

Radial growth of Norway spruce and Scots pine: effects of nitrogen deposition experiments

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Received: 1 December 2010/Revised: 6 July 2012/Accepted: 7 September 2012/Published online: 6 October 2012
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Abstract The growth patterns of annually resolved tree rings are good indicators of local environmental changes, making dendrochronology a valuable tool in air pollution research. In the present study, tree-ring analysis was used to assess the effects of 16 years (1991–2007) of chronic nitrogen (N) deposition, and 10 years (1991–2001) of reduced nitrogen input, on the radial growth of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) growing in the experimental area of Lake Gårdsjön, southwest Sweden. In addition to the ambient input of c. 15 kg N ha⁻¹ year⁻¹, dissolved NH₄NO₃ was experimentally added to a 0.52-ha watershed at a rate of c. 40 kg ha⁻¹ year⁻¹. Atmospheric N depositions were reduced by means of a below-canopy plastic roof, which covered a 0.63-ha catchment adjacent to the fertilized site. The paired design of the experiment allowed tree growth in the N-treated sites to be compared with the growth at a reference plot receiving ambient N deposition. Nitrogen fertilization had a negative impact on pine growth, while no changes were observed in spruce. Similarly, the reduction in N and other acidifying compounds resulted in a tendency towards improved radial growth of pine, but it did not significantly affect the spruce growth. These results

suggest that spruce is less susceptible to changes in the acidification and N status of the forest ecosystem than pine, at least in the Gårdsjön area.

Keywords Radial growth · Tree rings · Dendrochronology · N addition · Acidic exclusion · Field experiments

Introduction

Nitrogen (N) is one of the most abundant nutrients in the phytomass of terrestrial vegetation and is an important component in metabolic processes of a plant. Thus, the vitality of a tree is highly dependent on a balanced supply of N (Arnold and van Diest 1991). Although most ecosystems of Northern Hemisphere contain large stores of N bound in the soil organic matter, climate and soil conditions typical of these latitudes contribute to a rather tight N cycle in nearly all systems, characterized by an efficient internal cycling and a small loss in runoff. Tree growth in temperate forests has therefore been considered to be highly regulated by the availability of N (Mitchell and Chandler 1939). Increased pollution-derived atmospheric N loadings into an N-limited system may enhance the uptake of N by vegetation, leading to canopy expansion, increased primary production and an accelerated internal N cycle. Accelerated base cation uptake, which follows enhanced growth rates, may lead to nutritional imbalances and deficiencies of macronutrients such as phosphorus (P) and calcium (Ca), which will inhibit the vegetation growth (e.g. Burström 1968; Chapin 1980). When the input of N exceeds the total nutritional demand of plants and microbes within the ecosystem, N saturation will occur (Aber et al. 1989). The first sign of saturation is increased nitrate (NO₃⁻) leaching from

Communicated by A. Merino.

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below the rooting zone, accompanied by a net proton production and, subsequently, acidification. Leaching of NO_3^- may be followed by leaching of base cations, which, in the long term, may reduce the site fertility and result in ecosystem malfunction such as disturbances in the mycorrhiza development and function, reduced root growth and increased susceptibility to damage by animals, fungi, bacteria and viruses (Nihlgård 1985). Acidification may further cause mobilization of aluminium, particularly the Al^{3+} ion, leading to root damage and aluminium toxicity of many plants.

Even though the atmospheric deposition of N compounds has decreased by approximately 20 % during the period 1989–1998 over southern Scandinavia (Wright et al. 2001), there are still concerns for nitrogen saturation in forest and aquatic ecosystems in Sweden. The ecosystem-scale experiments in the area of Lake Gårdsjön, on the west coast of Sweden, were designed to obtain a better understanding of the relationship between the conditions of coniferous forest ecosystems, pollution and other stress factors (Wright and van Breemen 1995). Field experiments, including nitrogen fertilization, were conducted in several sub-catchments within the Lake Gårdsjön area as a part of the project. To overview the influence of the experimental treatments, responses of runoff (Moldan and Wright 1998a, b; Moldan et al. 2006), ground vegetation, soils and soil solution (Stuanes et al. 1995), N_2O emission (Klemmedtsson et al. 1997) and the internal nitrogen cycle (Kjønaas et al. 1998), fine root (Clemensson-Lindell and Persson 1995) and mycorrhiza (Brandrud 1995) have been assessed.

The present work examines the radial growth of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) in the experimentally treated watersheds at the Gårdsjön research site. The growth of a tree is a function of a range of environmental parameters, including climate, stand dynamics and exposure to pollutants (Fritts 2001). Thus, annual radial growth increments can provide valuable historical records of past local environmental conditions and be used to link alterations of various environmental parameters to tree health (Cook et al. 1987). Dendroecological methods have frequently been used to describe growth reductions associated with pollutant exposure on local scale (Ashby and Fritts 1972; Nash et al. 1975; Nöjd and Reams 1996; Hirano and Morimoto 1999; Long and Davis 1999; Boone et al. 2004), as well as regional scale (McLaughlin and Percy 1999; Dittmar et al. 2003). Here, dendroecological techniques were used to examine the effects on conifer growth of (1) 16 years of chronic nitrogen fertilization and (2) 11 years of exclusion of N deposition. The experimental effect was estimated by comparing the tree growth at the impact sites with that of an adjacent, non-treated reference site.

