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# Effect of nitrogen on drought strain and nutrient uptake in Norway spruce *Picea abies* (L.) Karst.) trees

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## Abstract

A field lysimeter study was established with the aim of investigating the effect of nitrogen availability upon drought strain in Norway spruce trees. Forest soil (Typic Udipsamment) was filled in lysimeters 1 m in diameter and 1 m deep. Small trees of Norway spruce from five different clones were planted in the lysimeters. Roofs under the canopy of the trees ensured full control of water and nutrient input. Three levels of nitrogen were given to the trees during five years; ambient rainwater, and five and fifteen times this N concentration, respectively. Additional N was given as $NH_4NO_3$ in irrigation water. Mean annual N-addition during the five years corresponded to 5, 27 and 82 kg per ha and year for the three treatments, respectively. During the third and fifth growth season drought was artificially induced. In addition to a watered control, two levels of drought were applied, representing water deprivation for 2 and 3 months, respectively, in 1990 and 3 and 4 months, respectively in 1992. A higher water consumption in the nitrogen fertilized trees during the droughts resulted in a significantly lower pre-dawn shoot water potential compared to the trees receiving ambient rain N. The interaction between drought and nitrogen fertilization was clear also for photosynthesis and transpiration. A decrease in height- and diameter increment caused by drought was most pronounced in the 82 kg N $ha^{-1}$ $yr^{-1}$ treatment. A water strain integral showed a strong positive correlation to the needle biomass of the trees. Foliar concentrations of several nutrients decreased significantly with increasing drought strain in the trees. Concentration of potassium and boron were especially low and visual symptoms of deficiency occurred.

## Introduction

The growth stimulating effect of nitrogen application to most coniferous forests has been known for several decades (see Tamm, 1991). A huge number of fertilizer experiments in middle- and northern Europe have demonstrated the growth promoting effect of nitrogen under various forest stand conditions. In the discussion of transboundary air pollution, the effects of nitrogen deposition has been focused on the last decade. A higher increment in spruce stands, compared to expected values derived from yield models, has partly been explained by the fertilizing effect of nitrogen deposition (Kenk, 1989). This has also been reported from southern Sweden in beech forests (Falkengren-Grerup and Eriksson, 1990). On the other hand, concern has been expressed about possible negative effects on forest ecosystems due to the increased nitrogen deposition in large areas around the world (e.g. Mohr, 1986; Nihlgård, 1985). Several factors have been focused on; effects on the trees mycorrhizae, shortage in mineral elements, growth of leaf algae, increased water demand due to increased growth and altered root to top ratio. Increased water use could thus leave the trees more susceptible to drought injury. Increases in soil acidification and leaching of nitrate are also effects of heavy nitrogen inputs that can occur.

This paper addresses the effects of increased drought strain in Norway spruce (*Picea abies* (L.) Karst.) trees that are exposed to increased N concentration in the precipitation water. Plant nursery experiments indicate a reduced drought resistance with increasing nitrogen application in *Pinus contorta* Dougl. var. *lat.* (Etter, 1969). Field experiments with

*Pinus radiata* D. Don trees in Australia have shown increased mortality during a hard drought due to fertilization (Linder et al., 1987). On the other hand, other authors have found an optimal level of nitrogen concentration in trees (*Pinus banksiana* Lamb. and *P. taeda* L.) in relation to drought resistance (Bensend, 1943; Pharis and Kramer, 1964).

The purpose of this investigation was to test the hypothesis that increased nitrogen deposition increases the crown growth of Norway spruce trees, leading to increased water consumption and thereby to increased strain during drought. Effects on tree uptake of other nutrients and on stem growth were also considered.

## Material and methods

### *The lysimeters*

An experiment consisting of 45 lysimeters was established at Ås near Oslo (59° 40'N, 10° 40'E). Each lysimeter, made of high density polyethylene, was 1 m in diameter and 1 m deep with a sloping bottom (5°). Runoff water was collected through a connected pipe on the lowest side. The lysimeters were filled with forest soil (Typic Udipsamment) taken at a site 60 km north of Ås. The different soil layers was mixed separately and the profile was reconstructed in each lysimeter. The E-horizon was excluded in the lysimeters because it was very thin and variable. The humus layer was homogenized and carefully mixed, then placed on top of the mineral soil in a 5 cm thick layer. This was to ensure low variability between the lysimeters.

The lysimeters were placed on each side of a lysimeter trench and the space between them was filled up with soil. About 15–20 cm of each lysimeter was left above the soil surface, both inside and outside.

### *Plant material and establishment period*

In the period May-July 1987 the trial was established and five clones of Norway spruce trees were planted, one clone for each of the 5 replications. Two ramets of the same clone were planted in each lysimeter. Tree height at planting was on an average 0.8 m. The trees were third generation of cuttings, rooted 6 years before start of the experiment. The provenance was well adapted to the environment at the site.

After planting the trees, seeds of *Deschampsia flexuosa* (L.) Trin. were sown to restore the dominant vegetation at the site were the soil was taken, and to avoid weeds establishing from the local flora.

From July 1987 until May 1988 all lysimeters were exposed to the precipitation at the site. In May 1988 small transparent roofs were built around the trees 15cm above the edge of the lysimeter to fully control the water and nutrient input to the lysimeters. During summer the lysimeters were added 10 to 30 mm rainwater a week each, depending on weather conditions. Each spring 150–200 mm of rainwater was given in a short period, to imitate a snow melting period.

In a few dry periods and during parts of the snow melting period tap water was used for the watering due to insufficient collection of rainwater. All water used for watering was analysed for nutrient content.

