S- and N -containing pollutants acidify forest soils in southern Sweden. It has been suggested that this may severely affect forest yield. Liming and/or application of specific nutrients, e.g. phosphorus (P) and potassium (K), have been proposed as countermeasures. The influence of such measures, and of nitrogen (N) addition, was investigated in two experimental series over 5–10 years. Stem growth and needle element concentrations were assessed, predominantly in high-yielding Norway spruce [*Picea abies* (L.) Karst.] and Scots pine (*Pinus sylvestris* L.) stands, 30–60 years old, growing on acidic mineral soils in southern Sweden. The effect on crown transparency was also evaluated in some of the Norway spruce stands. In all experiments a randomized block design was used. The treatments included liming (500–6,000 kg ha^{-1}), and N addition at low annual doses (2×10 kg N ha^{-1}) and in single shots (150 kg N ha^{-1}). Combinations of lime+N, lime+PK and lime+PKN were also tested. The effects were generally weak or negligible, except that growth was significantly increased by N fertilization in the Scots pine stands, and by lime+PKN in some of the Norway spruce stands.

In another study, the survival and growth of Norway spruce seedlings were found to be more or less unaffected when planted in pre-harvest acidified, limed or N fertilized soil, although the Ca and Zn concentrations in their needles rose after liming, while those of Mn and Al declined.

In closed-canopy stands of Norway spruce and Scots pine with N concentrations of more than 15–16 mg (g DM)$^{-1}$ in current-year needles, N fertilization was indicated to not necessarily stimulate increased growth. Other indicators of highly N-rich forests (e.g. elevated arginine levels) also start to appear above this level.

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Contents

Appendix

Papers I–V

This thesis is based on the following papers, which will be referred to by their respective roman numerals.

I. Nohrstedt, H.-Ö., Sikström, U., Ring, E., Näsholm, T., Högberg, P. and Persson, T. 1996. Nitrate in soil water in three Norway spruce stands in southwest Sweden as related to N-deposition and soil, stand, and foliage properties. Canadian Journal of Forest Research 26, 836–848.

II. Sikström, U. 1997. Effects of low-dose liming and nitrogen fertilization on stemwood growth and needle properties of *Picea abies* and *Pinus sylvestris*. Forest, Ecology and Management 95, 261–274.

III. Sikström, U., Nohrstedt, H.-Ö., Pettersson, F. and Jacobson, S. 1998. Stem-growth response of *Pinus sylvestris* and *Picea abies* to nitrogen fertilization as related to needle nitrogen concentration. Trees 12, 208–214.

IV. Sikström, U. 2001. Effects of pre-harvest soil acidification, liming and N fertilization on the survival, growth and needle element concentrations of *Picea abies* L. Karst. seedlings. Plant and Soil 00, 1–12. (In press).

V. Sikström, U. Effects of liming and fertilization (N, PK) on stem growth, crown transparency and needle element concentrations of *Picea abies* stands in SW Sweden. (Manuscript).

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Introduction

In Sweden, about 55% of the land area is covered by productive forests (Anon., 2000). The conifers Norway spruce [*Picea abies* (L.) Karst.] and Scots pine *Pinus sylvestris* (L.) are the dominant tree species, and in the period 1994–1998, they together yielded c. 77 million m^3 stem wood annually, of which c. 54 million m^3 was harvested and utilized (Anon., 2000). The southern part of Sweden, "Götaland", accounted for about a third of this annual yield and harvest. This region represents a fifth of the productive forest land in Sweden. As well as being an important resource for production of products such as timber and paper, the Swedish forests are valuable for biodiversity and recreation.

Nitrogen (N) and phosphorus (P) are the nutrients that are most important for plant growth in natural environments (Aerts & Chapin, 2000). On mineral soils in most boreal and nemoral coniferous forests, the major limiting factor for forest production is a shortage of plant-available N (Kenk & Fischer, 1988; Tamm, 1991). This shortage of N is referred to in the following text as "limited by N" or "N limitation". As well as N, several other essential elements are needed for synthesis of biomass. These elements are available to a greater or lesser extent to plants, as they are cycled in different forms, within organisms, and in and between ecosystems (cf. Kimmins, 1987). Human activities, especially during the last century, have altered the pools and fluxes of many elemental cycles. For example, the rate of N input into the terrestrial global N cycle has approximately doubled (Vitousek et al., 1998). The main sources of the additional N are fossil fuel combustion and various agricultural measures (such as the production and use of N fertilizer, and use of N_2-fixing crops). Fossil fuel combustion has also caused increased sulphur (S) pools and fluxes of S to rise.

Deposition of sulphur, nitrogen and heavy metals in Sweden

The southern part of Sweden has been subjected to a substantial deposition of air-borne S and N pollution for several decades. During the most recent decades up to 15–25 kg ha^{-1} yr^{-1} of each element has been deposited in forested areas (Lövblad et al., 1995). In Sweden, the amount of deposited S and N compounds decreases from the southwestern part in northeasterly and northerly directions. In the northern part of Sweden, the deposition amounted to less than 3 kg ha^{-1} yr^{-1} of S, and 3–6 kg ha^{-1} yr^{-1} of N in the beginning of the 1990s. However, species composition and the height of forest stands have strong influences on the amounts reaching the forest floor. In southern Sweden, it has been shown that the throughfalls of ammonium-N (NH_4-N), nitrate-N (NO_3-N) and sulphate-S (SO_4-S) to mature Norway spruce stands were 1.5–3 times greater than those to mature Scots pine, European beech (*Fagus sylvatica* L.) and Birch (*Betula sp.*) stands (Westling et al., 1992; Bergqvist & Folkesson, 1995).

Since the late 1970s, there has been a significant reduction in deposited S in most parts of Sweden. Between the years 1980 and 1990, the amounts deposited were estimated to have fallen by c. 40% in southern Sweden (Lövblad et al., 1995), and a further reduction is reported to have occurred in the last decade (Akselsson et al., 2000b). During the period 1980–1990, there were no clear trends in the deposition of N (Lövblad et al., 1995). However, in the last few years there have been indications of a slight reduction in the wet deposition of N (Lövblad, 2000). If planned emission cuts can be achieved, future amounts of deposited N may be substantially reduced, especially of oxidized N. At present in southern Sweden, most of the deposited S is probably leached (Eriksson et al., 1992), whereas the major part of deposited N is retained in the soil (Nilsson et al., 1988).

The deposition of heavy metals [cadmium (Cd), copper (Cu), iron (Fe), lead (Pb), mercury (Hg), nickel (Ni), vanadium (V), and zinc (Zn)] from anthropogenic sources has been substantial during recent decades, and is still well above 'natural' base-line levels except, possibly, for Zn (Rühling & Tyler, 2001). However, there has been a gradual decline in these deposits, especially in southern Sweden. In the year 1995, the concentrations of the previously mentioned metals, in moss carpets in Sweden were 11–52% of the values recorded in 1968/70 (Rühling & Tyler, 2001).

pH and exchangeable base cations in Swedish forest soils

Retrospective studies of Swedish forest soils have shown that pH (Hallbäcken & Tamm, 1986; Falkengren-Grerup, 1986, 1987; Falkengren-Grerup et al., 1987; Tamm & Hallbäcken, 1988; Eriksson et al., 1992), and exchangeable pools of base cations (Falkengren-Grerup & Eriksson, 1990; Falkengren-Grerup et al., 1987) have decreased in recent decades, especially in southern Sweden. The deposition of acid, and air polluting S and N compounds are potential causes of the changes that have been observed in soil chemical properties. Other factors are also involved in soil acidification, such as changes in land use, succession of forest stands (i.e. growth), and forest management (cf. Nilsson & Tyler, 1995; Binkley & Högberg, 1997). Tree harvest, especially whole-tree harvest, leads to a loss of base cations, which causes soil acidification. Nilsson (1993) estimated internal soil acidification processes, e.g. base cation accumulation in trees, to be of the same magnitude as the soil acidification associated with the deposition of strong acids. Other effects of soil acidification on soil chemical properties, except for decreased pH and base cation pools, may include reduced availability of certain nutrients, for example P, and some micronutrients, e.g. molybdenum (Mo), and increased concentrations of inorganic aluminium (Al).

Data from Swedish Forest Soil Survey samples taken during the period 1983–1987 showed regional differences within Sweden in pH(H_2O), especially in the mineral soil (Johansson et al., 1999). The most acidic soils were found in the southwestern part of Götaland where, on average, the pH(H_2O) was 3.7 in the humus layer and 4.4 in the B horizon. In the northern part of Sweden, the average

$pH(H_2O)$ values were 3.9 (humus) and 4.9 (B horizon). Approximately 20% (600,000 ha) of the forest soils in Götaland have a $pH(H_2O)$ lower than 4.4 in the B horizon (Johansson et al., 1999). The base saturation in the O horizon of podsolized soils seems to increase from the south of Sweden towards the north, and in the C horizon there are signs of increases in both south–north and west–east directions within the country (Nilsson, 1995). Data from the period 1983–1987 showed that approximately 30% of the forest soils in southern Sweden had a base saturation of less than 3% in the B horizon (measured at pH 7), and in northern Sweden the corresponding base saturation was 15% (Johansson et al., 1999).

Nitrogen in Swedish forest soils

A major part of the N pool in Swedish forest ecosystems on mineral soils is found as organic matter in the soil and amounts to 1,000–10,000 kg ha^{-1} (Nohrstedt, 1993). Since the last glaciation the historical 'natural' input of N might have averaged about 1–2 kg ha^{-1} yr^{-1}, consisting of biological fixation of N_2 and some base-line N deposition (Högberg et al., 2000). Today the deposition of N is substantially higher (see above). Most of the deposited N is retained in the soil (Nilsson et al., 1998). Generally, the N cycle in Swedish forests is closed and the small amount of leaching that occurs is mainly of organic N (Nohrstedt, 1993). However, quite high leaching of inorganic N has occasionally been observed in some areas, especially in southwestern Sweden (Nilsson et al., 1998). Denitrification, fires and harvest of biomass all cause losses of N. The turnover time of different N pools in the soil is highly variable, from days to centuries (Högberg et al., 2000).

Högberg et al. (2000) estimated the cumulated anthropogenic N deposition to be 500–1,000 kg ha^{-1} for the last 100 years in the most exposed areas of southern Sweden. This corresponds to an increase in the total N pool of ecosystems of between five and 100%, depending on forest type. There are concerns that the input of N into forest ecosystems will lead to saturation (e.g. Aber et al., 1992). However, the term N saturation has been defined in several different ways, by various authors, to refer to all of the following (cf. Högberg et al., 2000): (i) cases where the loss of N is larger or equal in magnitude to the input in an ecosystem, (ii) systems where an elevated level of N leaching can be observed in relation to a given natural background level, and (iii) states in which the supply of N exceeds the N requirements of plants and microorganisms. In this thesis, I have adopted the third definition, using it in the sense that N saturation occurs when N is no longer the factor limiting growth of forest trees.

N fertilization is practiced in Sweden in closed-canopy coniferous stands on mineral soils. N is generally the growth-limiting nutrient in these habitats (Tamm, 1991) and addition of N usually results in increased stem growth (Pettersson, 1994). About two million hectares have been N fertilized in Sweden in recent decades (Anon., 2000). Today the annual area subjected to N fertilization amounts to c. 20,000 ha (Anon., 2000).

Possible effects of some air pollutants on forest trees

Since the end of the 1970s, there have been several reports concerning signs of forest decline in central Europe (e.g. Schultze, 1989) and eastern North America (e.g. Joslin et al., 1992). The symptoms usually included needle yellowing and necrosis, together with premature needle loss, sometimes associated with severe mineral nutrient deficiencies [often magnesium (Mg)]. In some of the worst cases, tree and stand mortality has occurred (e.g. Schulze, 1989; Evers & Hüttl, 1990). These reports raised questions about whether air pollution, such as S and N deposits, caused the symptoms observed, and if they were a threat to sustained forest growth.

Aber and Melillo (1991) grouped the major forms of air pollution thought to affect terrestrial ecosystems, into three categories, (i) oxidant gases [sulphur dioxide (SO_2), nitrogen oxides (NO_X) and ozone (O_3)], (ii) dissolved acids [sulphuric acid (H_2SO_4) and nitric acid (HNO_3)], and (iii) heavy metals (Pb, Ni, Cu, Zn, Cd, and others). The trees in forest ecosystems may be affected by these pollutants either directly, through the crown, or indirectly through the soil. Several hypotheses have been proposed concerning direct and indirect tree responses to air pollution (cf. Tamm & Cowling, 1977; Schulze, 1989).