Materials and methods

Study site and treatment descriptions

The radial tree growth of Norway spruce and Scots pine was studied in the area of Lake Gårdsjön (58°04'N, 12°03'E, 135–145 m a.s.l.), located approximately 10 km east of the Swedish west coast and 50 km north of Gothenburg City (Fig. 1). Proximity to the sea yields a maritime climate in this region, characterized by mild winters and cool summers. Mean annual temperature and total annual precipitation are 6.4 °C and 1,100 mm, respectively. The area receives moderate depositions of sulphate, nitrate and ammonium; mean throughfall inputs (1989–1996) were estimated to be 25 kg $\text{SO}_4\text{-S}$ ha^{-1} year^{-1} , 7.3 kg $\text{NO}_3\text{-N}$ ha^{-1} year^{-1} and 4.8 kg $\text{NH}_4\text{-N}$ ha^{-1} year^{-1} (Moldan et al. 2006). The bedrock in the region is dominated by granites and granodiorites. Soils are dominantly thin (<0.5 m) sandy and silty podzols with inclusions of bedrock outcrops and thicker organic soils in the valley bottoms. The C/N ratio ranges between 34 and 38 (whole soil, mol/mol), and the soil N content is approximately 8,600 kg ha^{-1} (Moldan et al. 2006). The forest in the Gårdsjön area consists of mixed mature conifer trees, where Norway spruce dominates the stands and inclusions of Scots pine are found in the drier areas.

For this study, three sub-catchments, G1, G2 and F1, all situated at the southern end of the lake in the Gårdsjön basin, were chosen (Fig. 1). All the three catchments had relatively similar valley-shaped topographies, with flat or gently sloping bottoms and steep sides. As a part of the European NITREX project (NITrogen saturation EXperiments; Wright and van Breemen 1995), the G2 NITREX catchment (0.52 ha) was experimentally manipulated by the addition of ammonium nitrate (NH_4NO_3) from April 1991 onwards (Moldan et al. 1995). NH_4NO_3 was dissolved in deionized water and applied to the whole, originally N-poor, catchment area by means of a sprinkling system. The nitrogen was distributed in weekly and biweekly doses, in proportion to the volume of ambient throughfall. The volumes of the additional water corresponded to 5 % of the natural precipitation, and the experimental addition of N was approximately 40 kg ha^{-1} year^{-1} (Moldan et al. 2006). The second catchment, G1 ROOF (0.63 ha), was entirely covered between April 1991 and 2001 by a transparent roof, constructed at a height of 2–4 m beneath the forest canopy (Moldan et al. 2004). Here, the acidic throughfall was intercepted by the roof and replaced by water pumped from Lake Gårdsjön, deionized, spiked with sea salt and sprinkled by means of an irrigation system underneath the roof construction to simulate rain, typical of the region but under less-polluted conditions. The artificial throughfall contained small amount of added KNO_3 as the only N compound and