Leachate volume and concentration were measured approximately once a month during summer.

### *Experimental design*

Three levels of nitrogen application were given: N0 - control, ambient rainwater with an annual average concentration of 1.15 mg N L$^{-1}$, and treatment N5 and N15 with N concentrations of 5 and 15 times the ambient, respectively. The additional nitrogen was given as ammonium nitrate.

The third season after establishment (1990), drought was artificially induced at three levels: D0 - control with no restrictions on watering, and Dl and D2 with no watering for 2 and 3 months, respectively. Before the fourth growing season, one of the trees in each lysimeter was removed to provide more space for the remaining trees. No drought treatment was applied during the fourth growing season. During the fifth growing season (1992), the remaining trees were again exposed to drought, lasting 3 and 4 months for the Dl and D2 treatments, respectively.

Total input of water and nitrogen during the experimental period for the D0-treatment is shown in Table 1. The irrigation in 1990 was 470 mm and 420 mm for the D1- and D2-treatments, and in 1992 the corresponding figures were 300 mm and 170 mm.

### *Measurements during the drought periods*

During the drought periods pre-dawn shoot water potential was measured weekly. Small twigs were taken from the middle and lower parts of the crowns and the water potential measured using a pressure chamber. One twig from one tree in each lysimeter, 45 altogether, was measured each time.

*Table 1.* N addition (kg ha$^{-1}$), relative N addition and irrigation (mm) in the watered control treatment

| N-treatment | 1988 | 1989 | 1990 | 1991 | 1992 | Mean | Rel.N |
|---|---|---|---|---|---|---|---|
| N0 | 3.94 | 6.17 | 6.24 | 4.04 | 4.91 | 5.06 | 1 |
| N5 | 21.11 | 34.01 | 32.69 | 22.60 | 25.33 | 27.15 | 5.4 |
| N15 | 64.03 | 103.61 | 98.81 | 69.00 | 76.37 | 82.36 | 16.3 |
| Irr. (mm) | 370 | 600 | 570 | 400 | 440 | 476 | |

One month after the onset of drought the grass in the lysimeters was cut. This was done to reduce other water use than transpiration of the trees and the surface evaporation.

The accumulated water strain in each tree during the droughts was calculated using a water strain integral ($S_\Psi$) (Myers, 1988).

$$S_\Psi = \left|\sum_{i=0}^{i=t}(\bar{\Psi}_{i,i+1} - c)n\right|$$

where $\bar{\Psi}_{i,i+i}$, is the mean $\Psi_e$ (pre-dawn or 'equilibrium' water potential) for any interval i, i + 1, c is the maximum $\Psi_e$ during the season, t is the number of measurements and n is the interval in days between the measurements. (The term water strain integral is used instead of water stress integral that is used by Myers (loc.cit.)).

At intervals, photosynthesis and transpiration were measured by a LI-COR (LI 6200) portable $CO_2$-porometer with a 4 litre chamber. South facing branches of the third or fourth whorl from the top were selected for measurements. The same branches were used for the measurements on each occasion. About 15 cm of the branch end, with 6 to 10 small twigs, were enclosed in the chamber. The measurements were done under fairly high light intensities under a period of about one hour.

In autumn the twigs used for photosynthesis measurements was cut off. The needles were dried for 3 days at 103 °C, and their dry weights determined.

### *Needle sampling*

In November each year samples of current year needles from the third whorl were taken. In 1987 samples were taken from each tree and pooled samples for each of the 5 replications were made and analysed for nutrient concentrations. In 1988 and −89 pooled samples consisted of the 3 nitrogen treatments in each replication, 15 samples altogether. In 1990 samples from each tree were collected and analysed. In 1991 and −92 samples from both current and last year needles were collected and analysed from each tree. The relatively small size of the trees the first years after planting excluded a more intensive sampling.

### *Root sampling*

Three cores (6 cm in diameter) from the humus layer were taken from each lysimeter in three out of the five replicates in autumn 1992. All living fine roots (< 2 mm diameter) were sorted out.

From one of these replicates (9 lysimeters) 20 samples were taken from the humus layer and 10 samples from the mineral soil. The mineral soil samples were divided into 10 cm sections down to 40 cm depth, and one section from 40–80 cm depth. The average fraction of living fine roots in mineral soil out of total fine roots in this replicate, was used to give a rough estimate of the total biomass of living roots in the three replicates where only humus samples were collected.

### *Soil water content*

Soil cores of 1.5 cm in diameter were taken from different depths in the lysimeters just before rewatering of the D1-treatment in 1992. Fresh weight and weight after 3 days drying at 103 °C were measured to determine the water content in the soil.

