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EXPERIMENTAL MANIPULATIONS: FOREST ECOSYSTEM RESPONSES TO CHANGES IN WATER, NUTRIENTS AND ATMOSPHERIC LOADS

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ABSTRACT

In four Dutch coniferous forest ecosystems water and nutrient supply, as well as atmospheric loads, were manipulated for three or more years. Four approaches were used: (1) optimal supply of water and nutrients, (2) decrease of nitrogen and sulphur loads to pre-industrial levels, (3) increase of nitrogen and sulphur loads to excess levels (120 kg N ha^{-1} yr^{-1}). Nutrient supply was optimized according to tree demand in optimal proportions relative to ambient nitrogen supply. Tree growth was strongly enhanced (ca. 30%) by optimal water supply but not further enhanced by nutrient additions. Water additions tended to lower nitrogen concentrations in the needles by 5-10%, probably by growth dilution. Nutrient applications improved the nutritional balance in trees of phosphorus and potassium relative to nitrogen. Exchange of applied base cations with protons and aluminium from the soil, temporarily increased the acidity of the soil solution. Large applications of nitrogen in a Scots pine stand increased the nitrogen concentration in the needles. Excess nitrogen stimulated tree growth during the first two years, and depressed growth in the fifth treatment year. Phosphorus deficiency was induced but no visible tree damage occurred.

When atmospheric deposition of nitrogen and sulphur was reduced to pre-industrial levels in a nitrogen and sulphur saturated Scots pine and Douglas fir stand, a few months after reduction of the input, output to the groundwater was also strongly reduced. This implies a tight input-output coupling. As a result, leaching of aluminium and base cations (to counteract nitrate and sulphate leaching) decreased and the mineral balance in the soil solution improved. Consequently, tree health improved as shown by increased root and shoot growth and by reduced total-N and arginine-N concentrations as well as an improved mineral balance of the needles

INTRODUCTION

High atmospheric input of ammonium results in loss of base cations from the soil. due to either direct exchange at the soil absorption complex or indirect via acidification, as a result of nitrification. This may result in nutrient deficiencies in trees (Roelofs *et al.*, 1985; Schulze, 1989). The nutritional balance of trees can be affected even further by preferential ammonium uptake to supra-optimal levels and can be disturbed by the ion competition of ammonium, aluminium and protons on the potassium, magnesium and calcium uptake. Furthermore acid soils can have Ca/Al ratios that are unfavourable for roots. The high inputs of nitrogen can result in lower root/shoot ratios and may increase the drought sensitivity of trees.

This study deals with the growth and nutrition of two tree species, Scots pine (*Pinus sylvestris* L.) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), under influence of acidification and eutrophication. The aim was to determine whether the nutrient supply is growth-limiting, under the constraint of aluminium stress and competition with ammonium and how nutrition and root functioning are related to the water economy of the tree. Therefore, the effects of a change in input of water, nutrients and acidifying substances to the soil, on trees were quantified. Atmospheric loads were increased or decreased to study their impact on nutrient cycling and forest decline. Secondly, it was hypothesed that the effects of increased soil acidification and eutrophication on trees could be mitigated by optimization of the water and nutrient supply. Experimental variation of the water supply may elucidate the impact of water stress on tree functioning. Reducing the nitrogen input to pre-industrial levels may assess the reversibility of nitrogen saturation on the different compartments of the ecosystem. These ecosystem manipulation experiments were conducted within the EXMAN and NITREX framework (Beier and Rasmussen, 1992; Dise and Wright, 1992).

MATERIALS AND METHODS

Manipulations were carried out at four forest stands in the Netherlands. In a Scots pine stand near Harderwijk and in a Douglas fir stand near Kootwijk either water and nutrients were applied, or rates of soil acidification were changed by exclusion of atmospheric loads or by increasing acid loads.

Irrigation of demineralized water (I plot) amounted 3 to 4 mm day^{-1} maximally on days without rain. Fertigation (IF plot) consisted of a complete set of dissolved nutrients, given very frequently and in addition to irrigation during four growing seasons. The total annual application rate was equal to the estimated gross uptake in trees. Phosphorus and potassium additions were quantitatively the most important and ranged from 13 (P) and 65 (K) for Scots pine to 36 and 60 kg ha^{-1} yr^{-1} for Douglas fir respectively. A roof construction above the forest floor prevented the infiltration of throughfall water, being polluted with atmospheric substances, and clean rain was irrigated below in combination with a fertigation treatment (IF+R plot). Fertilization with dissolved $(NH_4)_2SO_4$ amounted to 120 kg N ha^{-1} yr^{-1} (treatment N+S). In the Harderwijk stand the treatments C (control), I, IF and N+S, in the Kootwijk stand C, I, IF and IF+R were carried out. In all treatments soil water contents and composition, tree growth, needle chemistry and needle fall were monitored. (see De Visser (1994) for details on treatments and measurements).

In 1989 two research sites were established in a Scots pine stand near Ysselsteyn and in a Douglas fir stand near Speuld in which ambient throughfall water was intercepted by means of a roof, and replaced by demineralized water to which all nutrients were added in the same amount as present in the throughfall, except for nitrogen and sulphur concentrations. Underneath the roof, two plots (10x10m) were designed to receive either clean water (roof-clean plot) or ambient throughfall (roof-control plot). Outside the roof a second control plot was established, receiving ambient throughfall (control plot).

A detailed description of the sites and of the methods has been given elsewhere (Dise and Wright, 1992; Van Dijk *et al.*, 1992a,b; Boxman *et al.*, 1994; Boxman *et al.*,1995). For statistical analyses the software packages Systat 5.0 and Statgraphics 6.0 were used.

RESULTS AND DISCUSSION

Ecosystem responses to changes in water and nutrients

Tree growth and nutrition in relation to water and nutrient supply

Three out of four irrigated forest stands showed a water-limited growth in the examined period. An increase of 40% for Douglas fir to 50% for Scots pine in basal area growth was observed upon irrigation of 3 to 4 mm day^{-1} (Figure 1; $p \leq 0.05$, analysis of variance, followed by LSD test; Statgraphics 6.0).

Figure 1

These data are in agreement with those found in a Norway spruce stand at Klosterhede (Denmark). In a Norway spruce stand at Höglwald (Germany) no response was observed, since the soil had a high water storage capacity (De Visser, 1994).

The concentrations of potassium and phosphorus in the needles were raised in all treatment years by fertigation. Needle nitrogen remained stable and consequently K/N (Figure 2) and P/N ratios increased, resulting in an improved nutritional balance in trees, with supra-optimal values (K/N > 50) in plot IF of Douglas fir.