Direct effects (1) of air pollutants may include:

(1a) Fumigation damage by oxidant gases, such as SO_2, NO_X and O_3. These gases are known to affect important physiological processes in plants (Darral, 1989; Wellburn, 1990), and may reduce tree growth (Roberts, 1984). In general, the ambient concentrations of SO_2 and NO_X in the air in Sweden (Kindbom et al., 2001) are much lower than threshold levels (Roberts, 1986; Anon., 1996) above which damage to forest trees is thought likely to occur. For O_3, concentrations occur in the spring and summer that may be harmful to forest trees, especially in southern Sweden (Kindbom et al., 1995). However, it has not yet been possible to quantify to what extent O_3 affects tree growth (Fuhrer et al., 1997).

(1b) Acids may cause erosion of the cuticle of leaves/needles, and induce other effects, such as increasing the leaching of nutrients (Tamm & Cowling, 1977). However, this effect on forest vegetation foliage seems to be minor as judged from the pH of todays rainfall (Hogan, 1992).

(1c) Increases in net losses of cations from leaves, twigs or bark because of NH_4^+ deposition (cf. Pearson & Stewart, 1993; Roelofs et al., 1985). Increased input of NH_4^+ has been suggested to increase the susceptibility of trees to various adverse influences, e.g. reduced frost hardiness and increased risk of attacks by insects and fungi, and even to be a trigger of forest decline (Nihlgård, 1985).

Indirect effects (2) on trees of deposited air-borne S- and N- containing pollutants, involve changes to the soil. Nutritional status, crown transparency, and growth of forest trees may all be affected. It has been suggested that all of the following indirect effects of pollutants may occur:

(2a) Root damage and deteriorations in root function, i.e. nutrient and water uptake, because of Al toxicity (e.g. Ulrich, 1983; Ulrich, 1986; Schædle et al., 1989), which may increase crown transparency and decrease the growth of forest trees. Al is known to impede the plant uptake of base cations such as calcium (Ca^{2+}) and Mg^{2+} (Schædle et al., 1989; Eriksson et al., 1995).

(2b) Nutrient depletion in the soil induced by deposited acids, and N and S compounds may cause nutrient deficiency in the foliage and reduce tree growth. Base cations in the soil (i.e. Ca^{2+}, Mg^{2+}, K^+ and Na^+) can be exchanged by other ions, notably H^+ and NH_4^+, and leached out, together with SO_4^{2-} and NO_3^- (e.g. Joslin et al., 1992). Furthermore, P and some micronutrients, e.g. Mo, may be locked up in the soil together with Al when the soil is acidified. Reductions in tree growth because of these kinds of potential nutrient deficiencies are probably limited to areas where N availability is not the primary factor limiting growth.

(2c) Increased tree growth may be induced by N inputs in areas where N availability limits growth (e.g. Nihlgård, 1995; Rosén et al., 1992), provided that increased soil acidification does not inhibit root function or adversely affect the availability of nutrients other than N. In Sweden, deposition of S and N co-vary. Increased growth would also increase the demand for, and uptake, of base cations. Hence, this would strengthen the depletion of base cations, which in the long run might cause nutrient deficiencies in the trees.

(2d) According to Rosén et al. (1992), many areas in Europe receive more N than is used by the trees. This surplus of N may cause imbalances in nutrient uptake, while increasing the leaching of NO_3^- and thereby contributing to soil acidification and the adverse effects of Al. Based on studies of tree seedlings grown in culture solutions, Eriksson (1995) suggested that root growth is favoured over above-ground biomass when there are deficiencies of N, P or S. If there are deficiencies of potassium (K), Mg or manganese (Mn), shoot growth may be favoured instead, indicating that a negative feedback mechanism links reductions in nutrient uptake and root growth.

(2e) In soils, a decrease in pH generally increases the solubility of heavy metals, in the form of cations, such as Cd^{2+}, Zn^{2+}, Pb^{4+}, Ni^{2+}, Hg^{2+}, cobalt (Co^{3+}) and chromium (Cr^{3+}) (Tyler et al., 1989). Impeded root development is most likely to be the first visible sign of heavy-metal injury, although elevated concentrations of carbohydrates in the foliage of trees might be an early sign of physiological changes (Tyler et al., 1989).

Schulze (1989) refers to some additional hypotheses that have been put forward regarding the observed forest decline in central Europe. These hypotheses suggest that natural climatic variation or fungal infections of the needles may be responsible for forest decline rather than anthropogenic air pollution. Furthermore, Schulze (1989) proposed that a combination of factors rather than one single process causes decline, defined as reduced growth per unit ground area for trees with needle yellowing. Other scientists have also argued for multiple-stress hypotheses (Prinz, 1987; Roberts et al., 1989).

It has been suggested that the growth of tree roots is related to the Ca/Al ratio in the soil solution (Ulrich, 1983; Cronan & Grigal, 1995), and that plant growth is related to the log(Ca+Mg+K)/Al molar ratio (Sverdrup & Warfvinge, 1993). At ratios of less than one the plant growth has been suggested to decrease. Based on the latter relationship, and a presumed future rate of deposition equal to the level recorded in 1988, Sverdrup & Warfvinge (1995) suggested that the growth rate of Swedish forests would decline by c. 15–20% on average, and locally much more, by the year 2040. However, the relevance of the log(Ca+Mg+K)/Al molar ratio as a growth predictor has been questioned (Högberg & Jensen, 1994; Örlander et al., 1994; Lökke et al., 1996; Binkley & Högberg, 1997).

Measures to counteract soil acidification and an excess of N

Large-scale liming has been proposed for southern Sweden, as a measure to counter the ongoing acidification of soils and lakes (Anon., 1994; Johansson et al., 1999). Acidity of soils can be reduced by addition of neutralizing compounds. Liming has been shown to affect several soil properties. For instance, it tends to increase pH, base saturation and exchangeable amounts of Ca and Mg (depending on Mg-content in the lime used), and to decrease exchangeable Al contents (Smallidge et al., 1993; Stuanes & Abrahamsen, 1994; Kreutzer, 1995; Nihlgård et al., 1996b).

Application of both lime and ash fertilizer, or addition of specific mineral nutrients such as P and K have been proposed as alternative measures to counter soil acidification and related nutrient depletion in some areas (Johansson et al., 1999). Liljelund et al. (1990) suggested application of nutrients other than N as a possible measure to increase the acquisition of N in soils with an excess of plant-available N. This could have additional benefits, since the potentially increased uptake of N it could induce would prevent or reduce leaching of N from the soil.

Aims and scope

Various mechanisms may be involved in the effects of air-borne S- and N-compounds on trees, as listed above. However, the work described in this thesis was mainly related to the indirect effects (2a–2d, above) mediated through changes in soil characteristics, and the following key questions were addressed:

1. Do additions of lime affect growth, nutrient status and crown transparency of coniferous trees growing on acidic mineral soils?

2. Do additions of N affect growth, nutrient status and crown transparency of coniferous trees growing on acidic mineral soils? Are the effects dependent on the ambient N status of the site and the stand? Where N is not the limiting factor for growth, do additions of P and K have an influence on these variables?

The presented data were obtained in studies undertaken in field experiments within the Nordic countries. Most of the experiments for which treatment effects are reported were located in southern Sweden. The studies mainly concern Norway spruce and, to a lesser extent, Scots pine stands on acidic mineral soils. The measurement of treatment effects was relatively short term, i.e. they covered not more than ten years.

Materials and methods

The approaches used consisted both of studies along environmental transects (Papers I and III) and studies in field experiments where the effects of different soil treatments were examined (Papers II, IV and V). The field experiments were designed mainly to establish differences in soil acidity, by application of neutralizing compounds, such as calcite ($CaCO_3$) and dolomite ($CaMg(CO_3)_2$) (Papers II, IV and V), or of elemental S, which is oxidized in the soil into sulphuric acid (H_2SO_4) (Paper IV). The effects of adding N (Papers II, IV and V), as well as P and K were also examined (Paper V).

A short description of the studies in Papers I–V is given below. For a complete account, see the papers in appendices I–V. As well as the experiments reported in these appendices, data from two more field experiments (designated 194 and 223) are included in the thesis (Tables 1 and 2). The two experiments belong to the same experimental series and were subjected to exactly the same experimentation and assessments as the experiments reported in Paper II.

Table 1. Experimental sites and stands reported in the thesis

Variable	Experiment								
	223	183	182	194	244	245	246	247	131[a]
Paper	-	II	II	-	I, V	I, V	V	V	IV
No. of blocks	3	3	3	3	3	1	2	2	3
Location									
Latitude (° ' N)	61 33	57 10	58 11	57 34	56 46	56 45	56 15	56 14	56 26
Longitude (° ' E)	16 17	14 50	11 44	15 39	12 56	12 45	13 06	13 04	14 35
Altitude (m a.s.l.)	300	210	110	210	140	70	110	100	150
Stand									
Species[b]	S.p.	S.p.	N.s.	N.s.	N.s.	N.s.	N.s.	N.s.	N.s.
Total age (yrs)	60	30	40	40	60	50	30	30	70
Volume (m^3 ha^{-1})	250	140	230	220	450	320	240	240	280
Site quality[c] (m^3 ha^{-1} yr^{-1})	6.3	7.8	11.9	13.9	12.0	11.3	12.6	13.2	10.6
I_v[d] (m^3 ha^{-1} yr^{-1})	9.2	9.6	21.4	19.2	13.1	13.0	18.8	23.8	10.1
Soil[e]									
pH(H_2O)									
O-horizon	4.3	4.2	4.7	5.5	3.8	4.0	4.1	4.3	4.2
Min. 0–5	4.7	4.6	4.8	5.2	3.9	4.0	4.0	4.2	4.1
Min. 5–10	5.0	5.0	4.9	5.0	4.2	4.0	4.1	4.3	4.3
C/N in O-horizon	36	28	21	21	31	20	27	24	30

[a] Stand data refer to the previous stand in the year 1989 and soil data in 1991. The stand was finally felled in 1992.

[b] S.p. = Scots pine and N.s. = Norway spruce.

[c] Site quality according to Hägglund and Lundmark (1982).

[d] I_v = Current volume increment on control plots during the experimental period.

[e] Data from two mineral soil layers (0–5 and 5–10 cm).

Responses of forest stands to liming and fertilization (Papers II and V)

Experimental sites and stands

The experimental sites (Table 1) in these experimental series (Papers II and V) were mainly located in the southern part of Sweden (Götaland). The altitude varied between 70 and 300 m a.s.l. The mean annual temperatures were 6–8 °C and the annual precipitation 600–1000 mm, except for the most northerly experiment (3.5 °C and 550 mm) (Alexandersson et al., 1991). The soils of the experimental sites were tills with sand and silt as the dominating fractions in the fine earth. The pH(H_2O) in the soils was generally low, especially at the experimental sites reported in Paper V. The C/N in the O-horizon varied between 20 and 36.

Table 2. Treatments in the experiments. All experiments included an untreated control

Treatment[a]	Experiment								
	223	183	182	194	244	245	246	247	131[b]
Paper II									
500 Lime	X	X	X	X					
1,000 Lime	X	X	X	X					
500 Lime + 150 N	X	X	X	X					
1,000 Lime + 150 N	X	X	X	X					
150 N	X	X	X	X					
Paper V									
3,000 Lime + 25 P + 80 K					X	X	X	X	
3,000 Lime					X	X	X	X	
5×(*2*×10) N					X	X	X	X	
3,000 Lime + 25 P + 80 K + *5*×(*2*×10) N					X	X	X	X	
6,000 Lime + 50 P + 160 K					X	X	X	X	
Paper IV									
12×50 S (600 S)									X
12×100 S (1,200 S)									X
12×500 Lime (6,000 Lime)									X
3×200 N (600 N)									X
12×50 S + *3*×200 N									X

[a] The values refers to kg ha^{-1} applied of the given element or compound, except for values in italics which are numbers of applications.

[b] Treatments started 16 years prior to the final felling in 1992, when the study in Paper IV was established.

The experimental stands were 30–60-year-old Norway spruce and Scots pine forests (Table 1). The Norway spruce stands were highly productive compared with Swedish standards. About 50% of the forested area in Götaland has a site quality within the range covered by the experimental stands (Anon., 2000). The southernmost Scots pine stand was also highly productive, whereas the northern Scots pine stand was only moderately productive.