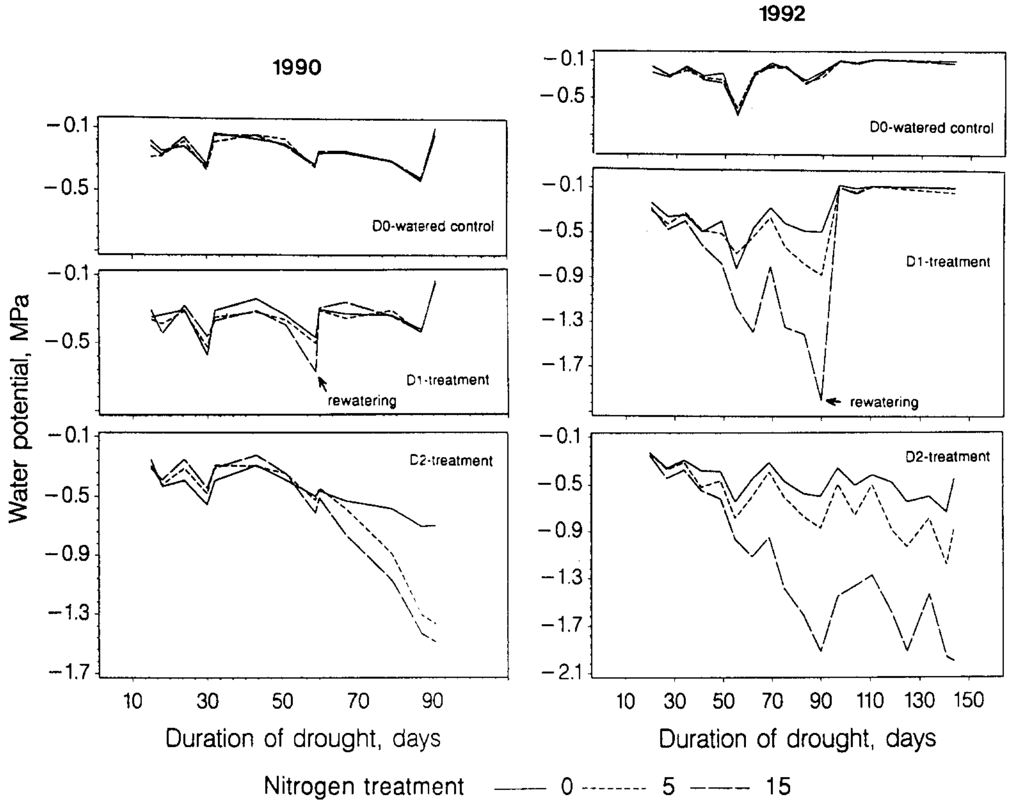

*Fig. 1.* Pre-dawn shoot water potential during the summers of 1990 and 1992 for different drought- and nitrogen treatments.

### *Chemical analysis*

Analysis of water and needles were done according to Ogner et al. (1991). In water samples the anions were determined by ion chromatography (Dionex 2001/SP) and ammonium by a modified flow injection method (FIAstar 5010 System). Total elements in water were determined by a simultaneous ICP-AES technique (Jarrel-Ash AtomComp 1100).

In needle samples total N was determined as ammonium after Kjeldahl digestion. Total elements in needles were determined by a simultaneous ICP technique in acid digested samples.

### *Statistical analysis*

The experimental design was factorial with two fixed effects (nitrogen and drought). A balanced ANOVA-model with fixed effects and an interaction term was used in analysing treatment effects. The different clones were treated as one in the analysis since they were represented in one replicate each. The Duncan multiple range test was used to identify differences between treatments. A non-linear regression analysis procedure was used to describe the relationships between needle nutrient concentrations and water strain integral. The statistical analysis program SAS was used (SAS, 1985).

## Results

### *Water potential during drought*

Pre-dawn shoot water potential at various intervals during the summers of 1990 and 1992 were rather similar (Fig. 1) The watered control D0 generally varied between −0.2 and −0.4 MPa. The variation was due to changing weather conditions and the low values during first part of the periods both years took place during dry weather conditions. No significant differences due to nitrogen application were noted for the D0-treatment.

*Table 2.* F-values from analysis of variance of pre-dawn shoot water potential. Results from selected days in 1990 and 1992 at varying duration of the drought

| | | Duration of drought, days | | | | | |
|---|---|---|---|---|---|---|---|
| Year | Treatment | 15 | 30 | 43 | 59 | 79 | 87 |
| 1990 | N | 1.66 | 1.76 | 0.92 | 5.67** | 3.49* | 3.47* |
| | D | 6.36** | 8.72*** | 27.00*** | 23.25*** | 46.65*** | 34.48*** |
| | N x D | 0.89 | 0.35 | 2.65* | 1.64 | 3.55* | 3.47* |
| | | Duration of drought, days | | | | | |
| | | 20 | 34 | 55 | 69 | 97 | 111 |
| 1992 | N | 0.02 | 1.39 | 6.06** | 31.80*** | 11.14*** | 10.78*** |
| | D | 10.55*** | 19.93*** | 4.89* | 34.10*** | 42.71*** | 63 .75*** |
| | N x D | 2.37 | 0.662 | 2.15 | 7.83*** | 10.99*** | 11.28*** |

Significant at level: *5%, **1%, ***0.1%.

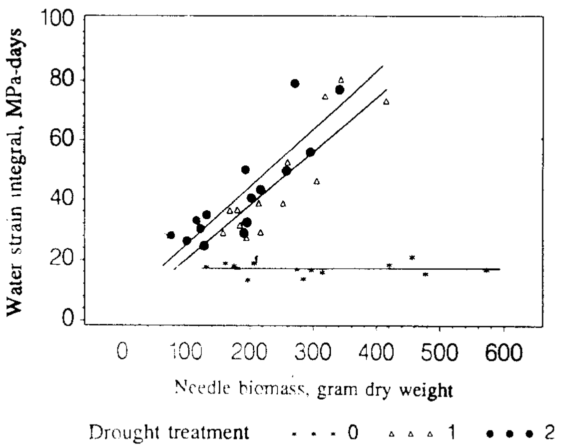

*Fig. 2.* Water strain integral for different drought treatments over a period of 90 days plotted agains needle biomass of the trees. 1992 data.