Figure 2

Fertigation did not increase total Douglas fir growth over the four-year period in addition to the growth effect of irrigation alone, and in Scots pine in one out of four treatment years only (Figure 1: 1992; $p \leq 0.05$, analysis of variance, followed by LSD test; Statgraphics 6.0). The lack of response did confirm that nutrient shortages were hardly present in the soil at the sites, although ratios of the base cations to nitrogen seemed unprofitable. Input-output budgets suggested that applied nutrients were mostly retained in the soil, although more potassium was returned with needle fall and some potassium losses were observed in the Scots pine stand. Litter fall in the Douglas fir stand decreased during the experimental period by irrigation, averaging 2.75 Mg ha^{-1} yr^{-1} (1989 to 1992), relative to 3.24 in the control. Fertigation increased aluminium concentrations in soil solution in both stands due to exchange of applied base cations with aluminium from soil. The same effect was found due to nutrient applications in a pot trial (De Visser and Keltjens, 1993) and so the treatment increased soil solution acidity, instead of ameliorating the root environment.

Tree growth at different rates of soil acidification

The application of $(NH_4)_2SO_4$ during five years to a Scots pine stand in Harderwijk (N+S plot) strongly increased soil acidification rates and resulted in aluminium concentrations up to 2.22 mM in soil solution from the third year onwards. Yet, diameter growth was first enhanced, probably by N-induced aboveground growth. In Figure 1 the cumulative basal area growth indicates whether a growth effect sustains during a number of years. It can be seen that after a slight initial stimulation, in the fifth treatment year growth was depressed at N+S relative to C. This coincided with phosphorus limitation, that might have resulted from Al-phosphates precipitates in soil and roots. Non of the mentioned acidifying treatments had changed the tree vitality (De Visser, 1994).

At the Douglas fir site near Kootwijk, growth increased drastically at decreased rates of soil acidification (Figure 1:plot IF+R). This growth effect added up to the positive effect of water+nutrient applications (De Visser, 1994). This growth increase was probably related to the decrease of NH_4 supply and uptake relative to NO_3, that resulted in slightly decreased soil solution concentrations of aluminium and protons, hence soil conditions were probably more favourable for roots. Soil solution concentrations of nitrate decreased under the roof in winter, in the summers upto 1992 nitrate concentrations rose due to small additions of fertilizer-N and due to mineralization (Figure 3).

Figure 3

Needle N concentrations decreased in irrigated and roofed plot (Table 1), whereas N uptake in biomass was estimated similar to (I) or higher than (IF+R) the control. Probably a growth dilution took place and growth was not hampered by the lower nitrogen contents.

Table 1. Nitrogen concentrations in current year, light adapted needles (% of D.W.) of Douglas fir at Kootwijk. Different letters between different treatment indicate means which are significantly different at $p \leq 0.05$.

Treatment	1989	1990	1991	1992
Control	1.86	1.99	1.74bc	1.90a
Irrigation	1.70	1.85	1.59c	1.62b
Fertigation	2.04	1.85	1.79ab	1.94a
Fert+Roof	1.95	1.87	1.57bc	1.70b

In a number of foreign coniferous stands, the rate of soil acidification was being increased or decreased as well. Acid irrigation (4 kmol H^+ ha^{-1} yr^{-1}) on a fertile soil in Höglwald (Germany) only slightly depressed element contents in needles of Norway spruce and no change in growth was observed (De Visser, 1994).

Nitrogen saturation

Fertigation, in combination with exclusion of atmospheric nitrogen and sulphur loads by a roof, decreased soil acidification slightly and increased tree growth considerably relative to fertigation at ambient nitrogen and sulphur loads. The reduction in nitrogen loads had reduced leaching losses of NO_3 to the same extent, whereas all other fertigation treatments showed that increased nitrogen inputs of approx. 30 to 40 kg N ha^{-1} yr^{-1} resulted in equally increased outputs (De Visser, 1994), suggesting a nitrogen-saturation of the ecosystems. The high growth rates in the stand at low nitrogen loads may have resulted from a higher supply ratio of NO_3^- to NH_4^+, that can result in less acid soil conditions and can increase stem growth, as was shown in a pot trial (De Visser and Keltjens, 1993).

Ecosystem responses to reduced nitrogen and sulphur inputs

Throughfall fluxes to the forest floor

Interception of throughfall in the roof-clean plot reduced atmospheric input of nitrogen and sulphur to a few kg's ha^{-1} yr^{-1} (Figure 4). During the experimental period the deposition to the ambient control plots was high (55-70 kg total-N ha^{-1} yr^{-1} and 35-40 kg S ha^{-1} yr^{-1} at Ysselsteyn and Speuld, respectively) and remained high, particularly in comparison with a critical load value of 15-20 kg N ha^{-1} yr^{-1} (Bobbink *et al.*, 1992).

Figure 4

Atmospheric deposition to the roof-control plot was somewhat lower than to the control plot but this was attributed to the way of watering and storage of the water, and some water losses during heavy showers. Input of the other nutrients was approximately equal in all plots (Boxman *et al.*, 1995).

Soil solution chemistry

At both locations the inorganic nitrogen and sulphur concentrations in the soil solution of the roof-clean plot responded within six months to a reduced input of nitrogen and sulphur (Figures 5 to 7). Unfortunately, no pretreatment soil solution data are available, but soil solution data (including pretreatment data) from the Solling NITREX site (Germany) show the same rapid response (Bredemeier *et al.*, 1995).

Figures 5,6,7,8

However, soil extracts made before the start of the treatment revealed no significant differences between the plots in availability of ammonium, nitrate or sulphur. During the first two years the way of watering determined differences between the control plots, but automation of the watering regime (early 1992) converged the data of these plots (Figure 5 to 10). NH_4^+ availability in the upper soil layer of control plots might have been determined by meteorological conditions. The ammonium concentration in the soil solution decreased rapidly in the very wet autumns of 1992 and 1993, which may be due to stimulated nitrification and/or leaching to deeper soil layers. The same seasonality was observed for nitrate. After an initial decrease of NO_3^- concentrations in the soil solution of the roof-clean plot a tendency was observed to increasing levels (Figure 6 and also Figure 4), which is related to increased dry-deposition to the plots (data not shown). In throughfall a dominance of ammonium over nitrate was found, in the soil solution the reverse situation was found probably due to nitrification, preferential uptake of ammonium by the vegetation or immobilization. As a result, the NH_4/K ratio in the soil solution of the roof-clean plot decreased to levels below 5, Figure 8) considered to be favourable for a balanced nutrient uptake (Roelofs *et al.*, 1985).