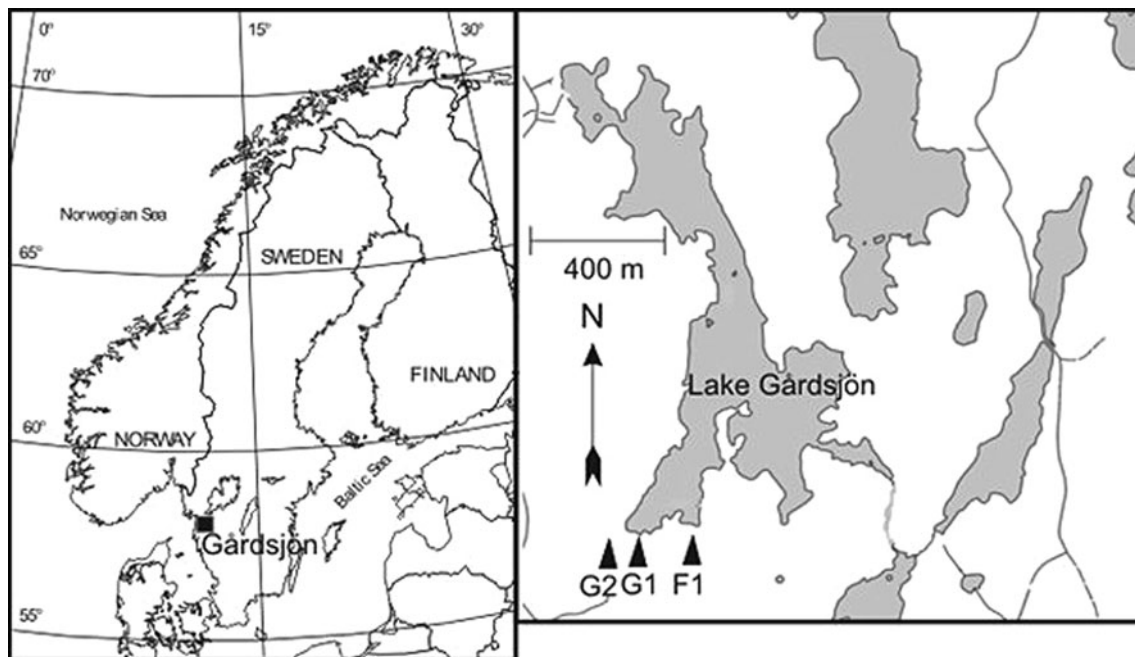


Fig. 1 Map showing the location of the experimental area of Lake Gårdsjön, on the west coast of Sweden. Black triangles in the southern part of the lake mark the position of the manipulated (G1 and G2) and the reference (F1) plots

had a lower concentration of sulphur (18–29 μM) compared with natural throughfall (125 μM) in the region (Moldan et al. 2004). The frequency and duration of each sprinkling event were dependent on the natural precipitation in the area. The litter intercepted by the roof was collected and placed on the soil underneath the construction (Bishop and Hultberg 1995). The third catchment chosen for this study, F1 CONTROL (3.7 ha), was not subjected to any experimental manipulation, but received ambient levels of atmospheric deposition and was consequently serving as a reference site for this study.

Chronology construction

In each of the three catchment areas, trees of Norway spruce and Scots pine, representing a fairly uniform age class of 93–121 years (Table 1), were randomly selected for tree-growth measurements. Using an increment borer, two-core samples, 4 mm in diameter, were sampled at a height of about 1.3 m from 12 to 16 trees from each species and at each site. To avoid reaction wood, the samples were taken in opposite directions of the trunk, parallel to the topographic contour. All the tree-ring data were collected in the early summer of 2007.

The tree cores were subsequently dried and mounted, and the cores were surfaced with a razor blade to enhance the appearance of ring boundaries and the cell structure. Annual tree-ring widths were measured with a precision of ± 0.001 mm using a stereomicroscope coupled to a Lintab measurement table connected to the Time Series Analysis

Program (TSAP) software (Rinntech, Heidelberg, Germany). To exclude possible measurement biases and to correctly ascertain the year in which each tree ring was formed, the samples were cross-dated through the matching of ring-width patterns of cores from each tree and among different trees of the same species. This procedure was performed visually and verified statistically using the COFECHA software (Holmes 1999). Since it was desirable to remove low-frequency age-related growth changes from the data, where the growth rate commonly declines monotonically with tree maturation (Fritts 2001), all individual tree-ring series were standardized using the ARSTAN software (Cook and Holmes 1986). The standardization procedure was performed by fitting a negative exponential curve, or a regression line, to the ring-width series and then dividing each observed ring-width value by the corresponding curve value. Standard-version chronologies were produced for each site and species as a biweight robust mean of the remaining dimensionless tree-ring indices and retained for the tree-growth assessment. For climate–growth response, residual chronologies were constructed after removing autocorrelation from individual series.

Tree-growth response

It is well established that climate is one of the most important factors influencing tree growth (Fritts 2001). Due to the close proximity between studied catchments, the same local climatic forcing most likely influenced the tree

Table 1 Statistical characteristics of the spruce and pine ring-width chronologies

	G1 (roof)		G2 (N addition)		F1 (control)	
	<i>P. abies</i>	<i>P. sylvestris</i>	<i>P. abies</i>	<i>P. sylvestris</i>	<i>P. abies</i>	<i>P. sylvestris</i>
No. of trees	12	14	16	14	13	13
Average age at 1.3 m height (years)	99	97	121	110	93	94
Average tree height (m) ^a	22.7	–	19.5	–	23.0	–
Ring width (mm)						
1910–2006	1.56 ± 0.49 ^b	1.40 ± 0.59	1.02 ± 0.27	1.03 ± 0.28	1.79 ± 0.47	1.63 ± 0.90
1910–1990	1.84 ± 0.33	1.73 ± 0.60	1.00 ± 0.24	1.09 ± 0.19	1.79 ± 0.49	2.15 ± 0.93
1991–2006	1.24 ± 0.19	1.03 ± 0.20	1.05 ± 0.14	0.98 ± 0.17	1.78 ± 0.27	1.05 ± 0.26
First-order autocorrelation ^c	0.801	0.818	0.806	0.741	0.773	0.869
Mean sensitivity	0.232	0.263	0.212	0.263	0.229	0.245
Interserial correlation						
Full chronology	0.60 ± 0.10 ^d	0.59 ± 0.10	0.58 ± 0.06	0.56 ± 0.05	0.52 ± 0.12	0.54 ± 0.10
1959–1974	0.62 ± 0.07	0.62 ± 0.07	0.59 ± 0.10	0.67 ± 0.10	0.41 ± 0.12	0.67 ± 0.06
1975–1990	0.60 ± 0.08	0.56 ± 0.11	0.69 ± 0.08	0.48 ± 0.11	0.62 ± 0.15	0.45 ± 0.10
1991–2006	0.59 ± 0.11	0.54 ± 0.11	0.61 ± 0.10	0.55 ± 0.11	0.63 ± 0.12	0.49 ± 0.12