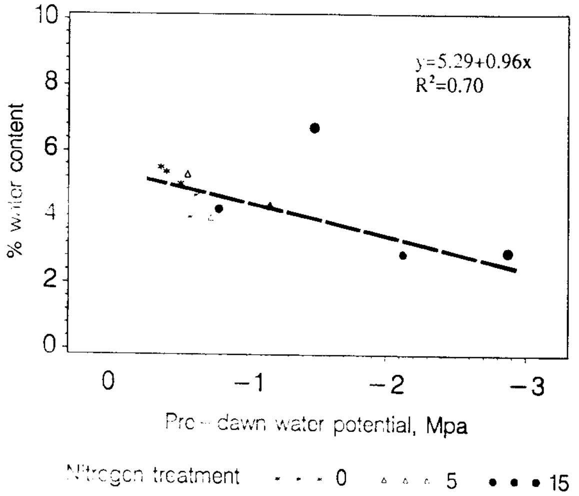

*Fig. 3.* Average water content in the mineral soil down to 40 cm depth in the D1-treatment after 90 days without watering versus pre-dawn shoot water potential at the same time. The outlier is not included in the regression analysis.

After about 60 days without irrigation the water potential decreased markedly, particularly in trees of the N15 treatments in 1992. The interactive effect of nitrogen and drought upon the water potential became more and more pronounced in the period from 60 to 90 days. The N5D2 and N15D2 treatments produced mean values of pre-dawn water potential down to −1.3 and −1.5 MPa, significantly different from the N0D2 that had a value of −0.7 MPa after 90 days in 1992. The interaction of nitrogen and drought was most pronounced in 1992 (Table 2). In 1992 the D2N5-treatment yielded results closer to the D2N0-treatment than what was the case in 1990.

Water potential of the D1-treatment followed those of the D2-treatment closely until rewatering which in both years resulted in a very rapid increase in water potentials, up to the values of the watered control trees (Fig. 1).

### *Water strain integral, soil water, needle biomass and increment*

In Figure 2 the water strain integral in 1992, up to the time for rewatering of the D1-treatment is plotted against the total autumn needle biomass. There is a positive correlation between water strain integral and needle biomass for the drought treated trees ($r^2 = 0.71$, $p < 0.01$). A simular correlation ($r^2 = 0.67$, $p < 0.01$) was also evident looking at the pre-dawn water

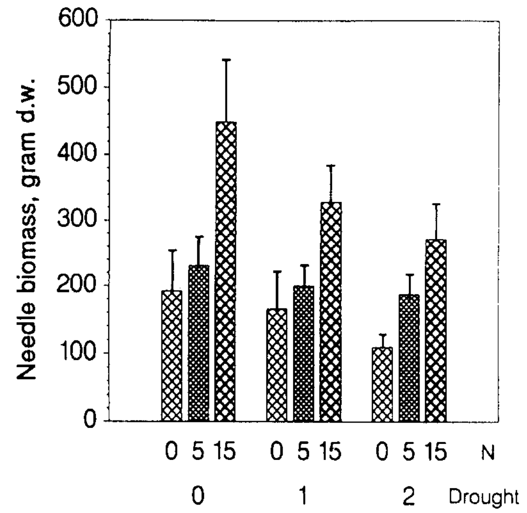

*Fig. 4.* Total needle biomass (+ 1 SD) in autumn 1992 for the different drought- and nitrogen treatments.

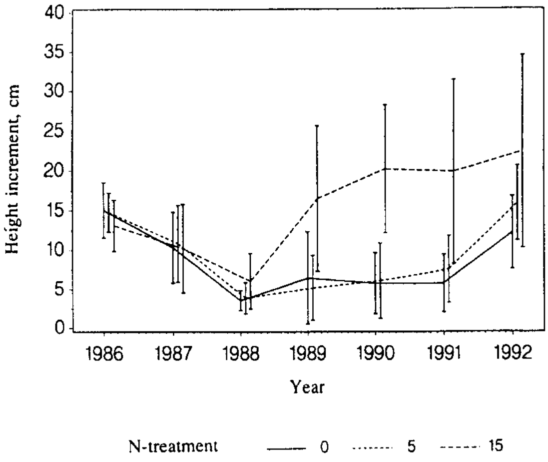

*Fig. 5.* Height increment (+/- 1 SD) of the trees one year before and during the experimental period for the different nitrogen treatments.

potential after 90 days and the needle biomass (not shown).

Average water content in the mineral soil after 90 days without watering correlated well with pre-dawn shoot water potential (Fig. 3). The single outlier was from a lysimeter having a high water content from 10 cm depth and downward and a much lower water content in the upper 10 cm of the mineral soil. This value is not taken into account in the regression analysis. The water content of the humus layer was much more variable and showed no clear correlation to shoot water potential in the trees.

The N-application resulted in a significant increase in total needle weight on the trees, while the effect of drought was opposite (Fig. 4). Shedding of needles before harvesting the trees was not measured, but from visual registration the shedding was rather small compared to total amount of needles on the trees.

The replanting in 1987 caused a reduction in height increment for all trees in 1987 and 1988 (Fig. 5). The N15-treatment resulted in an increased height increment from 1989 on. Nitrogen treatment effected height increment significantly in 1990, but in 1991 a delayed effect of the 1990 drought on height increment appeared (Fig. 6). In trees of the N15-treatment, the D0-treatment showed a significant higher increment than the D2-treatment. The N0 and N5 treatments showed the same trend but the differences were not significant. The same trend was observed in 1992. There was no significant interaction between N and drought upon height increment. There was a significant negative correlation between height growth in 1991 and water strain integral in 1990, although the variation was large (not shown).