Figure 9 and 10

Nitrogen and sulphur leaving the ecosystem at 90cm have decreased significantly as a result of the treatment. Because of this, the leaching of the accompanying cations (Al, Mg, Ca and K) was significantly reduced (Boxman *et al.*, 1995). This means that the mineral balance in the roof-clean plots improved.

Nutrients in the needles

Before the start of the manipulation experiment no significant differences were found in nutrient concentrations of the needles at both locations. At Ysselsteyn the needles had high nitrogen concentrations, whereas the other nutrient concentrations were very low. During the years of treatment the concentrations of nutrients can vary considerably, which may be related to meteorological conditions (Boxman *et al.*, 1995 and references therein). As yet, the needles in the roof-clean plot have responded to the treatment after a lag-time of approximately four years (Figure 11). The nitrogen concentration is still above 2%, which is considered as very high (optimal level is approximately 1.4-1.8%, Anonymous, 1990). The potassium and magnesium concentrations have increased significantly in the needles of the roof-clean plot as compared to both control plots (data not shown) and may be related to 1) a favourable NH_4^+/NO_3^- ratio in the soil solution, 2) a decreased leaching of base cations and 3) an increased root biomass (Boxman *et al.*, 1995). Consequently, the nutritional balance in the needles of the roof-clean plot has improved for potassium (Figure 12) and magnesium (data not shown) relative to nitrogen, the former even to a level above that is considered deficient (K:N>25, Anonymous, 1990).

Figures 11, 12, 13 and 14

Although the ecosystem at Speuld is also nitrogen-saturated the trees have normal nitrogen concentrations in their needles. In the control plot, however, nitrogen tends to increase (Figure 13). Since the trees are growing reasonably well, dilution effects in the needles may prevent nitrogen to become toxic. The nitrogen saturation effect is most pronounced in the older needles, which have higher nitrogen concentrations than the current ones (data not shown).

Potassium, magnesium and calcium are sufficient in the needles, while phosphorus is somewhat low. No significant differences were found between the plots. As a result the nutritional balance of potassium (data not shown) and magnesium (Figure 11) relative to nitrogen have improved, although ratios are above the levels that are considered deficient (25 and 5, respectively; Anonymous, 1990).

Nitrogen, taken up by the trees is incorporated into amino acids, and subsequently into proteins. The assimilation of ammonium is absolutely necessary as free ammonium is toxic because of its interference with many processes in the cell (see *e.g.* Puritch and Barker, 1967; Wakiuchi *et al.*, 1970; Van der Eerden, 1982). If the rates of nitrogen uptake and subsequent amino acid synthesis exceed that of protein synthesis, free amino acids accumulate. Upon changes in nitrogen supply these amino acids show more sensitive changes in concentrations than the total nitrogen content. In coniferous trees arginine is most important in this respect, because of the low C/N ratio.

When the nitrogen concentrations in the needles increased, arginine seemed to accumulate at nitrogen concentrations above 1.5 to 1.6% (Figure 15).

Figure 15

Irrespective whether total-N in the needles was still high, the treatment significantly decreased the arginine concentration in the needles at Ysselsteyn, while the same trend was observed at Speuld. The response of arginine-N was fast: within one year changes could be observed. In this respect arginine can be regarded as a good indicator of detrimentally high ammonium deposition (Van Dijk and Roelofs, 1988; Ferm *et al.* (1990); Näsholm and Ericsson, 1990; Pietilä *et al.*, 1991).

Figure 16 and 17

Diameter growth of the dominant trees in the roof-clean plot improved (p=0.06 for both roofed plots) and was inversely related to the arginine-N concentration in the needles (Figure 18). This is in agreement with the observation of Krauβ *et al.* (1986) who found a clear reduction in growth in relation to increasing arginine concentrations.

Figure 18

With respect to concentrations of arginine-N reported in the needles from pristine areas in northern Scandinavia (<0.06%) concentrations in the needles of Speuld were high (0.1-0.3%), but lower than at Ysselsteyn (0.65-0.9%). At the latter site this implies that almost 30% of total-N was stored in the form of arginine-N.

Fine root growth

A survey in 1992 revealed a significantly increased fine root biomass and number of fine root tips in the roof-clean plot at Ysselsteyn (Boxman *et al.*, 1995). Data from litter-bag experiments of the Vrije Universiteit of Amsterdam only confirmed these data. After one year more fine roots were grown into the litter-bags, contained more root tips and had a higher degree of mycorrhizal infection (data not shown). These data suggest an enhanced uptake capacity of the roots, which is in accordance with the improved nutritional balance in the needles.

Final conclusions

Decreasing the input of nitrogen and sulphur strongly reduced the output of nitrate, sulphate, aluminium and base cations from both ecosystems, implying a tight input-output coupling. The N-cycle changed from an open to a more closed one, indicating reversibility of nitrogen-saturation. However, the soil still contains a large amount of immobilized nitrogen and at this moment it is uncertain what will happen with this amount in the future. Both ecosystems are recovering from excess nitrogen availability, indicated by 1) a decreased leaching of base cations, 2) a more favourable NH_4^+/NO_3^- ratio in the soil solution, 3) increased root and 4) shoot growth, 5) a decrease in total-N and arginine-N in the needles and 6) an enhanced nutrient uptake and an improved nutritional balance in the needles.