^a From Kjønaas and Stuanes (2008). The data were collected prior to treatment and are based on all Norway spruce trees growing in each catchment

^b Mean ± SD

^c Based on raw ring-width measurements

^d Mean correlation ± SD

growth at each site, leading to the assumption that the tree-growth pattern among sites should be similar would the site treatments not have been introduced. This hypothesis was tested through an evaluation of the relationship between climate and tree growth. Long-term environmental disturbances, such as air pollution, likely manifest as a low-frequency variation in the ring-width data (e.g. McClenahan and Dochinger 1985; Sutherland and Martin 1990). In order to omit any potential low-frequency variations in the tree growth caused by the different manipulations and to enhance the climate-related year-to-year tree-ring signal, prewhitened residual chronologies were used to assess the climate–growth relationship. Response function analysis was performed between tree-ring indices and monthly and seasonal precipitation and temperature data from Säve meteorological station located c. 30 km from Gårdsjön (57°48'N, 11°54'E) and covering the 1911–2005 period. Analysis was carried out in DENDROCLIM2002 software (Biondi and Waikul 2004), which uses 1,000 bootstrapped samples to compute response coefficients and to test their significance at a 0.05 level.

The growth of pine and spruce at the control site represents natural (i.e. unaffected) conditions. If manipulation at sites G1 and G2 has affected the tree-ring chronologies, they would differ from control site in lower frequencies. Standard-version chronologies, retaining the time-persistence in the tree-ring data, were thus used to compare radial tree growth between sites. The control chronologies were compared with

the G1 and G2 site chronologies by means of product–moment correlation coefficient and paired *t* test to determine whether the mean difference between tree-ring series was significantly greater than 0. The statistics were calculated for two 16-year periods (1959–1974 and 1975–1990) before each treatment initiation and one 16-year period (1991–2006) after the onset of the manipulation. Furthermore, to highlight the low-frequency variability and to compare the chronologies graphically with each other, each chronology was smoothed using locally weighted regression (loess filter with a 10-year window; Cleveland and Devlin 1988).

Randomized intervention analysis

Randomized intervention analysis (RIA) (Carpenter et al. 1989) was used to investigate whether a non-random change had occurred in tree growth as a response to the artificial N addition and acidic throughfall exclusion in the G2 and G1 sites, respectively. This statistical test has especially been designed for ecosystem experiments, where it is desirable to detect possible impacts of an intervention. The RIA null hypothesis assumes that all observed alterations in a manipulated ecosystem are random, that is, any relationships apparent in the data are simply due to chance in the sampling process. Unlike many other statistical tests, RIA is not affected by moderate serial autocorrelation, heterogeneity of variance or non-normality. To estimate the test statistic, paired tree-growth index time series from

both the control and the manipulated sites were plotted. The time sequence used in the analysis covered the two 16-year periods before (1959–1990) and the 16-year period after (1991–2006) the treatment initiations at the G1 and G2 sites. Differences, $[(I_t(\text{exp.}) - (I_t(\text{ref.}))) = D_t$, for the time-paired tree-growth observations, I_t , were calculated, where exp. and ref. refers to the manipulated and the control sites, respectively. Mean intersystem differences before and during each intervention, $\bar{D}(\text{pre})$ and $\bar{D}(\text{post})$, respectively, were then computed. The absolute value of the difference between $\bar{D}(\text{pre})$ and $\bar{D}(\text{post})$ is the test statistic. Distribution of the test statistic was approximated by a Monte Carlo simulation, where the time series of differences, D_t , were randomly shuffled 1,000 times. For each shuffling, $|\bar{D}(\text{pre}) - \bar{D}(\text{post})|$ was examined. The proportion of the $|\bar{D}(\text{pre}) - \bar{D}(\text{post})|$ that exceeded the observed value was the P value (Carpenter et al. 1989).

Results

Radial growth

The spruce and pine chronologies, obtained from 12 to 16 trees from each site, ranged from 102 to 138 years (Table 1). Average sample age was just above 100 years, with the oldest trees found at the G2 site. Mean, unstandardized ring-width chronologies and their standard deviations for each site and species are given in Fig. 2 (to cover a common period, all chronologies were truncated before 1910). The tree-growth curves of individual series showed different trends (figure not shown), some exhibiting an exponential-like decay and some showing the effects of suppression–release common for a mesic, closed-canopy forest environment. Ring widths were averaged for two

periods, corresponding to a pre-treatment (1910–1990) and a treatment time interval (1991–2006; Table 1). Almost all sites showed the narrowest ring widths during the latter period, likely caused by the tree-ageing effect (Fritts 2001). A general decline in the standard deviations of the averaged ring widths during the treatment period provided an indication of a decrease in the sensitivity of each individual tree, suggesting a more homogenous response of the trees with increasing maturation (Table 1; Fig. 2). The mean sensitivity ranged from 0.212 to 0.263, with slightly higher values for pine.