Experimentation and analyses

In all experiments a randomized block design was used. The treatments (Table 2) included: liming with 500–6,000 kg lime ha^{-1} (Papers II and V); N addition in low annual doses, 2×10 kg N ha^{-1} (Paper V); and N given in single-shot applications, 150 kg N ha^{-1} (Paper II). In the study described in Paper II, some combinations of liming and N addition were also tested. In the experimental series described in

Paper V, P and K were applied together with lime and N. Soil treatments were done by manual top dressing.

In all experiments treatment effects were monitored within ten years, at most, with respect to tree-stem growth and needle element composition of current-year needles. In addition, crown transparency was assessed in the study in Paper V, in the five-year period following the treatments.

Treatment effects were evaluated by analyses of variance (SAS, 1987). In single experiments, the block and treatment factors were included as class variables in the statistical models. Where appropriate, and when pre-treatment data were available, one or more covariates were also included in the model. In Paper V, a more complex model was used, which also included the factor site and the interaction term site×treatment.

Soil sampling

In Paper II, there were no data on treatment effects on soil properties of the low-dose liming (500–1,000 kg ha^{-1}) at the time when the study was reported. In the autumn of 1997, soil was sampled in these experiments (182 and 183), as well as in experiment 223, which belongs to the same experimental series. In each experiment, soil of the control and one of the lime treatments (1,000 kg ha^{-1}) was sampled.

Within each experiment, 20 sub-samples were taken systematically with a corer from each control plot and limed plot. The corer diameter was 6 cm for the O-horizon and 3 cm for the mineral soil. The sub-samples were pooled into one sample per horizon representing each experimental plot. The composite samples were mixed and sieved through 5.6 mm (O-horizon) or 4 mm (mineral soil) meshes. pH(H_2O) was determined in 1:2 soil-water slurries. P, K, Ca and Mg were extracted with 1 M ammonium lactate solution.

For individual experiments, treatment effects were evaluated by analysis of variance (SAS, 1987). A model was developed which included the factors block (b), treatment (t), horizon (h) and the interaction terms b×t, b×h, and t×h. The model was reduced if the interaction terms were not statistically significant ($p<0.05$). This was the case for all variables tested, except for the element Ca in experiments 183 and 223. In these two cases, there was a significant t×h interaction. Therefore, the horizons were analysed individually, with a model including only b and t.

Responses of regeneration to pre-harvest treatment (Paper IV)

Norway spruce seedlings were examined at the time of planting in spring 1992 and during five subsequent growing seasons. The planting was done in pre-harvest acidified (600 S, 1200 S), limed and N fertilized soils (Table 2). The previous three stands (three blocks) consisted of about 55-year-old Norway spruce at the start of the treatment in 1976. 600 S consisted of annual applications of 50 kg ha^{-1} and 1200 S of 100 kg ha^{-1} elemental S powder (100% S) over a 12-year period (1976–1987). Liming also involved annual applications, of 500 kg ha^{-1} $CaCO_3$ powder during the same period. N was given in doses of 200 kg ha^{-1} as urea $[(NH_2)_2CO]$ on three occasions (1976, 1980 and 1985). All applications were done by top dressing. Survival, growth and needle element concentrations of the seedlings were recorded. Analysis of variance (SAS, 1987) was used in order to evaluate residual effects of the treatments. The statistical model included the factors block and treatment.

Studies along transects (Papers I and III)

The control plots in experiments 244 and 245 (Table 1), and in an additional experiment (241), were used in order to study N-cycling in Norway spruce (Paper I).

The study described in Paper III was based on N fertilization experiments in 28 Scots pine and 21 Norway spruce stands. The aim of the study was to evaluate the relationships between ambient foliar N concentrations and responses of stem growth to N application at doses between 120 and 180 kg ha^{-1}. Most of the stands (latitude 56 to 66 °N) were located in Sweden, but a few were in Norway and Finland. The experiments were distributed among sites with a large variation in site quality. The site quality varied between 2.5 and 8.2 m^3 ha^{-1} yr^{-1} and 4.6–13.9 m^3 ha^{-1} yr^{-1} in the Scots pine and Norway spruce stands, respectively. Linear regression (SAS, 1987) was used in the analysis of these relationships.

Methodological considerations

Treatments

Most of the experimental treatments were performed to alter soil acidity, and to evaluate their implications for important forest tree properties. However, changes in soil acidity influence many other soil properties, both chemical and biological (e.g. Tamm, 1989; Smallidge et al., 1993; Stuanes & Abrahamsen, 1994; Kreutzer, 1995; Nihlgård et al., 1996b). Hence, the effect on the studied variables of changes in soil acidity *per se* is difficult to distinguish.

Changes in ecosystems caused by deposition of anthropogenic air-borne S and N compounds, are probably fairly slow processes (with low doses added steadily, all year around) compared with artificial treatments in experiments (which usually involve quite high doses in one or a few applications). Thus, the experiments might produce artifacts, i.e. short-term shock effects, which may not occur in a natural forest ecosystem. This must be considered when recorded data are interpreted (cf. Skeffington & Wilson, 1988). Furthermore, some treatments, e.g. lime application, are known to have a long-term impact on soil properties (Kreutzer, 1995; Persson et al., 1995; Nihlgård et al., 1996b). Thus, long-term study periods, i.e. several decades, are needed in order to cover a complete effect.

The availability and plant uptake of added nutrients may interact with factors that show large between-year variations, such as water availability and weather conditions (e.g. temperature and precipitation). Thus, the response of a treatment may vary from one year to another, and the greatest variations may be associated with single-shot applications of easily soluble compounds, and with treatments that have short-term effects, i.e. a few years (cf. Tamm, 1985).

Tree growth

In order to obtain accurate estimates of the effects of fertilization on tree growth in field experiments it is highly important to have good comparability between experimental plots, in terms of both stand and soil properties. To some extent, it is possible to adjust for pre-treatment differences by using e.g. analysis of covariance. Many of the experiments were established in stands that were thinned quite recently before treatment. If the grade of thinning varied between different experimental plots, the effect of fertilization might have been confounded with the effect of thinning. Probably, this problem is greatest when the fertilization response is weak, the monitored period is short, or when the stand being considered is highly productive, since responses to thinning in these kinds of stands tend to appear and culminate quickly (Jonsson, 1995).

Results and discussion

Tree growth response to liming

Effects on forest stands

If liming is to have any effect on tree growth, it must first affect soil properties. One of the low-lime doses (1,000 kg ha^{-1}) examined in paper II was found to have some minor measurable influence on soil chemical properties ten years after the treatment in experiment 223, and thirteen years afterwards in experiments 182 and 183 (Table 3). Overall, the mean pH(H_2O) values were 0.2–0.6 units higher in the O-horizon and in the upper mineral soil (0–5 cm) of the limed plots than of the control plots. However, the effect of the treatment was statistically significant ($p<0.05$) only in experiment 223. The concentration of extractable Ca was almost doubled in most experimental sites and horizons examined. The effect was significant ($p<0.05$) in the O-horizon in experiment 183, in the mineral soil (0–5 cm) in experiments 183 and 223, and tended ($p=0.09$) to be greater in the 5–10 cm mineral-soil horizon in experiment 223. For Mg, the extractable concentration was approximately doubled (not statistically significant) in the upper soil horizons in experiment 182, and in the mineral soil in experiment 223, whereas it was more or less unaffected in experiment 183. There was a small significant reduction of extractable K in the whole soil profile in experiment 183.

Table 3. pH(H_2O), extractable P, K, Ca and Mg [mg (100 g DM soil)$^{-1}$] in the soil on control plots (C) and limed plots (L) in experiments 182, 183, and 223. Data refer to soil samples taken in autumn 1997, ten years (experiment 223) or thirteen years (experiments 182 and 183) after treatment. Means of three blocks per experiment

Experiment	Horizon[a]	Treatment[b]	pH[c]	P	K[c]	Ca[d]	Mg
182,	O	C	4.4	1.4	12	64	18
Norway spruce		L	5.0	1.4	12	130	33
	M 0–5	C	4.4	0.5	3.8	11	3.7
		L	4.7	0.6	3.7	26	7.2
	M 5–10	C	4.6	0.4	2.7	4.7	2.1
		L	4.6	0.4	2.3	6.3	1.6
183,	O	C	4.0	1.6	**11**	**45**	7.3
Scots pine		L	4.2	1.6	**10**	**98**	6.1
	M 0–5	C	4.3	1.6	**4.3**	**6.3**	1.2
		L	4.5	1.5	**4.0**	**23**	1.5
	M 5–10	C	4.9	1.7	**3.3**	4.7	0.63
		L	4.8	1.3	**2.5**	5.7	0.47
223,	O	C	**4.1**	2.5	21	72	9.5
Scots pine		L	**4.5**	2.3	21	130	12
	M 0–5	C	**4.6**	0.4	3.5	**8.8**	0.93
		L	**4.8**	0.4	3.0	**17**	1.5
	M 5–10	C	**5.0**	0.4	2.8	6.0	0.63
		L	**5.2**	0.4	3.2	10	1.1

[a] O = O-horizon; M 0–5 = Mineral soil 0–5 cm; M 5–10 = Mineral soil 5–10 cm.

[b] 1,000 kg $CaCO_3$ ha^{-1}, with 1% Mg in the form of $CaMg(CO_3)_2$.

[c] Bold letters indicate a statistically significant ($p<0.05$) overall treatment effect in the whole profile.

[d] Bold letters indicate a statistically significant ($p<0.05$) treatment effect within the corresponding horizon.

In the experiments reported in Paper V, several soil properties were significantly ($p<0.05$) affected by the liming after four years (Nohrstedt, 2001). On average, at the four experimental sites, the pH(H_2O) value of the O-horizon increased by 0.6–1 units, and by c. 0.1 unit in the upper mineral soil. No clear dose effect was found (3,000 and 6,000 kg ha^{-1} tested). The extractable amount of Ca+Mg increased three to six fold in the O-horizon, and almost doubled in the upper mineral soil. Furthermore, in the O-horizon, net N mineralization and potential nitrification rates were enhanced 1.5 and six fold, respectively (Nohrstedt, 2001). From the soil samplings, especially in the O-horizon, it can be concluded that the 3,000 kg ha^{-1} liming treatment caused some differences in soil chemical properties, and hence, could have affected soil biological properties. The low-dose liming (1,000 kg ha^{-1}) caused smaller changes (Table 3).

Many Swedish field experiments on liming have found indications that growth was unaffected, or reduced by 5–20%, during the 5–20-years following liming in Scots pine stands (Popovic´ & Andersson, 1984; Tamm & Popovic´, 1989; Andersson et al., 1996; Sikström, 1996; B. Popovic´, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden, pers. comm.). There are also reports of growth being increased by a similar degree (Popovic´ & Andersson, 1984). However, the effects of these treatments had low statistical significance, and in many cases the experiments did not include replicates. Most of the cited studies included stands growing on low-productivity sites, where SI_{H100}<T20 [i.e. the upper height at age 100 years for pine (T), was 20 m), and moderately productive sites (T20–T24). The liming compound was usually $CaCO_3$, and the doses, given as single-shot applications, varied between 5,000 and 10,000 kg ha^{-1}, i.e. up to 20 times more than in the experiments reported in this thesis.

In one of my studies (experiment 223 in Table 4), I found a similar growth reduction after the low-dose liming (500–1,000 kg ha^{-1}) in the less productive Scots pine stand (SI=T25). In the other of my experiments with Scots pine (experiment 183 in Paper II) on a more fertile site (SI=28), the response was of a similar magnitude, but reversed. This was in agreement with one of the experiments reported by Andersson et al. (1996). However, none of the effects were statistically significant ($p<0.05$).

An average stem growth reduction of 3% (non-significant), over a period of 15–25 years, was found in a comprehensive (n=68) Finnish study of Scots pine stands varying in age between six and 130 years (Derome et al., 1986). In these experiments the treatment involved application of about 2,000 kg ha^{-1} of dolomite. The data were also grouped into three site quality classes, roughly corresponding to the following site indices, and the growth responses for each class, compared with the control, were: class T12–20, -20% (n=9); class T19–27, -3% (n=29); and class T24–T30, -1% (n=24) (Derome et al., 1986; M. Kukkola, The Finnish Forest Research Institute, Vanta, Finland, pers. comm.). This indicates that growth was reduced on low-productivity sites, and unaffected on moderately and highly productive sites, more or less in accordance with the Swedish observations. However, all the differences showed low statistical significance (p=0.28–0.51) (Derome et al., 1986).