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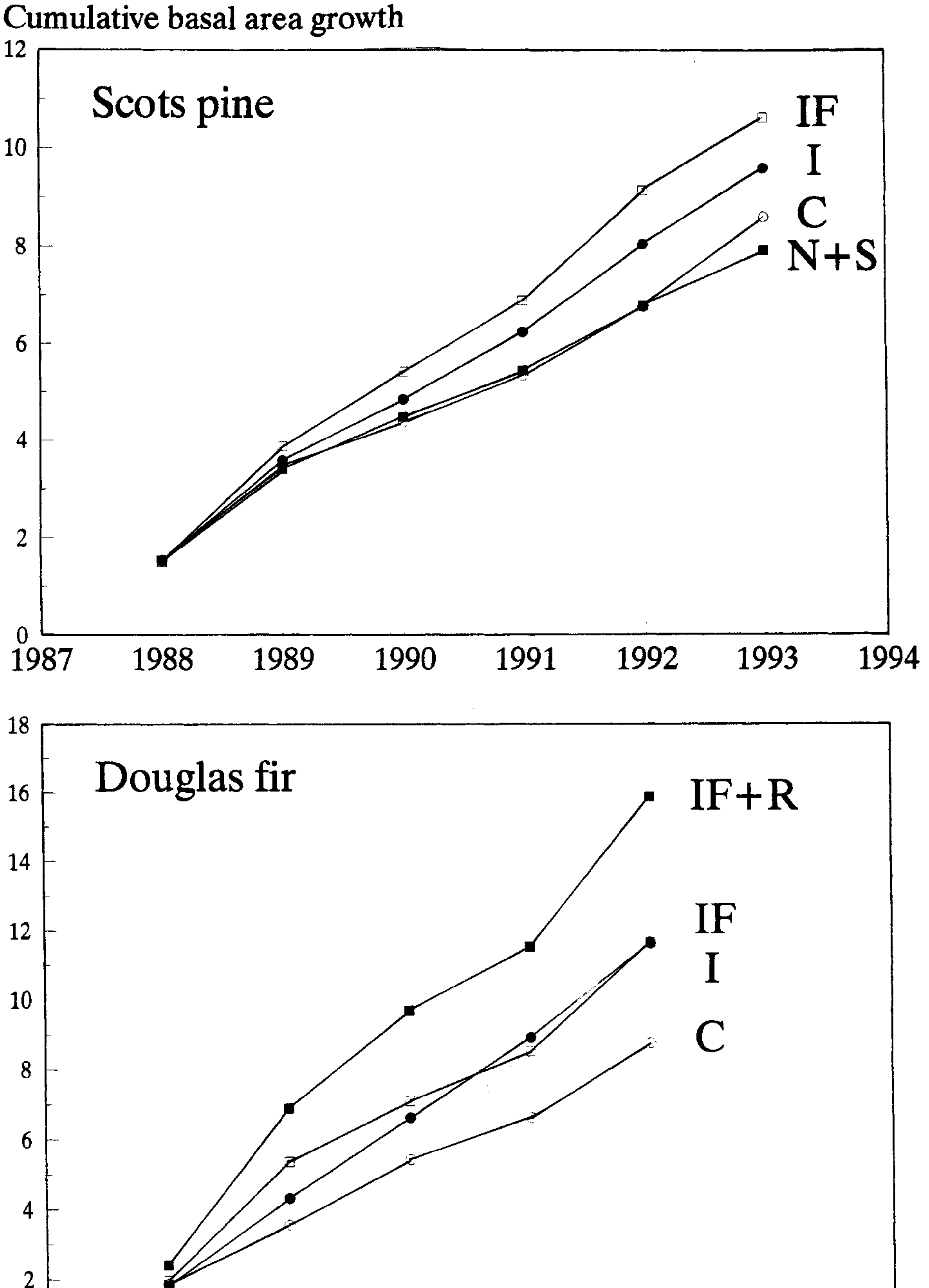

Figure 1. Cumulative basal area growth (m^2 ha^{-1} yr^{-1}) in the Scots pine stand at Harderwijk and the Douglas fir stand at Kootwijk. The treatments started in 1989.

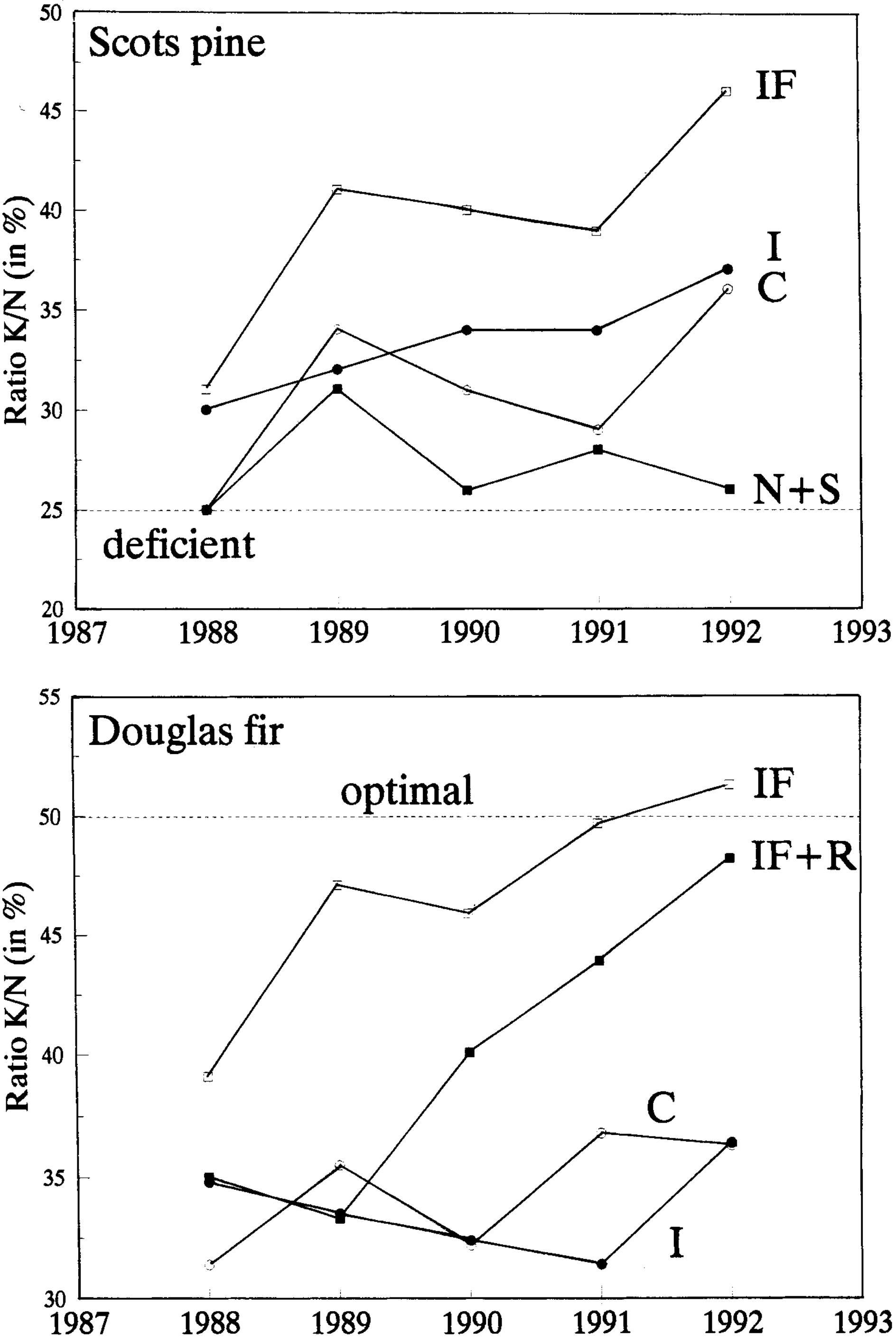

Figure 2. Elemental ratio of K to N (in %) in the Scots pine stand at Harderwijk and the Douglas fir stand at Kootwijk. For both tree species a ratio above 50% is judged optimal and a ratio below 25% insufficient for tree growth (Anonymous,