Comparison with the reference site

Similar tree-growth responses to climate were found at all sites; the growth of spruce was benefitted from enhanced June precipitation, while pine was positively affected by mild late-winter temperatures (Table 2). By establishing that the tree-growth variations are controlled by the same climate forcing, it can be concluded that the growth pattern in the treated sites would have been similar to that in the control site would the treatments not have been initiated. By reintroducing the persistence in the tree-ring data, the control and manipulated sites can be compared and intervention-related discrepancies in tree growth detected.

When comparing standardized chronologies developed for the manipulated sites with the reference chronologies, a rather synchronous growth pattern emerges (Fig. 3). The growth of spruce exhibited peaks in the 1960s and 1980s and a depression in the 1970s, while increased pine growth was conspicuous in the 1960s and in the early 1990s. Long-term growth trends were generally consistent among the experimental and control plots during the last decades (Fig. 4). The time period starting from 1990s onwards was characterized by a continuously decreasing radial pine

Fig. 2 Mean radial growth of spruce and pine from the G1 and G2 sites for the period 1910–2006. Standard deviations are illustrated by vertical bars

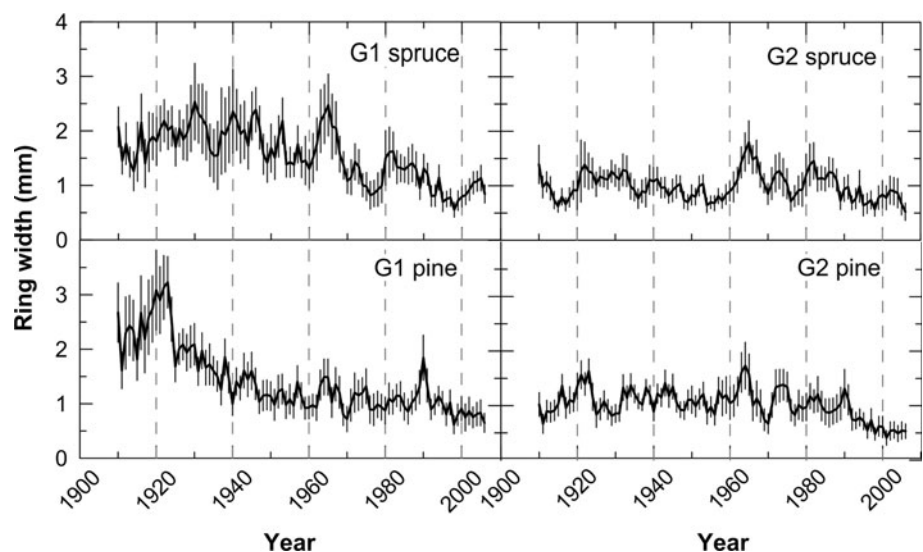
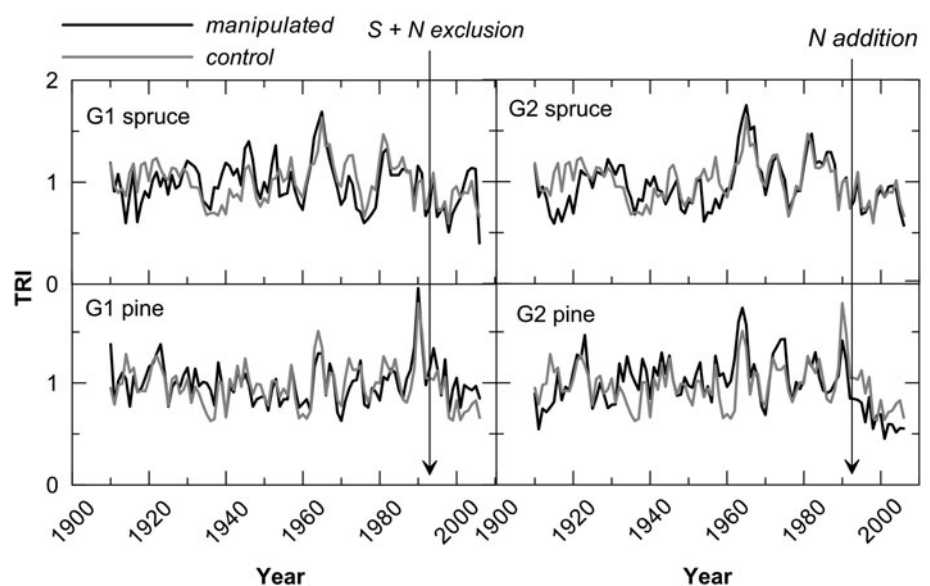


Table 2 Significant response functions ($P < 0.05$) between tree-ring indices (residual chronologies) and mean monthly temperature and total monthly precipitation (italicized) for a 12-month period extending from October of the year prior to growth to September of the growth year

	Previous year			Current year								
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
<i>P. abies</i>												
G1 (roof)									0.282			
G2 (N addition)									0.244			
F1 (control)									0.267			
<i>P. sylvestris</i>												
G1 (roof)					0.120	0.187						
G2 (N addition)					0.132							
F1 (control)					0.136	0.174						

Data are calculated over the 1911–2005 period

Fig. 3 Comparison of standardized tree-ring indices (TRI, standard version) of spruce and pine from the G1 and G2 sites (black lines) with growth indices of spruce and pine from the untreated F1 site (grey lines)

growth at all sites. A similar negative trend was apparent for spruce. However, in contrast to pine, the starting point for the spruce growth reduction was in the middle of the 1980s, while a gradual recovery was somewhat apparent from the middle of the 1990s.