The same tendency as for height growth was seen on the annual ring width at stem basis (not shown). The clearest effect was that of the N-treatment, but the interaction effect of N and drought was significant for the three-year period 1990-92. Trees of the N15 treatment had the largest decline in diameter increment due to drought.

The root biomass in autumn 1992 showed a tendency towards higher values for the N-treated trees, although no differences were significant. A decrease in root to shoot ratio due to the heaviest N-treatment was quite clear ($p < 0.06$, not shown).

### *Photosynthesis and transpiration*

It took more than 50 days before a tendency towards reduced photosynthesis and transpiration emerged in the most severe drought treatment (Fig. 7). Measurements after 71 days showed significant effects of both nitrogen and drought upon photosynthesis. The interaction between nitrogen and drought was also highly significant. Differences in transpiration rates showed the same pattern as for photosynthesis during the drought period, as shown in Figure 7 at 144 days. The water use efficiency (WUE) showed no significant changes due to the treatments, although it was a tendency to increased WUE due to drought and nitrogen treatments.

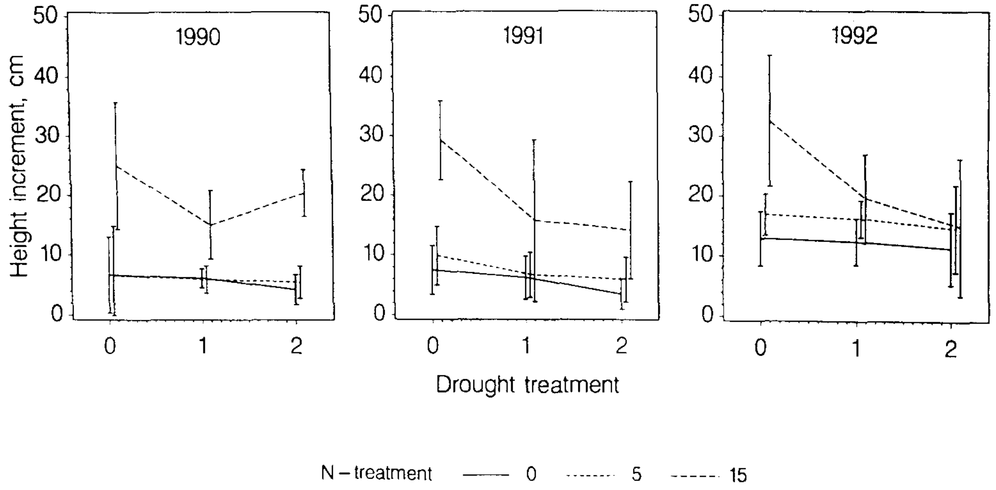

*Fig. 6.* Height increment (+/-1 SD) during the years 1990-92 for the different drought- and nitrogen treatments.