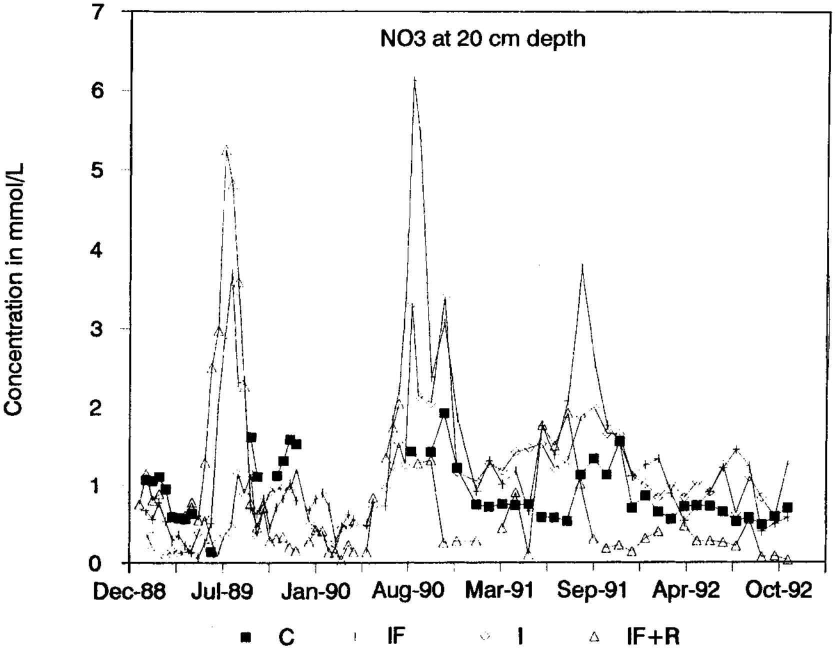

Figure 3. Nitrate soil solution concentrations at 20 cm depth in four treatment plots at Kootwijk.

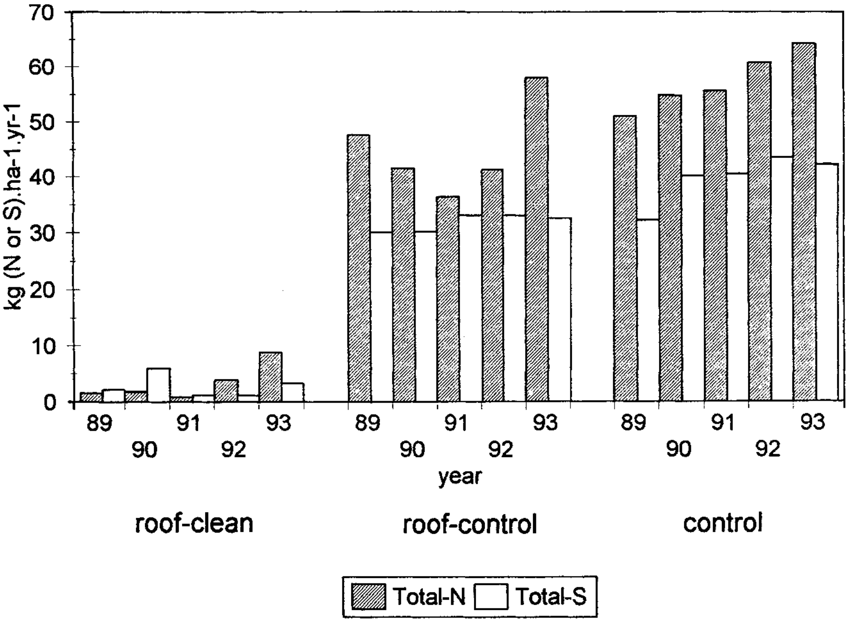

Figure 4. Deposition fluxes of total-N and total-S to the forest floor of the plots at Ysselsteyn.

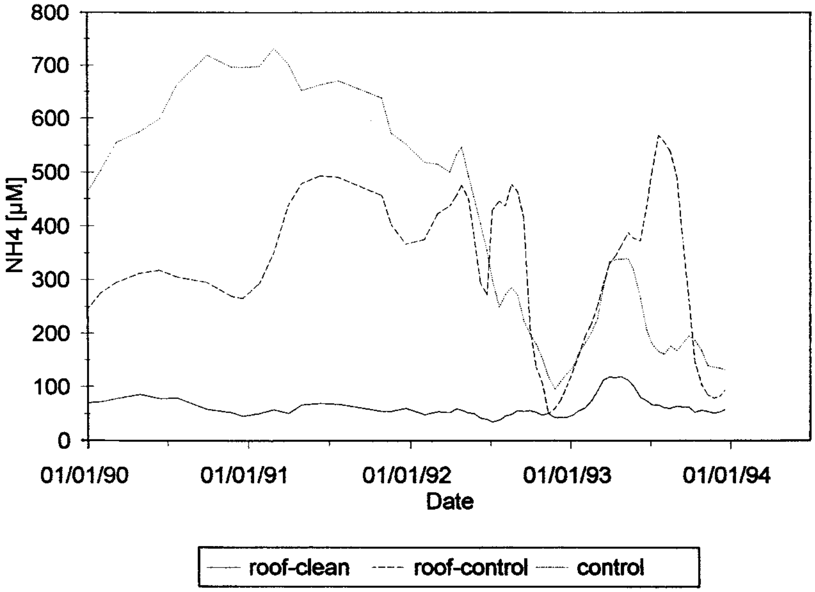

Figure 5. Ammonium concentrations at 10cm depth in the soil solution at Ysselsteyn.

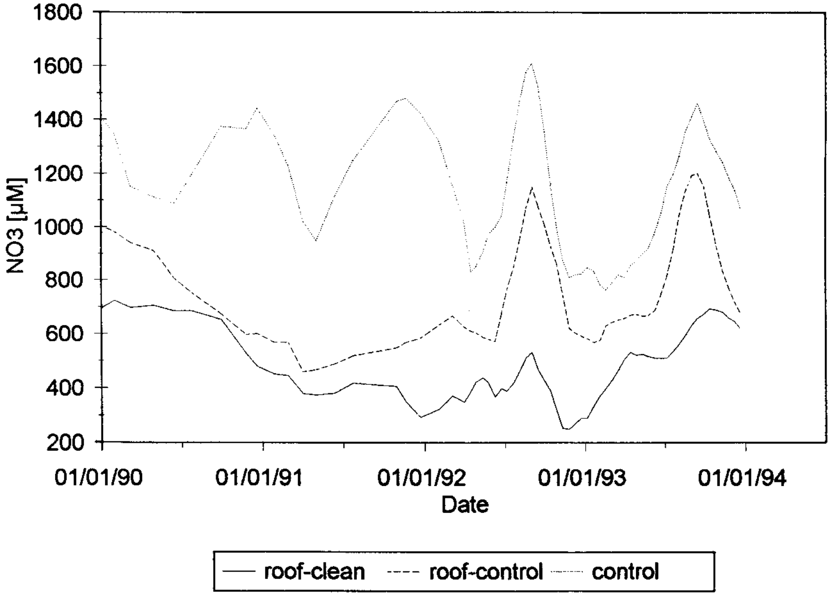

Figure 6. Nitrate concentrations at 10cm depth in the soil solution at Ysselsteyn.