Changes in the tree growth at the treated sites were evaluated by statistically comparing the growth series with those of the control site (Table 3). In the pre-manipulation periods, as well as in post-manipulation interval, the correlation between the chronologies was high and statistically significant at all sites ($P < 0.01$). The paired t test revealed that the mean pine growth at the G2 site, during the treatment period, was significantly ($P < 0.01$) lower than that at the control chronology, while the growth of spruce was slightly stronger ($P < 0.05$). At the G1 plot, only the mean growth of pine differed significantly ($P < 0.01$), in this case exceeding the reference site.

To further establish whether a non-random tree-growth change had occurred following the site treatments, RIA was performed on paired data sets from the treatment and the reference sites (Fig. 5). The probability of rejection of the RIA null hypothesis is shown in Table 4. Pine growth at the G1 and G2 sites had a rejection limit exceeding 99 % ($P < 0.01$). Hence, the pine growth could be rejected safely as exhibiting a non-random behaviour following the initiation of each experiment. Autocorrelation in the time series of intersystem differences might cause RIA to underestimate the true P value. It has been suggested that the P value from RIA should be less than 0.01 to reject the null hypothesis if a time series is autocorrelated (Carpenter et al. 1989). The spruce growth in the G1 and G2 sites had a rejection limit below 99 %. Hence, it could not safely be assumed that spruce exhibited a non-random growth change in either of the sites.

Fig. 4 Standard-version spruce and pine chronologies from the G1 and G2 sites. Data are been smoothed with a 10-year low-pass (first-order) loess filter (Cleveland and Devlin 1988)

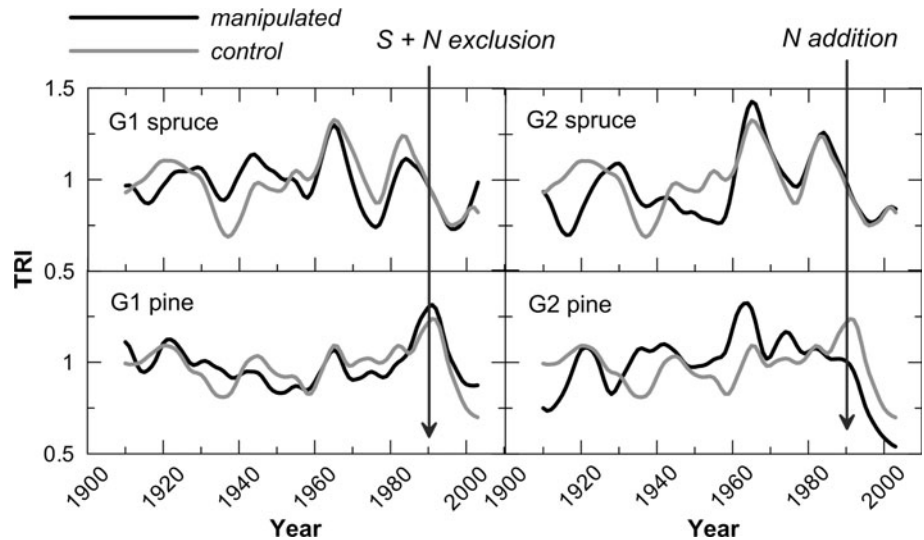


Table 3 Results from the statistical comparison of the radial tree growth at the experimentally manipulated sites with the control plot prior to (1959–1974 and 1975–1990) and after the onset of the each site intervention (1991–2006)

Period	G1 (roof)				G2 (N addition)				
	<i>P. abies</i>		<i>P. sylvestris</i>		<i>P. abies</i>		<i>P. sylvestris</i>		
	<i>n</i>	<i>r</i> ^a	Difference ^b	<i>r</i>	Difference	<i>r</i>	Difference	<i>r</i>	Difference
(1) 1959–1974	16	0.83*	−0.077	0.87**	−0.062	0.90**	0.048	0.80**	0.183**
(2) 1975–1990	16	0.88**	−0.082**	0.86**	−0.007	0.95**	0.033	0.78**	0.003
(3) 1991–2006	16	0.73**	−0.020	0.85**	0.130**	0.93**	−0.029*	0.93**	−0.185**