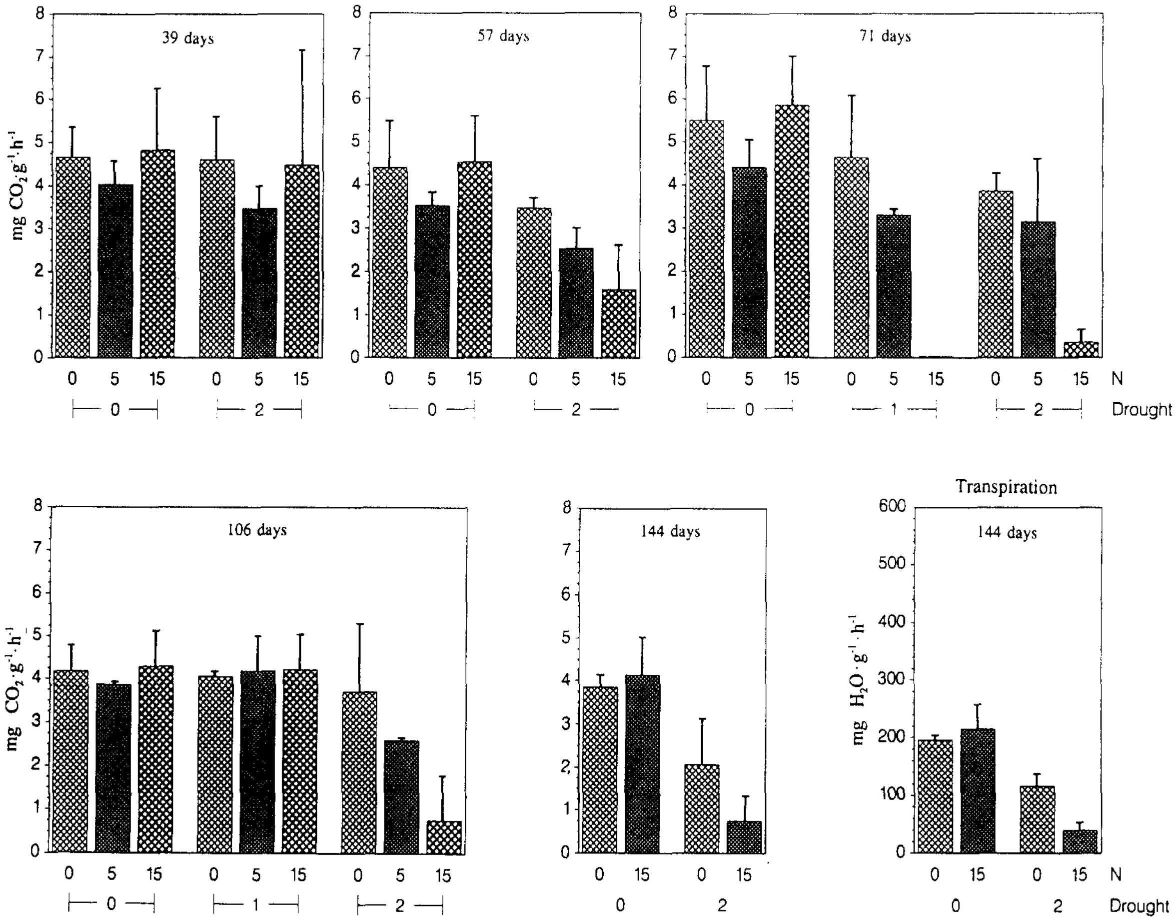

*Fig. 7.* Photosynthesis (+ 1 SD) in small twigs at different intervals after onset of drought during summer 1992 for the different drought- and nitrogen treatments. At 144 days transpiration is also shown. The measurements after 39 days without watering were done between 07.00 and 08.00 a.m. in the morning, the others were done between 12.00 and 14.00 p.m.

Rewatering of the D1-treatment after 90 days resulted in a fast recovery in photosynthesis. Two weeks after rewatering the D1-treatment the photosynthesis was on a level equal to the D0-treatment (Fig. 7, 106 days). The transpiration was a little lower causing a slightly higher WUE, but not significantly.

The differences in photosynthesis and transpiration between watered and drought treated trees lasted throughout the autumn. Moist weather and less intensive radiation reduced the differences to some extent (Fig. 7, 144 days).

Measurements from the first drought period in 1990 showed similar results (not shown here) as the 1992 data presented above.

### *Needle nutrient concentration*

The nitrogen level in current year needles was increased from rather low values through medium to high values due to the N-fertilization (Fig. 8). The N15-treatment was significantly different from the N0 treatment all years, whereas the N5-treatment fluctuated between N0 and N15. In 1990 and 1991 the N-concentration was significantly higher in the N5-treatment than in the N0-treatment.

An opposite effect can be seen on other macronutrients in the needles (Fig. 8). Concentrations of potassium, magnesium and boron were reduced in the N5- and N15-treatments compared to N0. The general level of these nutrients was also markedly reduced from 1988 to 1989. Calcium, manganese and zinc showed also a decrease in concentration due to nitrogen treatment. Sulphur and phosphorus concentrations were less influenced by the N-treatment.

A vector analysis (Timmer and Stone, 1978) was performed for the watered control trees in 1990. The result gave a clear "A-shift" for Mg, Ca, and K (not shown), indicating a dilution effect of the N fertilization. The vector analysis should be interpreted with care in this case since the fertilization had been done for three seasons and had also influenced the number of needles and number of shoots.

Looking at the main tendencies in the nutrient concentrations (Fig. 8), it should be remembered that effects of droughts are included, at least in 1990 and 1992. In Figure 9 the concentrations of some elements are arranged according to the total water strain integral during the summer 1992. The macro-nutrients calcium, magnesium and potassium showed a decline in concentration with increasing drought strain. Nitrogen was slightly affected and this was also the case for sulphur and phosphorus (not shown). Boron was the only micro-element that dropped to a level of possible deficiency symptoms. Of the macro-elements, potassium and magnesium decreased to values expected to cause visible deficiency symptoms. This was in fact the case for some of the trees, where needle- and needle tip yellowing was observed. Nutrient concentrations seemed to level out after the water strain integral exceeded 100 Mpa-days.

The concentration of magnesium in last years needles was on an average 15% lower than in current year needles. Calcium concentration was almost doubled in last year needles compared to current year needles. For nitrogen, phosphorus and potassium concentrations, just minor differences were found between current and last year needles. These ratios showed no correlation to the strain integral.

## Discussion

A positive significant effect of nitrogen application on needle biomass accumulation and height- and diameter increment during the experimental period was found, especially for the heaviest N-treatment. This is in agreement with a number of experiments, both in nurseries and in forest stands of many tree species. Increased N-availability usually results in a reduced root to shoot ratio (e.g. Brouwer, 1962; Glatzel, 1981; Linder and Rook, 1984). This was the case in the present study as well.

The differences in pre-dawn water potential between the N-treatments during the summers of 1990 and 1992 were obviously related to differences in water consumption during the first part of these summers, since transpiration was relatively equal on dry matter basis for all N-treatments during more than one month (cf. Fig. 7). The correlation between water strain integral and needle biomass strongly indicated that the larger crown and corresponding higher water consumption lead to a much more rapid depletion of soil water in the N15-treatment than in the other treatments. This could also be seen from the soil water measurements, which showed rather low values in the N15-treatment. A volumetric water content of approximately 2% corresponds to a soil water potential of $-1.5$ MPa in this soil type (Stuanes and Sveistrup, 1979). In 6 weeks old seedlings of *Pinus contorta*, increased water consumption was attributed to nitrate application (Etter, 1969). This lead to increased mortality when the seedlings were held for two weeks without watering.