Table 4. Basal area (BAI; m^2 ha^{-1} 10 yrs^{-1}) and volume increment (VI; m^3 ha^{-1} 10 yrs^{-1}) as means of three replicates per experiment. Values in the same row marked with different letters differ significantly statistically ($p<0.05$). Figures within brackets denote values in percent of the control

Experiment	Variable	Treatment[a,b]					
		0	Ca	2Ca	CaN	2CaN	N
194, Norway spruce[c]	BAI	14.0a (100)	13.5a (96)	15.6a (111)	14.3a (102)	15.3a (109)	16.8a (120)
	VI	192a (100)	186a (97)	207a (108)	193a (101)	201a (105)	220a (115)
223, Scots pine[d]	BAI	6.51ab (100)	6.13a (94)	6.06a (93)	7.91c (122)	7.25bc (114)	7.74c (119)
	VI	92.5a (100)	83.9a (91)	80.0a (86)	116a (125)	106a (115)	108a (117)

[a] Ca = 500 kg $CaCO_3$ ha^{-1}, with 1% Mg in the form of $CaMg(CO_3)_2$; N = 150 kg N ha^{-1} as NH_4NO_3.

[b] All mean values (least-square means) were corrected with a covariate: BAI before treatment or, for VI in experiment 194, also with the volume at the start of treatment.

[c] p-values for BAI ($p_{model} = 0.027$; $p_{treatment} = 0.097$), and for VI ($p_{model} = 0.004$; $p_{treatment} = 0.14$).

[d] p-values for BAI ($p_{model} = 0.021$; $p_{treatment} = 0.008$), and for VI ($p_{model} = 0.078$; $p_{treatment} = 0.040$).

Nilsen & Granheim (1988) found no distinct growth responses of 75 to 110 years old Scots pine stands in Norway, during the 11-year period following addition of 3,000–15,000 kg $CaCO_3$ ha^{-1}. All the experimental stands they examined were clearly growth limited by N. Some other Norwegian studies on liming showed growth in young stands of Scots pine and Norway spruce was unaffected by test doses of 500–6,000 kg crushed $CaCO_3$ ha^{-1} (Tveite et al., 1994a). In some of these experiments the height growth was given, and in others estimates of volume growth were recorded.

The liming treatments I examined in Norway spruce stands on fertile sites (Papers II and V, Table 4) were associated with small or negligible effects on stem growth. During the 5 to 10 year observation period after treatment, the volume increment (VI) was altered by between -9% and +12% in the individual experiments, but these effects were not statistically significant ($p<0.05$).

The results were consistent with other studies conducted in Sweden (Popovic′, 1992; Andersson et al., 1995; Andersson et al., 1996; Akselsson et al., 2000; B. Popovic′, pers. comm.; N. Salih, SLU, Uppsala, Sweden, pers. comm.). The cited experiments reported average growth responses per experimental site varying from reductions of 8% to increases of 17% in growth, compared with untreated control plots. The effect period varied between three and 14 years. In these cases too, the responses showed low statistical significance. Almost all of these experiments were located in Götaland on quite fertile sites [SI>G28 (G=spruce)]. All these experiments had 3–4 replicates, and the lime compounds examined were $CaCO_3$ and $CaMg(CO_3)_2$ at doses of, mainly, 2,000–6,000 kg ha^{-1}, and occasionally up to 12,000 kg ha^{-1}.

In contrast, Derome et al. (1986) found a statistically significant reduction in growth of 12–16% during a 14-year period after application of 2,000 kg ha^{-1} of lime, mainly as $CaCO_3$. The experiments were located in two c. 40-year-old Norway spruce stands on fertile sites (SI=G30–32) in southeastern Finland. However, Derome et al. (1986) point out that the treatment effect might have been overestimated in one of the trials, because growth trends differed on the experimental plots before treatment. Derome et al. (1986) also conducted a more extensive study on liming in Norway spruce stands (n=32), among which the fertility among sites varied substantially (SI=G17–G33), and the stand ages ranged from five to 111 years, even though a majority of them were 10–50 years old. The sites were located between 61 and 63 °N. On average, there was a growth reduction by 10% (not statistically significant), during the 15 to 20 year period examined after the treatment. The four classes of site indices analysed showed the following average relative stem-growth responses compared with the control: G17–21, -24% (n=4); G22–25, -12% (n=12); G27–31, -8% (n=14); G32–33, -13% (n=2) (Derome et al., 1986; M. Kukkola, pers. comm.). As for Scots pine, the lowest fertility class showed the greatest mean relative growth reduction, and even at the more fertile sites there were reductions on average, albeit non-significant (p=0.12–0.24). It should be noted, of course, that the same relative growth reduction renders different reductions in absolute terms on low- and high-productivity sites.

In a summary of observations from various liming experiments in SW Germany, Spiecker (1991) noted that there was no decrease in stem growth, but rather a small increase in even-aged high-productivity Norway spruce stands. The overwhelming majority of German and other mid-European liming trials found no, or only slight, indications of growth increases associated with liming for Norway spruce and Scots pine (Nebe, 1972; Hüttl & Zöttl, 1993). Smallidge et al. (1993) reported various responses of coniferous trees to liming in a review of several North American studies, including both greenhouse studies and field experiments. They concluded that the responses depend on several factors such as soil type, type of lime applied and duration of the observations.

After liming, the magnitude of changes in soil chemical properties, such as pH, base saturation, and exchangeable Ca, Mg and Al depend on several factors, such as the dose applied (Nihlgård et al., 1996b; Hallbäcken & Popovic´, 1985). This was also indicated in a comparison of the effects in the two experimental series reported in this thesis (Table 3). The liming by 3,000–6,000 kg ha^{-1} (Nohrstedt, 2001) caused larger changes in soil chemical properties than low dose liming with 1,000 kg ha^{-1} (Table 3). However, there were no major differences after four years between the effects of applying doses of 3,000 and 6,000 kg ha^{-1} in the study reported in Paper V, except in the exchangeable amounts of Ca and Mg (Nohrstedt, 2001). The tree-growth responses in relative terms did not seem to be affected by the lime dose given, at least not within about a decade following treatment (Papers II and V). This is consistent with results from other experiments where different doses (up to 15,000 kg ha^{-1}) were tested in Scots pine and Norway spruce stands (Andersson et al., 1996; Nilsen & Granheim, 1988; Akselsson et al., 2000). Furthermore, no clear differences between the growth responses elicited by the two compounds used in liming [$CaCO_3$ and $CaMg(CO_3)_2$] have been demonstrated (B. Popovic´, pers. comm.; Andersson et al., 1996).

Persson & Wirén (1996) suggested that liming results in (i) reduced net N mineralization in soils poor in N (C/N in humus c. 40), (ii) reduced or unaffected mineralization in soils less poor in N (C/N in humus about 30), and (iii) increased net N mineralization in soils rich in N (C/N in humus 20–28). In Figure 1, the relative stem growth responses after liming with $CaCO_3$ or $CaMg(CO_3)_2$ at doses of 500–9,000 kg ha^{-1} were plotted against corresponding C/N ratios in humus. Data come from 15 liming experiments in Scots pine and Norway spruce stands in Sweden. Linear regression indicated there was a threshold ratio, C/N 30, at which the stem growth was unaffected, while growth was slightly reduced above this ratio, and slightly increased below it. The site quality also seemed to be correlated with the relative growth response after liming (Figure 1), with an apparent threshold of 9 m^3 ha^{-1} yr^{-1}. The data demand cautious interpretation, since the analysis includes two tree species, and the sampling of the humus may not have been consistent among experiments. However, there might be a link between the effect of liming on net N mineralization and growth responses of Scots pine and Norway spruce after liming.

Other factors, except for reduced net N mineralization, that may cause reductions in tree growth after liming include boron (B) deficiency (Lehto & Mälkönen, 1994) and adverse effects on roots and mycorrhiza (e.g. Persson, 1988; Finley, 1995). Furthermore, nutrient uptake may be affected by ion antagonism, e.g. Ca^{2+}/K^{+} interactions. Data on these kinds of phenomena are not available for experiment 223 (Table 3), where there was a small, non-significant growth reduction. In experiment 245 (Paper V), the B concentration in the needles did not indicate any deficiency that could explain a decreased growth. However, the estimates of growth for this site are uncertain (for instance there were no replicates).

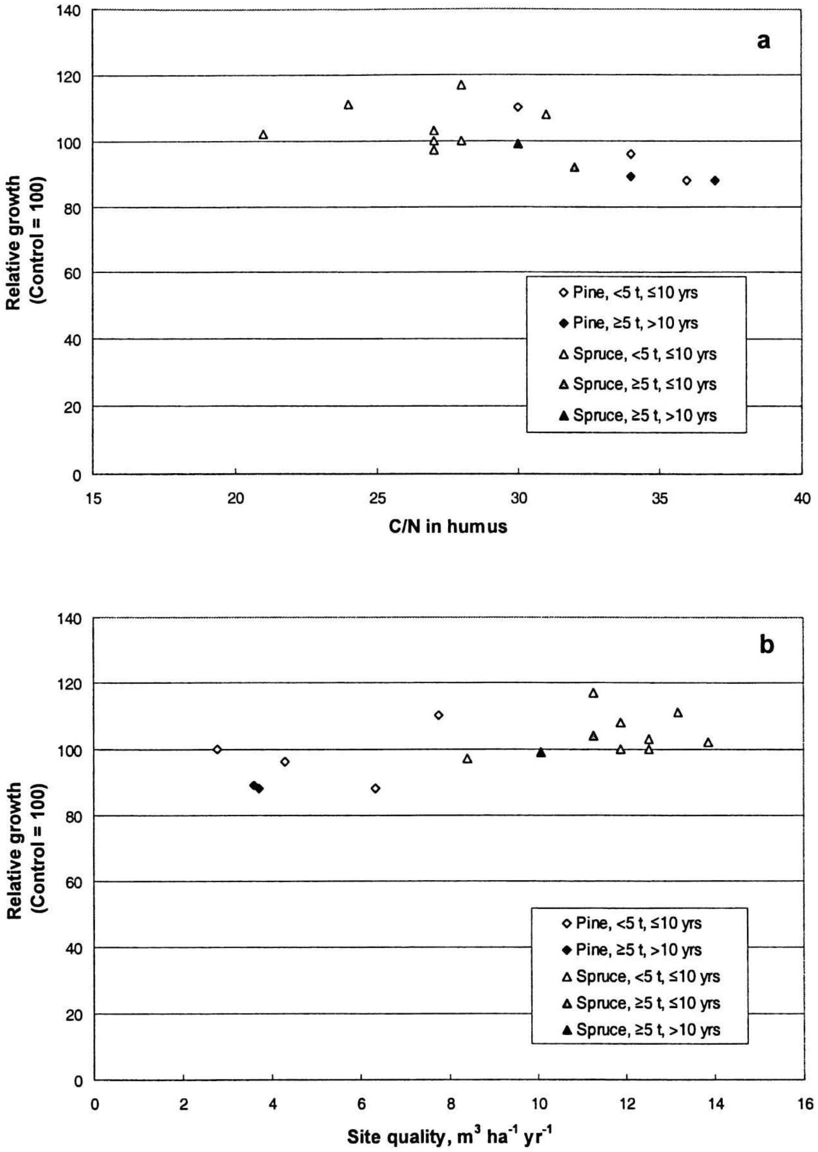

Figure 1. Relative stem growth after liming in relation to (a) C/N in humus (CN) and (b) site quality (SQ). Data from Swedish liming experiments with two–four replicates. Data were grouped according to lime doses and response periods [less than 5,000 kg ha^{-1} (< 5 t), and equal to or more than 5,000 kg ha^{-1} (≥ 5 t); less or equal to ten years (≤ 10 yrs), and greater than ten years (> 10 yrs)]. (Data from: Popovic´ & Andersson, 1984; Tamm & Popovic´, 1989; Andersson et al., 1995; Sikström, 1996; Akselsson et al., 2000; Papers II and V; B. Popovic´, pers. comm.; N. Salih, pers. comm.; T. Persson, SLU, Uppsala, Sweden, pers. comm.). The following equations were derived by linear regression:
(a) Relative growth = 137 - 1.25×CN; n = 15; $R^2 = 0.39$; $p_{\text{slope}} = 0.012$
(b) Relative growth = 88.3 + 1.36×SQ; n = 17; $R^2 = 0.39$; $p_{\text{slope}} = 0.007$

Popovic´ (1988) & Andersson et al. (1996) stated that an initial growth decrease after liming might be reversed, leading to an increase in the future. However, it is difficult to find any conclusive data to support their suggestion. Firstly, there are only a few experiments available in which effects have been followed for more than 20 years. Secondly, the significance of the relatively scarce long-term results that have been reported is uncertain because of the lack of replicates. There are also uncertainties regarding how mortality and thinning were treated in these analyses. Based on available data (discussed above), the value of any predictions of growth responses beyond a 20-year period after liming would be doubtful. Indeed, there are reports of tendencies for pools of total N in the soil to decline after liming on fertile sites (Kreutzer, 1995; Persson et al., 1995). Also, net N mineralization rates have tended to be lower than in controls even c. 40 years after some lime applications, at least at high doses, of 9,000–10,000 kg ha^{-1} (Persson et al., 1995). This implies that N availability in the soil may decrease in the long term after liming on fertile sites, and that tree growth may consequently be reduced in cases where N availability limits growth.