*, ** Significant levels at $P < 0.05, 0.01$

^a Two-tailed product–moment correlation coefficient between indices from the control and the manipulated sites. The sample size has been adjusted to account for the first-order autocorrelation conserved in the ring-width data before the significance of the correlation was assessed (Dawdy and Matalas 1964): $N' = N [(1 - r_{1x}r_{1y}) / (1 + r_{1x}r_{1y})]$, where N is the number of paired observations and r_{1x} and r_{1y} are the coefficients of the first-order autocorrelation of each tree-ring series

^b Difference between the means of experimental and control chronologies (paired-sample t test)

Discussion

Since the G2 plot was initially N-limited, enhanced tree growth was expected to accompany the increased N input. However, while no prominent discrepancy between the growth of spruce at the fertilized and the reference sites was observed, the pines at the G2 plot seemed, on the contrary, to show a N-saturation effect by significantly decreasing the wood productivity during fertilization with NH_4NO_3 . Previous N-fertilization studies on the stemwood growth of conifer and deciduous trees have showed various results: increased and decreased growth (Mälkönen et al. 1990; Nilsson and Wiklund 1992; Nohrstedt et al. 1993; Pettersson 1994; Sikström 1997; Magill et al. 2004; Wallace et al. 2007) and small or no effects (Sikström 1997; Persson et al. 1995) have been observed. Reduced growth of Norway spruce in German forests (Wright et al. 1995) has been attributed to ambient input of N, reaching levels of approximately $50 \text{ kg N ha}^{-1} \text{ year}^{-1}$. Binkley and

Högberg (1997) suggested that this deterioration might be associated with nutritional problems such as magnesium (Mg) deficiency. Reduction in the pine growth at the G2 site is not likely related to Mg shortage. Mg concentration at the G2 plot was optimal at the start of the experiment (Kjønaas and Stuanes 2008), and, due to the proximity to the sea, the area received moderate input of Mg from the sea salt deposition throughout the whole treatment period (Binkley and Högberg 1997).

Previous results from the area suggest that the system of the G2 plot reached an N-saturation point in a relatively short time after the onset of the experiment. Increased NO_3^- concentrations were observed in the runoff immediately after the treatment initiation (Hultberg et al. 1994; Moldan et al. 1995; Wright et al. 1995) and proceeded to rise throughout the treatment period from $<1 \mu\text{eq L}^{-1}$ in April 1991 to c. $70 \mu\text{eq L}^{-1}$, accounting for approximately 10 % of the total input, in 2004 (Moldan et al. 2006). Moreover, the N content in litter and foliage increased

Fig. 5 Calculations for randomized intervention analysis. The *thick lines* represent the difference, $[(I_t(\text{exp.}) - I_t(\text{ref.}))]$, between standardized tree-ring indices (I_t) from each manipulated site (exp.) and the untreated F1 site (ref.). Mean differences for the pre-treatment period (1959–1990) and the treatment period (1991–2006), $\bar{I}_t(\text{pre.})$ and $\bar{I}_t(\text{post.})$, are represented by *dashed lines*

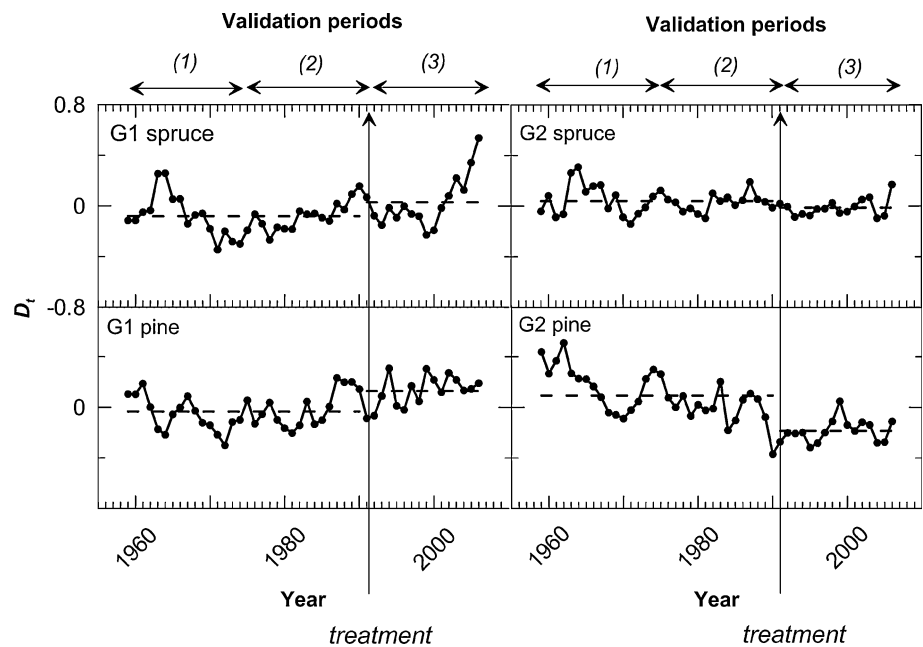


Table 4 Results of RIA—the probability of rejection of the null hypothesis

	G1 (roof)		G2 (N addition)	
	<i>P. abies</i> (%)	<i>P. sylvestris</i> (%)	<i>P. abies</i> (%)	<i>P. sylvestris</i> (%)
Probability of rejection	97	>99	92	>99