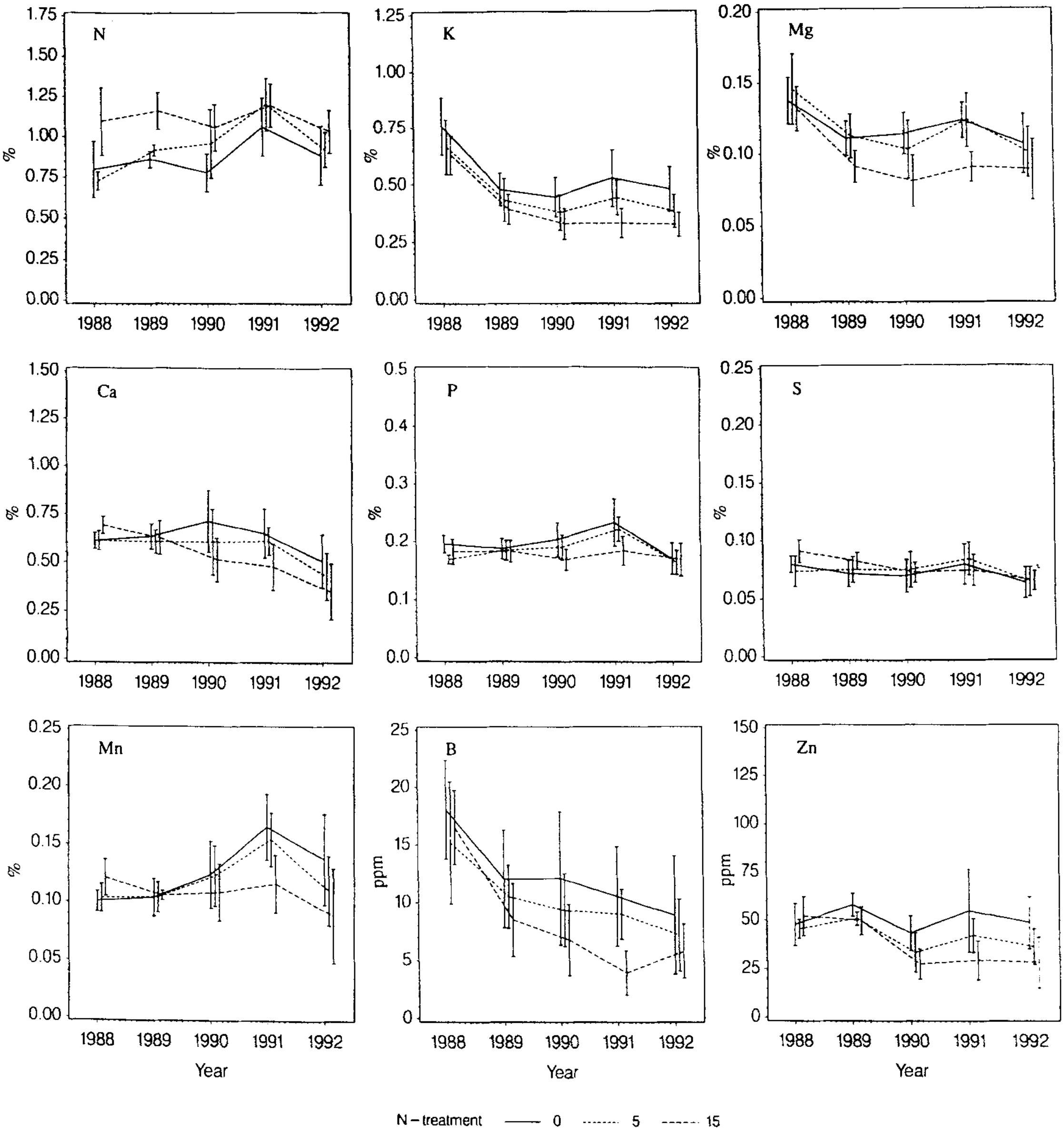

*Fig. 8.* Concentrations (+/- 1 SD) of some elements (% of dry weight) in current year needles for different nitrogen treatments in different years.

A small negative effect on drought resistance (defined as mortality rate) was also found when the seedlings were stressed to the same low moisture content in the soil. However, in small plants of *Pinus taeda*, an optimum needle N-concentration for drought resistance was found (Pharis and Kramer, 1964). Drought resistance was defined as the ability to endure severe water stress and recover with a minimum reduction in growth and yield. In *Pinus banksiana* an optimum nitrogen level for drought resistance has also been found (Bensend, 1943).

These earlier results appear a little contradictory. However, the definition of drought resistance varies, the species in question differ, and the methods used for drying differ among the investigations. The general conclusion must be that the water consumption of N-fertilized seedlings and trees increases, leaving them more susceptible for stress during acute droughts. The question of changes in drought resistance, according