In summary, the growth in Scots pine stands on low- and moderate- productivity sites (SI<T24) seems to be unaffected or slightly reduced (0–20%) over a period of 5–20 years following liming with $CaCO_3$ or $CaMg(CO_3)_2$. Results from more fertile sites are sparse, but indicate that growth is more or less unaffected. In Sweden, growth responses in Norway spruce stands are best investigated on fertile sites (SI>G28), where the stem growth has been unaffected or slightly increased (0–10%). There might be a link between the observed small changes in growth and the effect of liming on net N mineralization in soil. It should be stressed that most reported treatment effects have shown low statistical significance. Furthermore, many of the older experiments in Scots pine did not have replicates. Thus, the results from many studies may be uncertain, as stateded by Popovic´ & Andersson (1984). Observations of the long-term effects (>20 yrs) of liming are sparse and uncertain.

Effects of pre-harvest liming on regeneration

The pre-harvest liming treatment (6,000 kg ha^{-1} in total) caused large and persistent effects on soil chemical properties (Table 1 in Paper IV; Andersson et al., 1995). The field-layer vegetation was more abundant in the limed plots compared with the controls during the first years after final felling and planting (Paper IV; B. Olsson, SLU, Uppsala, Sweden, pers. comm.). This suggests that liming altered the growth conditions. Nevertheless, the survival and growth of the planted four-year-old Norway spruce seedlings were more or less unaffected (Paper IV). The seedlings were examined during a five-year period following planting. In this case the seedlings were planted only a few months after the final felling of the former stand. However, the more abundant field-layer vegetation associated with the liming implies that competition may be more severe and, thus, the regeneration patterns may be more complex in limed than in untreated areas if the planting is done some years after the final felling.

Variable results have been reported for growth responses of seedlings to lime applied at the time of planting or some years later (e.g. Ljungström et al., 1996; Podrázsky and Balcar, 1996; Tveite et al., 1994). The soil type probably has a strong influence on the growth response, as suggested by Smallidge et al. (1993), and, possibly, on how the addition of lime affects net N mineralization (cf. Persson & Wirén, 1996).

Is tree growth related to soil acidity?

The study reported in Paper IV included treatments in which elemental S was applied at two doses. These pre-harvest treatments still had detectable effects on some soil chemical properties at the time of final felling, even though the soil had recovered to some extent after the S addition, which had terminated five years earlier (Andersson et al., 1995). At final felling, pH(H_2O) in the upper mineral soil was reduced by 0.1–0.2 (control 4.1–4.4) units, and exchangeable concentrations of Mg and of K in the humus were 20–30% lower than in controls, respectively. Furthermore, the previous S addition had caused a reduction in the biomass of field-layer vegetation, both before (Hallbäcken & Zhang, 1998), and after (Paper IV; B. Olsson, pers. comm.) the final felling of the former Norway spruce stands. Thus, the results indicate that the S treatment made growth conditions less favourable, although it reduced competition between field-layer vegetation and planted Norway spruce seedlings. Nevertheless, during the five-year period examined after planting, neither the survival nor the growth of the planted Norway spruce seedlings were significantly ($p<0.05$) affected by the pre-harvest soil acidification (Paper IV).

Originally, the experiment in Paper IV was established in three Norway spruce stands, about 55 years in age, and it is one of few acidification experiments located within the southern part of Sweden, where the mineral soils are the most acidic in the country. However, in spite of the additional acidification caused by the S treatments at the two different doses tested (600 and 1200 kg S ha^{-1}), the growth in stem volume was not significantly altered during a 14-year period after the start of the treatments (Andersson et al., 1995). However, there was an indication that the high S addition was associated with a reduction in basal area increment. If all the S supplied in this treatment was oxidized into SO_4^{2-} in the soil, it would correspond to an extra 150 years of H^+ input at ambient levels (H.-Ö. Nohrstedt, Skogforsk, Uppsala, pers. comm.). Moreover, in two other similar acidification experiments in Norway spruce stands, in the southern part of Sweden, no differences in stem growth were found 13–14 years after the start of the treatments (250–300 kg S ha^{-1}) (Tamm and Popovic´, 1995; N. Salih, pers. comm.).

There are also some experiments on increased soil acidification in forest stands located further north within the Nordic countries. In these experiments too, no significant reductions in stem growth have been observed, except at very high inputs of acid, corresponding to several decades or even one or two centuries of ambient deposition (Tveite et al., 1994b). The Swedish acidification experiments in Scots pine have not documented any reduced stem growth during the 15 to 20 year observation periods (Tamm & Popovic´, 1989). In these cases, pH and base saturation in the upper mineral soil were reduced by c. 0.2 units (control 4.5–5.4) and by 4–12 percent units (control c. 20%), respectively. Exchangeable base cations (mainly Ca^{2+} and Mg^{2+}) were also reduced. In the humus, these variables tended to change in the same directions. Similar results on soil properties and stem growth of Norway spruce, Scots pine and Lodgepole pine (*Pinus contorta* Dougl.) were obtained in some Norwegian studies on increased soil acidification, except at very high acid loading in the form of dilute H_2SO_4 (pH 2–2.5), which reduced growth (Tveite et al., 1994b). When the treatment was terminated, the growth reduction was reversed to some extent at later stages. The authors did not identify any clear cause for the observed growth reductions, but suggested several possible explanations. One was that the availability of Mg had been reduced, as indicated by both reductions in the exchangeable amounts of the element in the soil and decreased concentrations in the needles. However, these observations were not consistent across the different tree species and sites. Another suggestion was that reduced needle biomass was responsible, as an adaptation to changed nutrient conditions, which would not be detected by diagnostic foliar analysis. A third suggestion was that an increased concentration of Al in the soil may have hampered nutrient uptake, either by ion-antagonism or by negative effects on the root biomass. However, the latter process would be expected to affect the total nutrient uptake, not solely that of a specific element (Tveite et al., 1994b).

Örlander et al. (1994) found no influence on tree growth of pH, base cations in the soil water, concentrations of Al or the Ca/Al ratio. Their study included 20 sites with Norway spruce and Scots pine stands in southern Sweden ranging in age from 28 to 89 years. Similarly, in an analysis of data from the Swedish National Forest Survey and the Forest Soil Survey including 1,100 observations, Olsson et al. (1994) found no strong correlation between pH(H_2O) in the mor layer and current growth in mature spruce stands at sites with podzolized and glacial tills. Furthermore, Binkley & Högberg (1997) pointed out that increased growth after N fertilization is often accompanied by a decline in soil pH.

In conclusion, there are no clear indications among data available from field experiments or field surveys that moderate increases in soil acidification adversely affect the growth of Scots pine or Norway spruce at ambient soil pH values observed in Sweden and Norway. However, at very high inputs of acids the growth has been hampered (Tveite, 1994b). This suggests that the acidification of Swedish forest mineral soils seen in recent decades (Nilsson & Tyler, 1995) has had a minor or negligible effect on the growth of Norway spruce and Scots pine stands. Thus, some other factor, or factors, must exert more important influences on the stem growth of these species growing on mineral soils. Furthermore, the effect of liming on tree growth seems to be negligible or slight (see above). When the growth is altered, either positively or negatively, the change seems to depend on the effect of liming on soil N turnover and availability. There are also data, both on regional (Dahl et al., 1967; Lahti & Väsinen, 1987) and local (Giesler et al., 1998) scales demonstrating a positive correlation between soil pH and base saturation on the one hand, and plant productivity and plant community composition on the other. The mechanism and causal relations between base cation availability and N turnover are not fully understood. It has been suggested that soil pH and the supply of base cations affect plant productivity via effects on N availability (Giesler et al., 1998). However, the fact that liming may sometimes reduce levels of plant available N, at least in the short-term, seems to conflict with these suggestions.

Needle nutrient composition responses to liming

Increases or decreases in needle nutrient concentration may reflect changes in uptake patterns or leaching of nutrients, as well as changes in needle mass. In addition, nutrients are often re-translocated within plants.

In current-year needles of mature Norway spruce trees, the N concentration decreased (experiment 182 in Paper II), or tended to decrease (experiment 194, data not shown), during the year following the application of low doses of lime (500 and 1,000 kg lime ha^{-1}). This was not the case in the Scots pine stands (experiments 183 and 223). Reduced N concentrations in current-year needles after liming have been reported earlier, although only at quite high total lime doses (5,000–10,000 kg ha^{-1}), and mainly on low-productivity sites (Popovic´ & Andersson, 1984). However, results from a previous study of a quite productive Norway spruce stand (Andersson et al., 1995), are consistent with the findings in Paper II. In all the Norway spruce stands, where the N concentrations decreased temporarily in the foliage, the stem-growth was not affected (Paper II; Table 4). However, the growth was decreased in some of the Scots pine stands for which reduced N concentrations in needles were reported by Popovic´ & Andersson (1984).

The low-dose liming had no effect on needle Ca concentrations (Paper II). However, all the treatments including lime in the study in Paper V (3,000 and 6,000 kg lime ha^{-1}) were associated with increased concentrations of Ca in current-year needles of Norway spruce. Concentrations of Cu were also raised (especially by the high dose of lime). There are several examples of increased concentrations of Ca after liming with higher doses than the 500–1,000 kg ha^{-1} examined in Paper II (Tamm & Popovic´, 1989; Andersson et al., 1995; Nihlgård et al., 1996a; Nilsen & Granheim, 1998; Salih & Andersson, 1999; Akelselson et al., 2000a), and of Mg levels in needles rising after addition of Mg-containing lime (Derome et al., 1986; Kaupenjohann et al., 1989; Nihlgård et al., 1996a).

Following liming there are usually reductions in needle concentrations of Mn (Schierl & Kreutzer 1991; Andersson et al., 1995; Nilsen & Granheim, 1998), and B (Aronsson, 1983; Lehto & Mälkönen, 1994). In the study described in Paper V, treatments including lime were associated with reduced Mn and B concentrations in the spruce needles six–seven years after treatment. Reduced B concentrations may decrease growth, and at levels less than 4–5 μg (g DM)$^{-1}$ may cause visible damage (Aronsson, 1983).

Most of the changes in nutrient concentrations of needles that I found in limed experimental stands with closed canopies have been reported earlier. Also the Norway spruce seedlings in the study in Paper IV showed increased Ca and a tendency to have elevated Cu concentrations in one-year-old needles, as well as reduced concentrations of Mn, after the pre-harvest lime addition (6×500 kg ha^{-1}). Furthermore, concentrations of Zn increased and that of Al decreased, as reported for older Norway spruce trees by Akselsson et al. (2000a).

The observed changes in nutrient concentrations in needles following liming are probably due to altered availability of the corresponding nutrients in the soil, either as a direct effect of the addition (Ca and Mg), or via changes in solubility (Zn, Cu, Mn and B) induced by a rise in soil pH (e.g. Lehto & Mälkönen, 1994). For N, the change in net N mineralization and N availability (Persson & Wirén, 1996) may be crucial factors. The observed changes in nutrient concentrations after liming, except those of N and B, are not likely to influence tree growth.

Is needle nutrient composition related to soil acidity?