within a few years of the treatment (Boxman et al. 1998; Kjølneas et al. 1998). These observed responses, typical for an N-saturated system, indicate that the N cycle had been affected in the G2 plot. Even though the N treatment might have caused a fertilizing effect in the G2 plot in the short run, our data suggest that the duration of this effect was not long-lasting enough to enhance the radial wood production. Kjølneas and Stuanes (2008) proposed that the slow tree-growth response at the G2 plot might partly be explained by the fast immobilization of incoming N into the soil pool; only about 9 % of the added N was incorporated into the spruce biomass during the first years of the experiment. The increased NO_3^- leaching shortly after the initiation of the treatment has likely caused alterations in the nutrient status of the system so that the tree growth is now more or less inhibited by a nutrient shortage and therefore presumably more susceptible to secondary stress factors such as drought, frost, fungi and parasites (Nihlgård 1985). Tree growth in the Gårdsjön area was already limited at the start of the experiment by the restricted availability of major nutrient elements (N, P, K, Ca). The decrease in the N/nutrient ratios (Mg/N, P/N, K/N) in the spruce needles at the G2 plot throughout the experimental period, especially in the P/N ratio that, at end of the experiment, reached proportions falling well below the critical level (<10–12;

Kjølneas and Stuanes 2008), has proved that the nutrient uptake has indeed become even more limited at the G2 site.

Previous findings from the G1 site demonstrate an improved quality of the runoff following the roof construction; the concentrations of S, Al and base cations declined, while the pH slightly rose (Moldan et al. 2004). Fine roots are sensitive to changes in the soil environment. Thus, different root parameters such as tree fine root biomass and fine root Ca/Al molar ratio have been used as indicators of plant nutritional status (e.g. Lamersdorf and Borken 2004; Helmisaari et al. 2007; Vanguelova et al. 2007; Zang et al. 2011). Increased percentage of living fine roots in the organic soil layer within the G1 plot (Clemensson-Lindell and Persson 1995) and better mineral nutrient status of fine roots (increased K, P and Ca levels in relation to N; Persson et al. 1998) suggest that tree-growth conditions had improved in the G1 site following the roof construction. Indeed, pine growth at this site significantly exceeded that of the reference site throughout the treatment period. The G1 site was N poor before and during the experiment. The improved growth at the site might therefore indicate that changes in the acidification rather than in the N status of the system are important for the tree growth in the area.

In contrast to the results obtained for pine and despite observed signs of reduced and increased amounts of spruce

fine roots in the G2 and G1 sites (Clemensson-Lindell and Persson 1995), respectively, the growth of spruce showed no distinct tendency towards either improved or reduced growth following the site interventions. Fine roots may be the first biological components to respond to changes in the soil environment (Persson and Ahlström 1999). The increased amount of fine roots in the G1 plot may have improved the tree water uptake, thereby increasing the assimilation rate, especially on dry summer days. However, the energy cost associated with the root growth may, on the other hand, have ceased the growth rate of the aboveground tree structures.

Our results could be interpreted as an indication of a somewhat stronger sensitivity of pine trees to changes in the N status of the forested ecosystem, which, on the other hand, may seem contradictory since it has been showed that Scots pine is well adapted to conditions of poor nutrient availability and that the productivity of pine exceeds that of Norway spruce at sites with low fertility (Ilvessalo 1927). The lack of any response in the case of spruce could also simply be attributed to the site characteristics of each individual tree-growth spot. The sensitivities of individual trees and microsite conditions may partly determine whether fertilization with N will cause tree mortality or increased wood productivity (Wallace et al. 2007). It is important to remember that trees were sampled randomly in the whole watersheds with no regard to the soil moisture status, topography, soil depth, ground vegetation or other factors potentially influencing the sequestration and leaching of N and thereby the tree exposure to N and the nutrient availability. For instance, trees growing in the lower parts of the terrain in the G2 plot were probably more exposed to N, since any added N into the system was eventually drained through this region.

Conclusions

Earlier studies have suggested that elevated N input in previously N-limited temperate forests often results in initially increased tree N uptake and subsequently enhanced productivity. Our results showed, on the contrary, that 16 years of fertilization with $40 \text{ kg N ha}^{-1} \text{ year}^{-1}$ did have a significant negative impact on radial pine growth (N-saturation effect), but not on spruce. N saturation of the system shortly after the treatment initiation followed by a reduction in site fertility was a probable cause of the decline in pine growth.

Excluding inorganic N and other acidifying substances significantly enhanced the productivity of pine, but not spruce, which, in consistent with previous findings from the site, suggests that the growth conditions for pine improved following the acidic exclusion. The absence of any

significant tendency of either improved or deteriorated growth of spruce following the treatment initiations suggests that the radial growth of spruce is less susceptible to changes in the N status of the forest system, compared with that of pine. However, the lack of any significant responses to the interventions may also be explained by the characteristics of the sites.

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