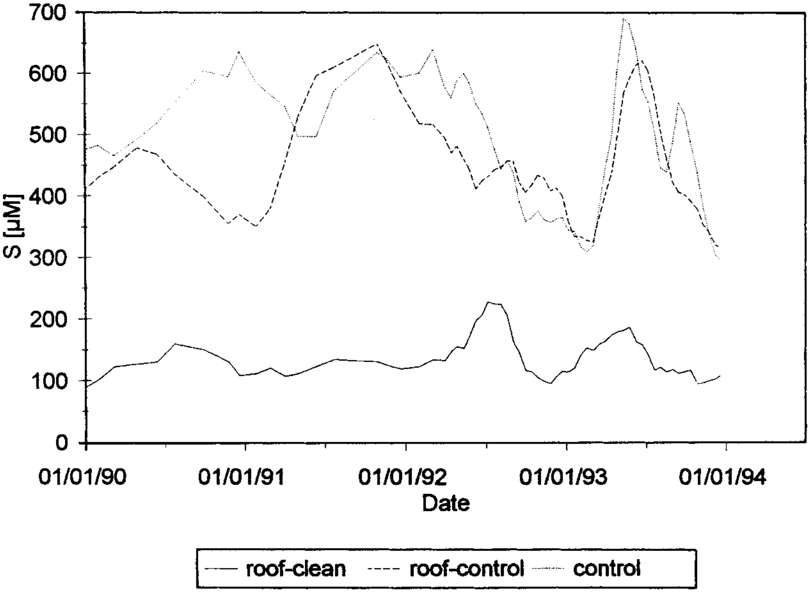

Figure 7. Total-S concentrations at 10cm depth in the soil solution at Ysselsteyn.

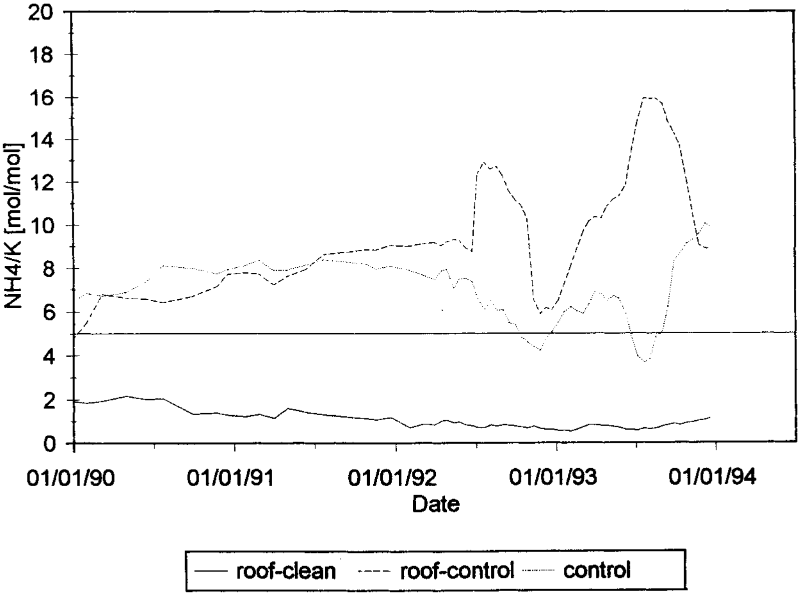

Figure 8. NH_4/K ratio at 10cm depth in the soil solution at Ysselsteyn.

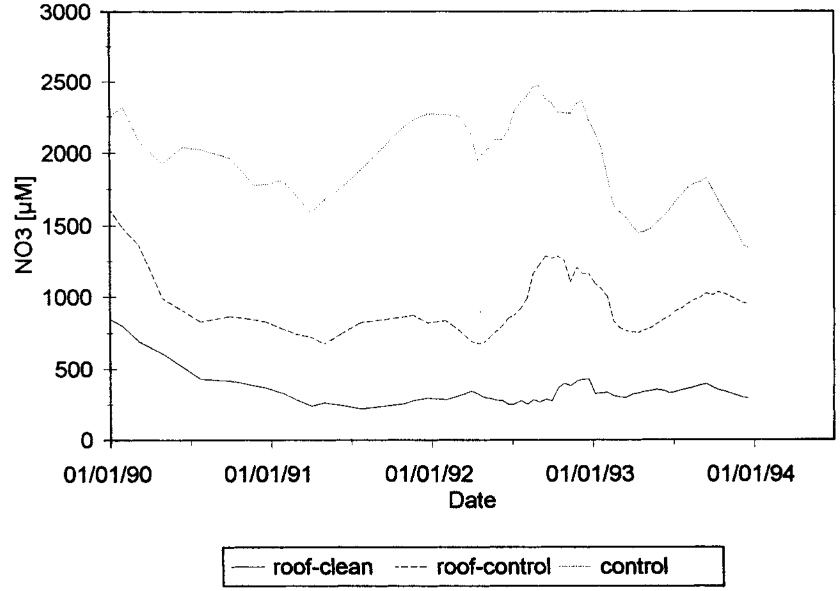

Figure 9. Nitrate concentrations at 90cm depth in the soil solution at Ysselsteyn.