Mg is the element that has been shown to decrease most often in current-year needles of Scots pine and Norway spruce after artificially induced increases in soil acidification (Tamm & Popović, 1989; Tveite et al., 1994a; Andersson et al., 1995). This probably reflects the reduced amounts of exchangeable Mg observed in the soil in some of these experiments, which may, in turn, be an effect of increased leaching. Mg deficiency has been a commonly reported symptom in spruce foliage in central Europe (cf. Roberts et al., 1989). In my regeneration study, the Mg concentration was not reduced in the one-year old needles of the Norway spruce seedlings on the pre-harvest acidified plots (Paper IV). This was despite a reduction in the Mg concentration in the foliage of the previous mature stand on the acidified plots (Andersson et al., 1995). However, the soil had recovered to some extent at the time of final felling, and the turnover rate of organic matter may have increased after the harvest, possibly increasing plant available Mg. In the same study, the Norway spruce seedlings on the limed plots showed significantly ($p<0.05$) higher K concentrations than the seedlings on the most acidified plots. This was not seen in the old stand. As for Mg, K may have been leached from the soil because of the increased acidification, although it is difficult to explain how the liming could have caused K concentrations to increase. However, regardless of the explanation, this did not cause any differences in seedling survival and growth between the two treatments (Paper IV).

Tree growth response to addition of N and other nutrients

Effects on forest stands

It can be hypothesised that the supply of plant-available N in the soil and the ambient nitrogen status in the stand influence the growth response of trees to added N. This was supported by the study reported in Paper III, which indicated that the relative growth response of Scots pine and Norway spruce to N fertilization (120–180 kg N ha^{-1}) decreased as the N concentration in current-year needles of control plots rose. The results suggested that N fertilization would not necessarily stimulate growth if the N concentrations in the needles were greater than 15–16 mg $(g\ DM)^{-1}$. A similar threshold has been suggested for Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] (Hopmans & Chappell, 1994; Turner et al., 1998), whereas a lower value [13 mg $(g\ DM)^{-1}$] was indicated in a study on Lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) (Brockley, 2000). The threshold interval we found [15–16 mg $(g\ DM)^{-1}$] was in the same range as the optimal N concentration in the foliage for maximum growth of Scots pine derived from a field experiment with different N doses (Tamm, 1985). Brække (1994) and Linder (1995) suggested 18 mg $(g\ DM)^{-1}$ was the optimal N concentration for maximal growth, in situations where no other nutrient is growth limiting. However, these kinds of empirically derived intervals or threshold values probably have large degrees of uncertainty and should be seen only as crude guidelines for evaluating the nutritional status and potential fertilization responses of coniferous trees under field conditions. Higher thresholds and intervals have been suggested for seedlings (Tamm, 1968; Swan, 1972). Miller & Miller (1981) found optimal foliar nutrient concentrations to be dependent on the stage of stand development.

Montañés et al. (1993) suggested that the DOP-index (Deviation from Optimum Percentage) could be used as a tool to evaluate diagnostic needle nutrient concentrations. This index is calculated from the formula $DOP = [(C \times 100) / C_{ref}] - 100$, where C is the nutrient concentration in the sample being assessed, and C_{ref} is the optimal nutrient concentration for maximum growth. A DOP-index equal to zero indicates an optimal nutritional status for an element, a positive value indicates an excess and a negative index a deficit. The different nutrient elements are then ranked in order to identify the growth-limiting nutrient (Montañés et al., 1993). However, it is important to stress that a prerequisite for a correct evaluation of DOP-indices and nutrient concentrations *per se* is that the reference values must be sufficiently well known.

In all my experimental stands the N concentration in current-year needles was less than 18 mg $(g\ DM)^{-1}$ so, according to the DOP-index, growth was N limited in most stands (Table 5). The Scots pine stands (experiments 182 and 223) had among the lowest N concentrations and DOP-indices for N. In these stands, a single-shot application of 150 kg N ha^{-1} resulted in increased stem growth (Paper II; Table 4). Such a response is commonly obtained in Swedish coniferous forests on mineral soils with a site index below about 32 m, whereas the effect is more variable on sites with indices above this value (Pettersson, 1994; Nilsson & Wiklund, 1992; Nohrstedt et al., 1993; Persson et al., 1995). In the two Norway spruce stands where the same fertilization regime (150 kg N ha^{-1}) was applied, the stem growth was 15% greater (non-significant) than in the control in one (experiment 194 in Table 4), but there was no apparent growth response in the other (experiment 182 in Paper II). According to the N concentrations and the DOP-indices for N (Table 5), growth should have increased after this N fertilization. However, the lack of response was consistent with the relatively high productivity of these two stands (Pettersson, 1994). SI ranged from 28 to 35 m in experiment 182, and was even higher (36 m) in experiment 194.

All the Norway spruce stands reported in paper V were highly productive (SI=32–35). Stem growth was about 15% greater in N treated than in control plots in experiments 244 and 246, and about the same in experiments 245 and 247. In this series of experiments the N dose (100 kg N ha^{-1} in total) was lower than in the experiments reported in Paper II, and it was applied on several occasions, twice per year for five years. Splitting the dose has been shown to give a lower stem-growth response than a single-shot dose (Pettersson, 1994). In addition, some of the experiments represent sites that were very rich in N for Swedish conditions, especially experiment 245 (Papers I and V). At this site, the leaching of nitrate-N was nearly of the same magnitude as the throughfall of inorganic N, suggesting that the conditions were near N-saturation. This is unusual in Sweden (Nohrstedt, 1993). Furthermore, at the site of experiment 245 there were high concentrations of N and arginine, as well as high ^{15}N abundance levels in the needles, all of which are indicators of sites rich in N (Paper I, Näsholm et al., 1997). Nevertheless, the stand showed growth levels that were consistent with predictive functions for similar Norway spruce stands in the region (Paper I).

At the point where N ceases to be the growth-limiting factor, another factor should become limiting, if the law of limiting factors (Liebig´s principle) is valid. In the experiments reported in Paper V, P and K were added in some of the treatments. However, this additional PK (representing the difference between the treatments lime and lime+PK) did not unambiguously promote growth in any of these stands (Paper V), although their DOP-indices indicated that they were growth limited by P or K (Table 5). In experiments 244 and 245, P ought to be limiting, and K in experiment 247 (Table 5). This shows that it may be difficult to assess nutrient growth limitations solely according to diagnoses of foliar concentrations, and DOP-index rankings. However, one uncertainty for the PK fertilization was whether the added P and K were available and taken up by the trees. This was likely at the higher dose, since soil analyses (Nohrstedt, 2001) showed there were elevated amounts of easily extractable P four years after treatment, and the P concentration in the needles was increased. The lower doses of P and K gave less pronounced effects.

Table 5. Concentrations [mg (g DM)$^{-1}$] of N, P, and K, (i) in current-year needles of Scots pine (S.p.) and Norway spruce (N.s.) from the experimental stands sorted in ascending N concentration (means of three–six years of sampling on one–three control plots per experimental site), (ii) suggested threshold concentrations, and (iii) values taken from surveys in Sweden

	N	P	K	Reference
(i)				
Exp. 223, S.p.	11.0 (-39)[a]	1.4 (-22)	5.1 (-15)	Sikström (1992)
Exp. 182, Block 3, N.s.	11.5 (-36)	1.2 (-33)	5.7 (-5)	Paper II
Exp. 183, S.p.	12.8 (-29)	1.5 (-17)	5.1 (-15)	Paper II
Exp. 182, Block 1, N.s.	13.0 (-28)	1.4 (-22)	5.0 (-17)	Paper II
Exp. 182, Block 2, N.s.	13.0 (-28)	1.5 (-17)	6.4 (7)	Paper II
Exp. 194, N.s.	13.0 (-28)	1.9 (6)	6.3 (5)	Sikström (1992)
Exp. 246, N.s.	14.0 (-22)	1.5 (-17)	5.2 (-13)	Paper V
Exp. 244, N.s.	14.5 (-19)	1.3 (-28)	5.3 (-12)	Paper V
Exp. 247, N.s.	16.8 (-7)	1.6 (-11)	4.7 (-22)	Paper V
Exp. 245, N.s.	17.1 (-5)	1.5 (-17)	5.4 (-10)	Paper V
S.p. (n = 28)	9.3–14.4	-	-	Paper III
N.s. (n = 21)	10.2–15.6	-	-	Paper III
(ii)				
Optimum	>18	>1.8	>6.0	Brække (1994; revised 1996)
Pre-optimum	15–18	1.5–1.8	5.0–6.0	
Deficiency	12–15	1.2–1.5	3.5–5.0	
Strong deficiency	<12	<1.2	<3.5	
(iii)				
S.p. (n=21–43); ALL	8.4–13.8	1.1–1.9	4.1–6.2	Nohrstedt (1990)[b]
N.s. (n=11–15); ALL	8.6–13.5	1.0–2.1	4.2–7.0	
S.p. (n=21–43); N	10.3–15.3	1.0–1.4	3.5–5.0	Jacobson and Nohrstedt (1993)[c]
N.s. (n=17); SW	11.7 [±1.3]	0.9 [±0.2]	4.6 [±0.5]	Eriksson et al. (1993)[d]
N.s. (n=60); S (NFI)	10.9 [±1.3]	1.1 [±0.2]	3.8 [±0.6]	Eriksson et al. (1995)[e]
N.s. (n=47); SW (NBF)	12.9 [±1.8]	1.1 [±0.2]	4.3 [±0.8]	
N.s. (n=5); S (IVL)	13.0 [±2.6]	1.1 [±0.3]	3.4 [±0.6]	
S.p. (n=9); S	14.2–15.3	2.6–2.7	5.0–7.7	Thelin et al. (1998)[f]
N.s. (n=31–33); S	13.3–14.5	1.6–1.8	4.0–6.4	
N.s. (n=22); S	11.0–15.5	1.0–1.7	3.9–9.3	Näsholm et al. (1997)[g]

[a] DOP-index (Montañés et al., 1993). Reference values according to optimum concentrations in section (ii) of the table. For further explanation see text.

[b] Range of maximum and minimum values from control plots in fertilization experiments all over Sweden (ALL) for current-year needles from middle-aged and old stands.

[c] Range of maximum and minimum values from control plots in fertilization experiments, mainly located in northern Sweden (N), for current-year needles from middle-aged and old stands.

[d] Mean values [±SD] of samples taken in 1990 in southwestern Sweden (SW) for two- and three-year old needles from stands that were older than 30 years.

[e] Mean values [±SD] from three different data sets (NFI, NBF and IVL) sampled in 1990 in southern (S) and southwestern (SW) Sweden for two- and three- year old needles from stands that were older than 30 years.

[f] Range of mean values from four years sampled between 1985 and 1994 in Scania, the southernmost (S) part of Sweden, for current-year needles from stands averaging 30 years in age.

[g] Range of maximum and minimum values from samples taken in 1994 in southern (S) Sweden for current-year needles from stands between 35 and 90 years of age.

In southern Sweden, there have been no reports of cases in which N-free fertilization alone clearly stimulated the growth of Scots pine and Norway spruce stands on mineral soils. However, there are a few cases in which growth of Norway spruce tended to be increased (Nilsson & Wiklund, 1992; Nohrstedt et al., 1993). In this region, addition of water has also been demonstrated to slightly increase growth of Norway spruce (Nilsson & Wiklund, 1992; Bergh et al., 1999). For Norwegian conditions, Nilsen (1998) concluded that the vast majority of coniferous stands respond to N addition by increasing growth, although P may occasionally be growth limiting in young Norway spruce stands. Dralle & Larsen (1995) suggested that that there may have been a shift from N limiting growth into K-, and possibly P-limitation in recent decades in some regions in western Denmark. However, in a Norway spruce stand in the same region, it was impossible to be certain which of the two elements, N or P, was limiting growth (Ingerslev, 1998). The concentrations of both of these nutrients were lower than suggested thresholds, but adding them did not clearly stimulate growth. Salih & Andersson (1999) had similar problems in a Norway spruce stand in SW Sweden, when they tried to establish which element was growth limiting. They used different techniques for evaluating nutrient concentrations in the foliage.

In Paper V, on average for all the experimental sites, there was a statistically significant ($p<0.05$) increase in stem-growth (possibly somewhat overestimated; see Paper V) when lime, PK and the annually applied low-N doses were combined. If this was a genuine effect, one explanation may be that N availability increased as an additive effect of both liming and N addition, which may have been further enhanced by the addition of PK. An additive growth response of Norway spruce to P plus N has also been reported, since NP treatments have sometimes induced stronger growth than N alone (Kukkola & Saramäki, 1983), but in other cases no such response was found (Nohrstedt et al., 1993; Jacobson & Pettersson, 2001). Where N fertilization has been very intensive, an additive effect of simultaneous PK addition has been shown for Norway spruce (Tamm, 1985; Tamm and Popovic´, 1995), but this has not always been the case for Scots pine (Tamm, 1985).