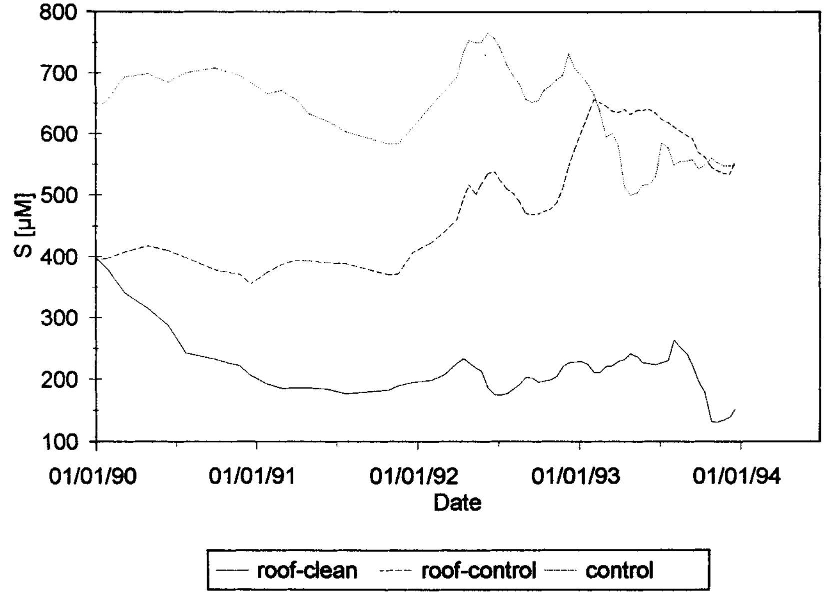

Figure 10. Total-S concentrations at 90cm depth in the soil solution at Ysselsteyn.

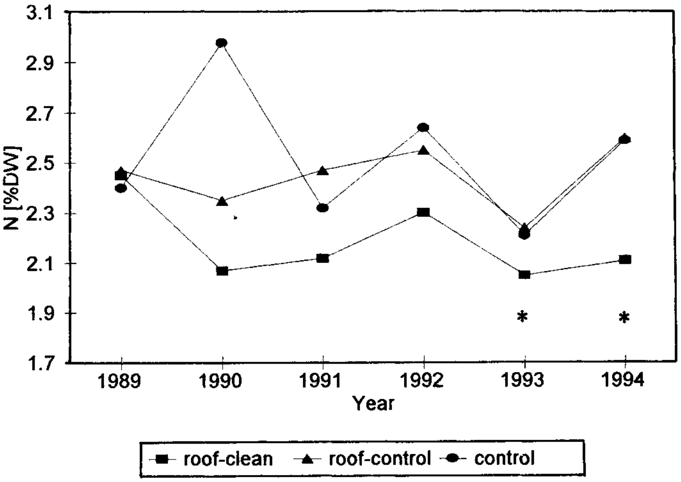

Figure 11. Nitrogen concentration in the ½-year-old needles at Ysselsteyn. *: roof-clean plot is significantly different from both control plots at p≤0.05. Systat 5.0: ANOVA correlation.

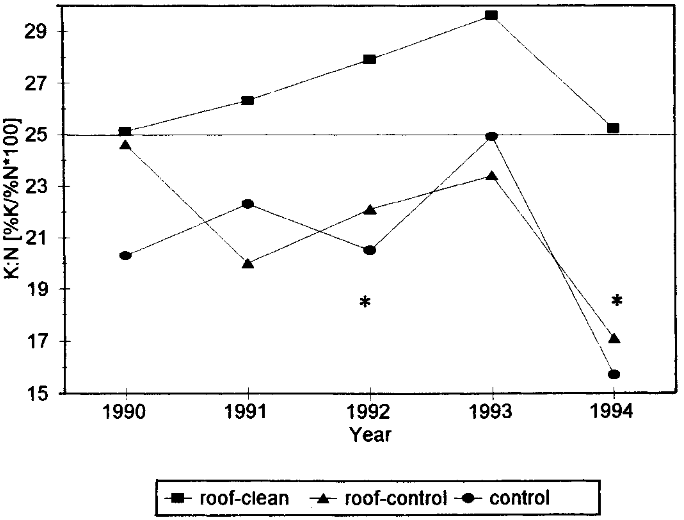

Figure 12. K:N balance in the ½-year-old needles at Ysselsteyn. *: roof-clean plot is significantly different from both control plots at p≤0.05. Systat 5.0: ANOVA correlation.

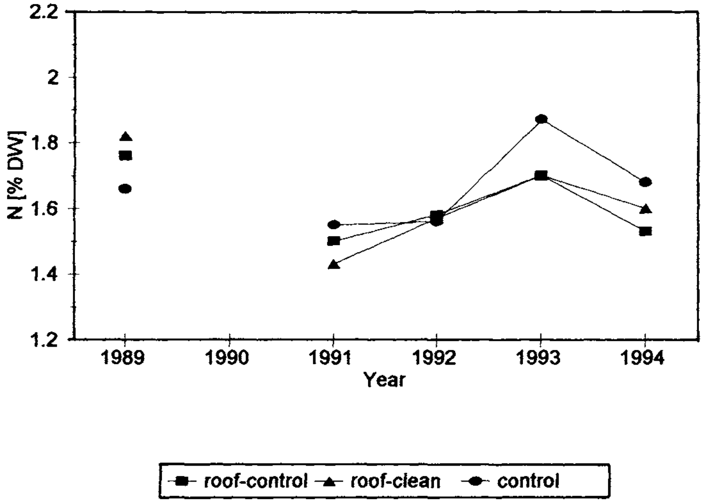

Figure 13. Nitrogen concentrations in the ½-year-old needles at Speuld. Plots are not significally different. Systat 5.0: ANOVA correlation.

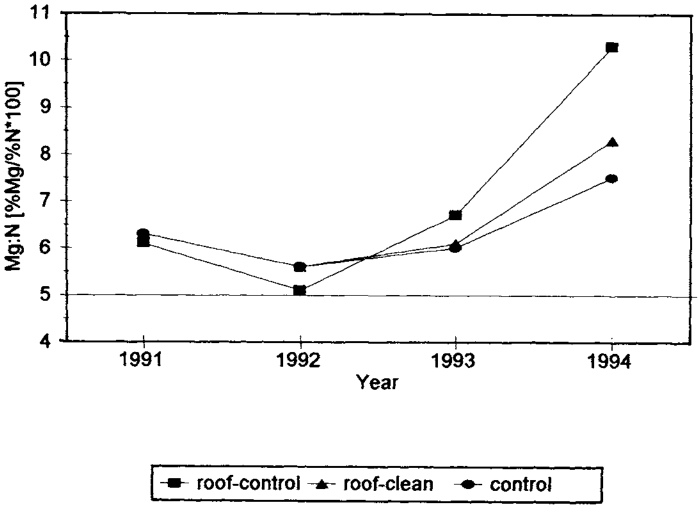

Figure 14. Mg:N balance in the ½-year-old needles at Speuld. Plots are not significally different. Systat 5.0: ANOVA correlation.