An increase in growth (+15%) was associated with the combined treatment, i.e. low-dose liming plus N, in the Norway spruce experiment (182) reported in Paper II. It is difficult to find a straightforward explanation for this effect. However, it might have been a similar response to that seen in treatment CaPKN in the Paper V study, assuming that the PK addition in the latter did not contribute to the growth response.

There have been numerous fertilization experiments in which several tonnes of N have been applied to coniferous stands per hectare, without causing specific growth abnormalities or site deterioration (Kenk & Fischer, 1988; Miller & Miller, 1988; Tamm, 1985). Thus, Scots pine and Norway spruce, and many other coniferous trees, show great tolerance to N addition, even at heavy doses.

Effects of pre-harvest addition of N on regeneration

The study reported in Paper IV evaluated the effect of pre-harvest N-fertilization (3×200 kg N ha^{-1}) on regeneration. The growth of the Norway spruce seedlings was not affected during the first five years after planting. The added N corresponded to an extra input of 25% in relation to the ambient N store in the topsoil (i.e. down to 20 cm in the mineral soil) at the start of treatment. Similar results on growth have been obtained in two other studies on Norway spruce (my own unpublished data) and Scots pine seedlings (Högbom et al., 2001) during the first 4–11 years after planting. In the Norway spruce plantation, the total pre-harvest-N doses were up to 2,400 kg N ha^{-1}, corresponding to an extra input of 130% in relation to the total store down to 10 cm in the mineral soil. In the Scots pine plantation up to 1,800 kg ha^{-1} was added pre-harvest, i.e. 250% extra input in relation to the N-store down to 25 cm in the mineral soil (Högbom et al., 2001). In the last study cited, several changes of soil N variables were documented in the clearcut 11 years after the final felling and 17 years after the last N addition. For example, the C/N ratio in the humus was reduced, while both the amount of inorganic N in the soil and net N mineralization was elevated in the pre-harvest fertilized plots (Högbom et al., 2001). Despite this, seedling growth was unaffected. The results indicate that the seedlings were not N limited or that they were weak competitors for available N. Young Scots pine seedlings may show small growth responses, at least in height growth, to N addition (Pettersson 1984). As regards the studies on Norway spruce seedlings, they were planted on fertile sites where, within a few years, abundant field-layer vegetation was established. In the study in paper IV, the total biomass of the field layer vegetation was slightly higher (non-significantly) on the N fertilized plots during the first three years after planting (B. Olsson, SLU, Uppsala, pers. comm.). Thus, at these sites in Paper IV the competition from field-layer species might have been severe and N may possibly have been growth limiting for the seedlings.

Does deposition of atmospheric N affect tree growth?

Opinions differ (e.g. Eriksson & Johansson, 1993; Nadelhoffer et al., 1999) on the contribution made by deposits of air-borne N-containing pollutants to the increases in tree growth observed over time in many boreal and nemoral forests (Kenk & Fischer, 1988; Spiecker et al., 1996). On sites where N does not limit tree growth, deposition of N would not be expected to increase growth. For sites where N is growth limiting, it seems plausible to assume that an extra N input in the form of deposition would increase growth. However, the fate of the added N plays an important role in determining the growth response. Several studies have shown that the tree biomass is a minor primary sink for the input of different N sources (Melin, 1986; Nadelhoffer et al., 1999; Nohrstedt et al., 2000). There is an established more or less linear relationship (depending on site quality) between the stem-growth responses of Norway spruce and Scots pine and the amount of N added as a single shot of between 60 and 150 kg N ha^{-1} (Pettersson, 1994). Extrapolating to even lower doses suggests that they should have a minor or negligible effect on growth. Furthermore, the proportion of added N taken up by the trees appears to decrease with reductions in the dose of N (Melin, 1986). Thus, N inputs supplied as small pulses throughout the year may not be major short-term contributors to increased tree growth. This means that hypothesis 2c in the introduction is based on questionable grounds, i.e. the assumption that growth will increase following N inputs in areas where N availability limits tree growth may not always be true.

Another possibility is that increased tree growth may be more likely to occur directly after low-dose N additions on fertile sites that are quite rich in N, but do not have N in excess, compared with sites where plant-N availability is very low, since the trees may have a better chance to compete for the extra N input in an environment that is already quite rich in N. However, the growth response might be weak. This was also indicated in the study in Paper V.

On the other hand, increased net N mineralization has been observed after soil N enrichment, at least after fairly high inputs with an accompanying decrease in soil C/N ratios (Andersson et al., 2001; Högbom et al., 2001). It is possible that this might stimulate tree growth in a more long-term perspective. However, whether or not net rates of N mineralization increase after rates of N addition similar to those of N deposition is unclear. In the study reported in Paper V, the net N mineralization was not affected four years after annual low-dose N additions (Nohrstedt, 2001).

An increase in growth due to N deposits would also induce additional demand for, and uptake, of base cations (see hypothesis 2c in the introduction). Hence, such deposits would accelerate depletion of base cation pools in the soil, which in the long run might cause nutrient deficiencies in the trees, unless weathering compensated for base-cation acquisition. However, if deposited N does not trigger growth, increased uptake of base cations would not be a problem. In the experimental series reported here (Paper V), the amounts of easily extractable Ca, Mg and K in the soil were unaffected by four years of low additions of N (Nohrstedt, 2001). In other studies on repeated N fertilizations with very large total doses (up to 2,400 kg ha^{-1}), the amounts of extractable base cations have been found to be unaffected for 10–20 years after the last fertilization (Nohrstedt et al., 2000; Högbom et al., 2001).

In a multiple-site study (NITREX), some watersheds and forest plots have been sheltered by a roof from the ambient precipitation and then subjected to rainfall of pre-industrial quality. At one of the Dutch sites (Ysselsteyn), which was N-saturated (with 60 kg ha^{-1} of throughfall N and 66 kg ha^{-1} of leached N), growth was found to be increased for four years after this sheltering (Boxman et al., 1998a). The increased growth coincided with reductions in needle N and arginine concentrations, together with increases in Mg and K concentrations of current-year needles. Both the initial and the reduced N concentrations were much higher than the suggested optimal concentration. At the other NITREX-sites, the growth was unaffected (Emmet et al., 1998), including both the 'clean rain' roof plots (10–55 kg N ha^{-1} yr^{-1} removed), and plots given annual N additions (35–90 kg N ha^{-1}). However, the experimental designs may have introduced uncertainties in the estimates of treatment effects on growth in some of the cited studies. For example, the study in Ysselsteyn included a comparison between non-replicated 10×10 m plots, where only the five widest trees in diameter per plot were assessed (Boxman et al., 1998a). Furthermore, at another experimental site (Gårdsjön, Sweden), trees growing in different catchment areas, with differences in pre-treatment stand age and site index, were compared (Stuanes et al., 1998). These variations might have confounded the results.

Needle nutrient composition responses to addition of N

The N fertilization with 150 kg N ha^{-1} increased the N concentration in current-year needles of both Scots pine and Norway spruce as reported in Paper II. These species showed the same response in experiments 194 and 223 (data not shown). The increase was detected in the first year or a few years after the fertilization, and was most pronounced in experiment 183, where the concentration was elevated for the whole five-year period examined. Increased stem growth was most clearly obtained in the Scots pine stands (Paper II; Table 4). Elevated needle N concentrations, a few years after a single-shot application of similar N doses have been commonly reported (Nohrstedt et al., 1993; Jacobson & Nohrstedt, 1993; Salih & Andersson, 1999). After more intensive N fertilization, the N concentration increases even more (Nilsson & Wiklund, 1994; Rosengren-Brink & Nihlgård, 1995). In N-limited young Scots pine and Norway spruce stands, annual N additions of doses of at least 30–60 kg N ha^{-1}, raised N concentrations in the foliage to higher levels than in untreated control plots (Tamm, 1985, 1991; Linder, 1995). However, when the addition was terminated in one case, the N concentration decreased rapidly again (Quist et al., 1999). Hence, several studies have demonstrated that addition of N at quite high doses increases the N concentration in Scots pine and Norway spruce needles, but the effect seems to last only as long as the addition continues.

After the annual low-dose N applications described in Paper V (2×10 kg N ha^{-1}), which were equivalent to approximately double the ambient deposition rate of N, there was no significant ($p<0.05$) effect on the needle N concentration of Norway spruce, as measured during the six–seven years following the start of the N addition. This was in agreement with some, but not all, of the NITREX-sites. In some cases needle N concentrations were reported to increase three–four years after annual N addition of 35–70 kg N ha^{-1} yr^{-1} (Boxman et al., 1998a).

At the Gårdsjön NITREX-experimental site, the nutrient concentrations in current-year and one-year-old needles were not affected by sheltering the ground from ambient throughfall (10–11 kg ha^{-1} yr^{-1} of inorganic-N and 18 kg ha^{-1} yr^{-1} of SO_4-S) (Stuanes et al., 1998). The stand comprised 80–100 years old Norway spruce and the last assessments were made four years after the start of the treatment. Similar results were reported from another NITREX-site, also located in a Norway spruce stand, at Klosterhede (Denmark) (Beier et al., 1998), whereas a reduction in needle N concentrations were indicated at Sollingen (Germany), (Breidemeier et al., 1998). Furthermore, the needle N concentration of the Scots pine stand in Ysselsteyn fell, from a very high initial level [28.9 mg $(g\ dw)^{-1}$], when the ground was sheltered from most of the ambient deposition of c. 60 kg $ha^{-1}\ yr^{-1}$ (Boxman et al., 1998a). In this case, K and Mg concentrations increased.

A few years after the N fertilization was applied in my study reported in Paper II, the P concentration increased in the Scots pine current-year needles, although no P had been added, and stem growth increased. Thus, an increased uptake of P seems to have been triggered by the N fertilization. Usually, the concentrations of macronutrients other than N are marginally affected by N fertilization (c. 100–200 kg N ha^{-1}), even at repeated applications (Jacobson & Nohrstedt, 1993; Nilsson & Wiklund, 1994; Andersson et al., 1995; Rosengren-Brink & Nihlgård, 1995). Tamm et al. (1999) report depressed concentrations of P, K, Ca, Mg and Mn in Scots pine current-year needles following annual addition of N during a long period (c. 20 years). However, no severe deficiencies were developed, possibly with the exception of Mg at the higher doses applied. Furthermore, Jacobson et al. (2000) found no residual effects in macronutrient concentrations in above-ground parts of a Norway spruce stand 13 years after the last N addition, which amounted in total to at most 2,400 kg N ha^{-1}. This was also true for the needle nutrient composition of Scots pine (Högbom et al., 2001) and Norway spruce (Paper IV) seedlings planted in pre-harvest N fertilized plots.

In the study reported in Paper I, there were no major differences in most nutrient concentrations in current-year needles, apart from N, among the three Norway spruce stands that differed in N status. The stand least rich in N (experiment 241) had the lowest K concentration and the stand richest in N (experiment 244) the lowest Zn concentration.

The concentration of B is known to decrease in coniferous foliage after N fertilization. Severe deficiencies following N fertilization have been reported, especially in the inland regions of the central and northern parts of Sweden (Aronsson, 1983; Möller, 1984). Nowadays, B is added to the fertilizer in practical N fertilization regimes, thus avoiding this problem. In southern Sweden, even high and repeated N doses do not seem to induce B deficiency, although the B concentrations are reduced (Nilsson & Wiklund, 1994; Andersson et al., 1995; Rosengren-Brink & Nihlgård, 1995). Concentrations of Mn, Zn and Cu have been shown to decrease after repeated N additions at intervals of 5–10 years between applications (Jacobson & Nohrstedt, 1993). However, deficiencies were not usually induced, at least according to the deficiency thresholds suggested by Braekke (1994) except, possibly, for Cu.

Does deposition of atmospheric N affect needle nutrient composition?

The deposition of air-borne N pollutants may have a minor direct influence on the N concentration in coniferous foliage, at least in a short-term perspective. However, the observed increase in net N mineralization that generally follows repeated N additions (Andersson et al., 2001; Högbom et al., 2001) may induce long-term retention of N in the trees, and possibly raise N concentrations in the foliage of coniferous trees. However, a small, gradual increase in foliar biomass may keep the concentration constant, as hypothesised by Aber et al. (1989).