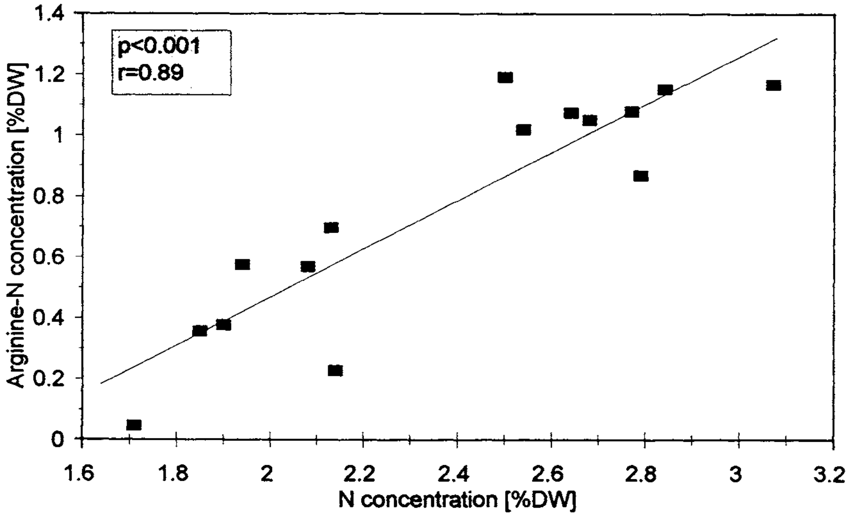

Figure 15. Correlation between the total-N and arginine-N concentration in the ½-year-old needles (collected January 1994) at Ysselsteyn. Systat 5.0: Spearman correlation.

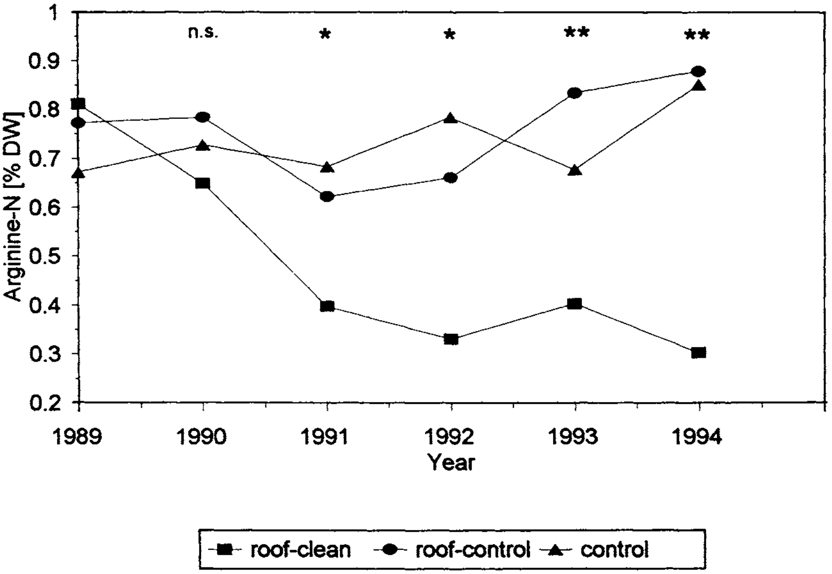

Figure 16. Free arginine-N concentrations in the ½-year-old needles at Ysselsteyn. Roof-clean plot is significantly different from both control plots at *: p≤0.05, **: p≤0.01, n.s.: not significant. Systat 5.0: ANOVA correlation.

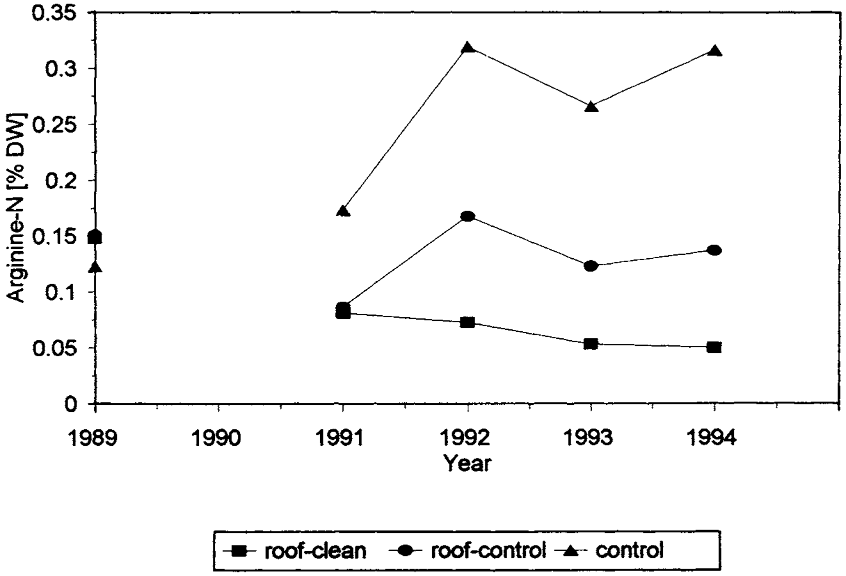

Figure 17. Free arginine-N concentrations in the ½-year-old needles at Speuld. Plots are not significally different. Systat 5.0: ANOVA correlation.

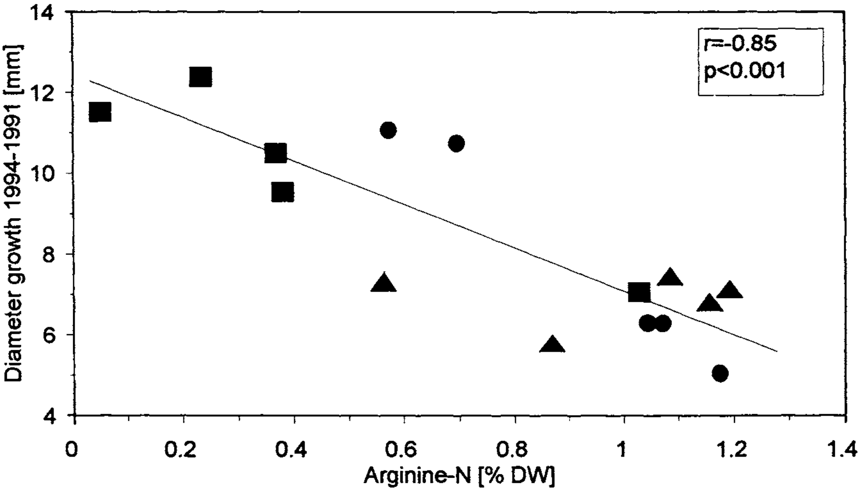

Figure 18. Correlation between arginine-N concentration in the ½-year-old-needles (collected in January 1994) and diameter growth of five dominant trees at Ysselsteyn. ■: roof-clean; Δ: roof-control; ●: control. Systat5.0: Spearman correlation.