A set of data from southern Sweden indicates that N concentrations have increased over time in current-year needles of Norway spruce and Scots pine (Aronsson, 1985), but another set from this region suggests they have not changed (Thelin et al., 1998). One problem when evaluating time trends in these data, is the relatively short time periods (10–20 years) and the infrequent samplings assessed, since the inter-annual variation in concentrations should be considered (cf. Tamm, 1991; Linder, 1995). Furthermore, sampling in permanent plots may be influenced by the ageing of the trees, which can affect both the ambient 'natural' concentrations (Höhne, 1964) and the demand (Miller et al., 1981) for different nutrients. However, several German studies indicate that N concentrations have increased over time, according to Hüttl & Schaaf (1995) and Evers & Hüttl (1990), even if there are exceptions to this generalisation (Hüttl & Wiesniewski, 1987).

In contrast to N, a temporal reduction in concentrations of P (Aronsson, 1985), K and Zn (Aronsson, 1985; Thelin et al., 1998) has been reported in southern Sweden, whereas changes in Cu have been variable. The Ca and Mg concentrations in Norway spruce needles increased during the same period in the study by Thelin et al. (1998).

Thus, it is difficult to establish, from the available data on nutrient concentrations in needles, whether there has been a long-term change in the nutrient composition of coniferous foliage in southern Sweden. A major problem is the lack of extensive data sets that describe both spatial patterns and long–term temporal trends.

Crown transparency responses to liming and to addition of N and PK

In the study reported in Paper V, crown transparency in the four Norway spruce stands was found to be unaffected in the five years following treatment by addition of lime (3,000 kg $CaCO_3$ ha^{-1}), lime plus PK (at two different doses), or the combination of lime, PK and N. Application of low annual N doses also had no effect on crown transparency.

Based on a study in northern England, Harrison et al. (1999) suggested that crown transparency in Sitka spruce [*Picea sitchensis* (Bong.) Carr.] and Scots pine may decrease with reductions in P stress. This was not confirmed for Norway spruce in my study, although there may have been differences in the P status, both of the stands and soils, in the two studies that may explain the difference in results.

In agreement with my results, crown transparency was not affected by annual doses of 35 kg N ha^{-1} yr^{-1} added in weekly batches to one of the NITREX sites (Gårdsjön, Sweden) (Stuanes et al., 1998). Similar results were obtained by sheltering the ground from the ambient throughfall of inorganic-N and SO_4-S, amounting to 10–11 kg ha^{-1} yr^{-1} and 18 kg ha^{-1} yr^{-1}, respectively (Ferm & Hultberg, 1998). The catchments were dominated by Norway spruce stands 80-100 years of age.

Bonneau et al. (1990) found variable responses of needle biomass and needle yellowing to Mg and Ca additions in a study of mature Norway spruce and Silver fir [*Abies alba* (Mill.)] stands in the French Vosges mountains. The treatments induced increased needle biomass or regreening in some stands with low Mg concentrations [0.4–0.5 mg (g DM)$^{-1}$], but caused further deterioration in other stands, while in still other cases the fertilization had no affect on needle biomass or discoloration. Furthermore, in some stands the control plots continued to decline, while in other cases the controls recovered in a similar way to the fertilized plots, indicating that factors other than Ca and Mg deficiency had caused the stands to deteriorate before the treatments had begun. Bonneau et al. (1990) concluded that it was difficult to judge which stands should be fertilized in order to reduce crown transparency, since annual fluctuations in the nutrition level occurred and the exchangable content in the soil was not a very good predictor. Also, in other studies in central Europe variable effects on crown transparency are reported to have occurred after liming and after addition of various nutrients, especially of P, K and Mg, and sometimes N (see Paper V).

Needles from trees with differing degrees of crown transparency did not show any major differences in needle nutrient concentrations in stands in SW Sweden examined by Aronsson (1985). Furthermore, neither Carlén et al. (1995), nor Hägermark (1995) found any significant relations between crown transparency and soil chemical properties, e.g. pH in the soil, for Swedish forests. On the contrary, the crown transparency tended to increase with an increasing part of cation exchange capacity being occupied by Ca in the soil, and to decrease as the part being occupied by Al increased in the soil (Hägermark, 1995). Furthermore, the crown transparency has been shown to co-vary with factors such as age of the forest stand and site index (Thomsen & Nellemann, 1994; Carlén et al., 1995), and water availability (Strand, 1997).

Thus, neither my own data nor other available measurements clarify the extent to which crown transparency is related to nutrient concentrations in needles, or the factors that govern whether or not changes in nutrient status will affect crown transparency in a short-term perspective.

Implications for liming and fertilization

Most of the examined nutrients (Ca, Mg, S, Mn, Fe, Zn, B and Cu) in the foliage of the experimental stands covered by this thesis were not likely to limit growth. This conclusion is based on comparison of measured elemental concentrations in current-year needles of Scots pine and Norway spruce with levels suggested to affect growth (Brække, 1994, revised 1996). In almost all stands the concentrations of N, P and K were below the proposed thresholds for optimal growth (Table 5). However, the examined stands did not show any severe nutrient deficiencies, except for N in the least productive Scots pine stand.

Comparing measurements of the nutrient concentrations (N, P and K) in needles of the experimental stands with available reference data shows that they were within ranges that commonly occur in Sweden (Table 5). The observed P and K concentrations are commonly found in Swedish coniferous stands on mineral soils, but they were somewhat higher than those recorded in a sampling of other stands in the region. In experiments 244 and 246, the N concentrations were fairly high for coniferous stands on mineral soils in Sweden as a whole, but they were common for the region. The N concentrations in experiments 245 and 247 were quite high, even for the region.

A nutrient budget for a forest stand includes the inputs from deposition, weathering, and fertilization, and the losses from leaching and removal of nutrients, by processes such as harvesting and, in some cases, fire. Many factors affect the nutrient availability and productivity of a forest stand. Abiotic factors, such as bedrock, water availability and climate are important determinants of weathering rates and nutrient turnover. Human land use, both historic and present, such as grazing, burning, litter raking and forestry also influence the nutrient status.

When evaluating the present nutrient status of Swedish coniferous forests, one has to keep in mind that forest trees in 'natural' situations seldom, or never, have an unlimited supply of mineral nutrients or, therefore, maximal growth. On the contrary, there is always some element in shortage, usually N, in Swedish mineral soils. Today, we have methods, e.g. fertilization, available to increase forest production. Therefore, it is important to decide what rates of forest growth should be deemed reasonable, acceptable, and sustainable.

Data from our own and other field experiments and surveys give no clear indications that increases in soil acidity have any adverse effect on the growth of Scots pine and Norway spruce stands, unless very high doses of acid are supplied (Tveite, 1994). Furthermore, in stands of these species, field experiments have shown that the effects of liming on growth are weak or negligible for periods of up to 20 years. All this suggests that the acidification of Swedish mineral soils that has occurred in recent decades (Nilsson & Tyler, 1995) has had a minor or negligible effect on the growth of Norway spruce and Scots pine. Thus, factors other than soil acidity must be more important determinants of nutrient uptake and stem growth of these species. However, liming may have some indirect effect on growth rates via changes in the net N mineralization in the soil.

A shortage in available N has commonly been, and still is, a factor limiting the growth of Scots pine and Norway spruce on mineral soils in Sweden, and it affects most of these soils in southern Sweden (Nilsson & Wiklund, 1992; Pettersson, 1994). There is no evidence suggesting that growth responses to N fertilization have diminished during the period 1960–1990 (Pettersson, 1994; F. Pettersson, SkogForsk, Uppsala, Sweden, pers. comm.). During the same period, variable effects (ranging from no effect to substantial increases) have been obtained on fertile sites. In these cases, the main factor(s) that regulate(s) growth are not fully understood. In southern Sweden, addition of water has sometimes been shown to stimulate growth, whereas addition of nutrients other than N has not been unambiguously shown to increase growth. Sites rich in N, where growth is not likely to be limited by N, do not seem to occur only in southern Sweden, but also in some areas in the northern parts (Giesler et al., 1998).

The experiments reported in paper V were located in southern Sweden, where it has been suggested that measures should be taken to counter the ongoing soil acidification (Anon., 1995; Johansson et al., 1999). One of the reasons given for taking acute measures was to maintain sustainable growth and vitality of the forests. All my experimental sites (Paper V) had pH values in the mineral soil (20–30 cm) that were at or below the suggested threshold of pH 4.5, and thus, qualified for such measures (Johansson et al., 1999). The suggested measures included liming with a dose of 3,000 kg ha^{-1}, applying a mixture of lime and ash fertilization, and adding specific mineral nutrients (Johansson et al., 1999). However, the results (shown in Paper V) of these treatments on the short-term responses of tree growth and crown transparency, as well as needle nutrient status, do not indicate any great need for the suggested measures to be taken in Norway spruce stands on similar sites in the region. Results from the Farabol experiment reported by Andersson et al. (1995) also suggested that liming would not give any great benefits.

This thesis has focused on ambient conditions, and analysed relatively short-term effects of treatments. However, further increases in soil acidification and eutrophication because of N may in the long run provoke unwanted effects in the studied variables. This may happen if further inputs of N contribute significantly to increased growth, and if weathering cannot compensate for the depletion of base cations caused by natural acidification and deposition of acidifying compounds. The time frame in which such conditions may arise is an open question. However, the facts that severe nutrient disturbances have not so far arisen on the most acidic soils in Sweden and that there has recently been a large reduction in S deposition implies that air pollution may have a successively weaker impact in the future.

Summary and conclusions

The survival and growth of Norway spruce seedlings was not significantly affected by pre-harvest acidification, liming or N fertilization, in the first five years following planting in a field experiment in southeastern Sweden. In the limed plots, the Ca and Zn concentrations in the needles rose, while those of Mn and Al declined.

The stem growth of 30–60 year old Norway spruce (two experiments) and Scots pine (two experiments) was not significantly affected by low-dose liming with 500–1,000 kg ha^{-1} as calcite, plus some admixture of dolomite, during a ten-year period following treatment. In one of the Norway spruce stands, the N concentration in current-year needles was significantly reduced during the year the lime was applied.

In the same experiments, N fertilization with 150 kg N ha^{-1} significantly increased the stem growth in the Scots pine stands, which had moderate, or high productivity. The response was consistent with expectations from predictive functions. In the two experiments in highly productive Norway spruce stands, the same treatment did not significantly affect growth. N fertilization is known to give variable effects in highly productive Norway spruce stands. The N concentration in current-year needles increased during the first 2–5 years after the N fertilization.

The combination of low-dose liming and N fertilization (150 kg N ha^{-1}) significantly increased the stem growth in one of the Norway spruce experiments, although Mg concentrations in the current-year needles were lower than in the controls for some years. A reduction in Mg was also detected in two of the other experimental stands, where the growth was not affected by the combined treatment.

In another experimental series, including four 30–60 year old Norway spruce stands in southwestern Sweden, the stem growth was not significantly affected during a five-year period following treatment with 3,000 kg ha^{-1} as a mixture of calcite and dolomite. Growth was also not altered by addition of the same lime dose plus P (25 kg ha^{-1}) and K (80 kg ha^{-1}), or by this combined treatment at doubled doses. Furthermore, annual addition of N (2×10 kg ha^{-1} yr^{-1}) during the five-year period did not change the growth rate. However, a treatment including the combination of the lower doses of lime and PK, plus the annual N addition increased the stem growth by 21%, on average, for all experiments. The most plausible cause of the increased growth was increased N availability in the soil. None of the tested treatments affected the crown transparency of the Norway spruce stands.

In the same series of Norway spruce experiments, liming was associated with increased Ca and Cu concentrations, and reduced B and Mn concentrations in current-year needles. However, these changes were not likely to affect growth. The P concentration was found to be significantly higher in the sixth–seventh year after addition of PK at the high dose.

One of the sites in this experimental series was judged to be very rich in N, and close to N saturation, i.e. with inputs of N equal to outputs. This is uncommon in Swedish forests. The growth of the stand was similar to expectations for similar stands in the region. Except for N, the nutrient concentrations examined in the needles did not substantially deviate from those in other stands. In the needles, both the concentration of arginine and the relative abundance of ^{15}N were high. Both variables have been suggested to be indicators of ecosystems with an excess of inorganic N.

A multi-site study indicated that N fertilization (120–180 kg N ha^{-1}) will not necessarily increase growth when the N concentration in current-year needles of Scots pine and Norway spruce is above 15–16 mg (g DM)$^{-1}$.

The closed-canopy experimental stands growing on the most acidic soils showed no signs of severe damage or nutrient deficiencies. As regards stem growth, needle element concentrations and crown transparency, there seems to be no acute need for liming and/or PK addition in Norway spruce stands on similar sites in SW Sweden. This conclusion is based on the observed status of the investigated stands, and on the minor or negligible treatment effects recorded in the studies described in this thesis, and in other relevant investigations.

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