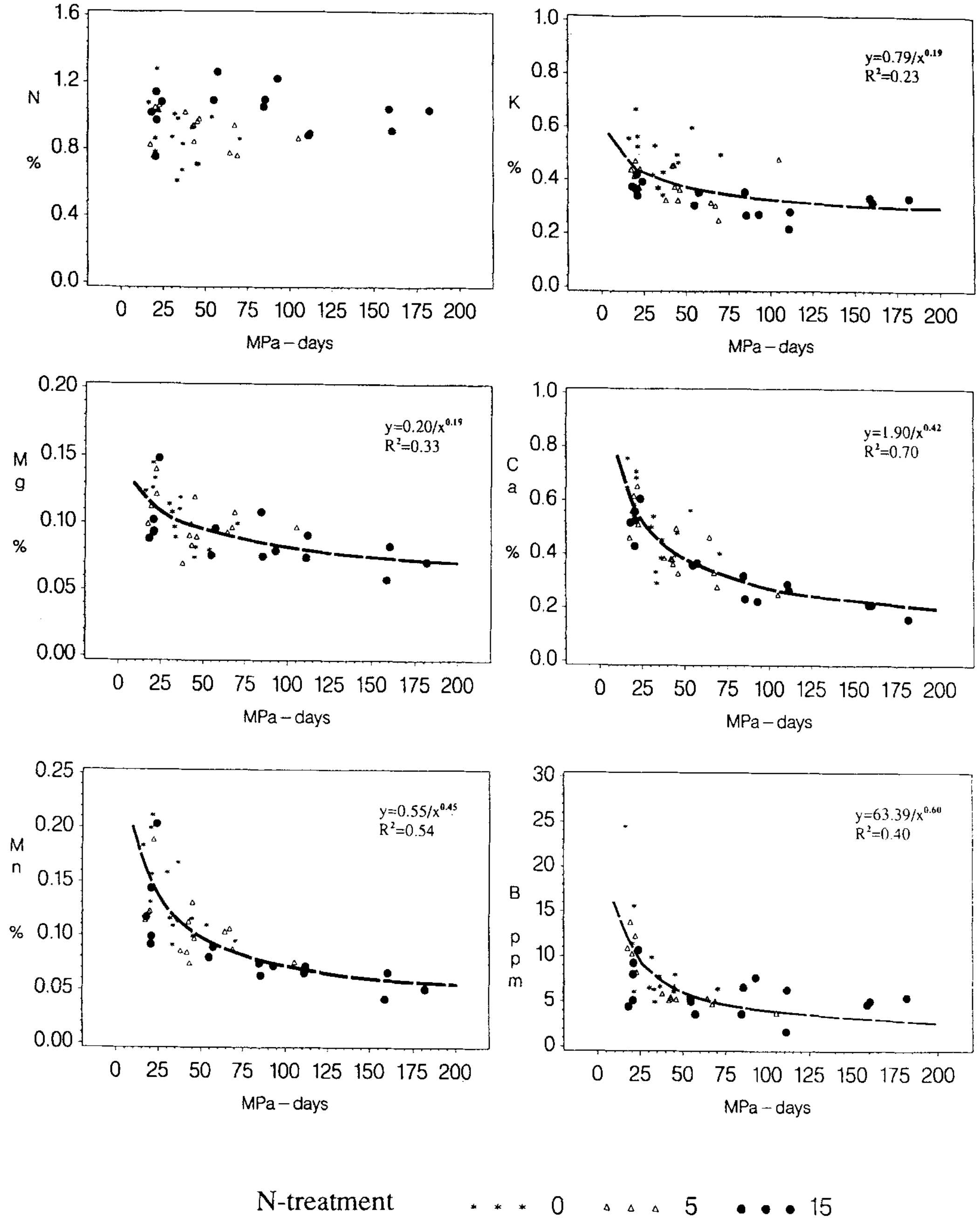

*Fig. 9.* Concentrations of some elements (% of dry weight) in current year needles of individual trees in autumn 1992, in relation to water strain integral (MPa-days).

to the definition of Levitt (1980), with increased N-availability is more difficult to answer. Larsen (1983) found a small positive effect on total drought resistance in *Pseudotsuga mensiezii* with increasing N-concentration in needles, using a soil freezing technique. This was mainly due to increased drought avoidance. The positive effect of increased potassium concentration, however, was much more pronounced on the drought resistance than the effect of nitrogen. In *Pinus radiata* a higher pre-dawn water potential, at the same soil water deficit, was found for fertilized trees (Linder et al., 1987). This at least indicates an increased drought avoidance with increasing N availability.

From field experiments few examples have been given on the nitrogen and drought interaction. In a fertilizer experiment in a 10 year old *Pinus radiata* stand, a decreased shoot water potential, a decrease in growth and also an increased mortality was observed in fertilized trees compared to control trees during a very dry summer (Linder et al., 1987). From fertilization trials with Norway spruce in Germany, Spiecker (1987) found a very small and even slightly negative growth response to nitrogen fertilization in the dry summers of 1975-77. In an analysis of Norwegian fertilizer experiments in old stands of *Picea abies* and *Pinus svlvestris* no negative growth response, compared to control plots, were found in fertilized trees during two very dry summers (Nilsen, 1990). Although some examples of negative effects on production of N-fertilization in dry periods can be found, the positive effect still seems to dominate under field conditions. Results from field experiments, even under relatively high N-deposition rates, still show positive fertilizer effect of nitrogen (e.g. Nilsson and Wiklund, 1992).

The height increment in 1991 correlating to the water strain integral in the present study, is in agreement with other investigations. Myers (1988) showed that the water strain integral gave a good link between short term water strain and long term growth measures like needle length and basal area increment in *Pinus radiata*. High correlation has also been found between both leaf area and dry matter production and water strain integral in two eucalyptus species (Myers and Landsberg, 1989).

The nitrogen concentration in the needles was rather low compared to optimal values under controlled conditions (Ingestad, 1979). It increased with N-application and the values in autumn 1989 before onset of the drought in spring 1990, varied between 0.7% to 1.3%. This must be said to cover the range from low to high nutrient levels. Values exceeding 1.2%–1.3% are in the upper range under field conditions in Norway (Aamlid et al., 1992). The relatively low N concentrations of the control trees could be due to a high microbial demand for nitrogen in the reconstructed soil profiles. Higher values for N in the control trees could possibly led to smaller differences between the treatments in the measured parameters. However, it is likely that also the N-treated trees would have shown higher N concentrations in undisturbed soil profiles.

The effect of N application on concentration of other nutrients was clearly negative in the present study. This is very likely a dilution effect since the vector analysis (Timmer and Stone, 1978) performed on the watered control trees in 1990 showed a typical “A-shift”. However, the differences in number of needles per shoot and number of shoots between the control and N-treated trees may influence on the results of the vector analysis.

The dilution of other elements than N is not necessarily a negative factor for the trees. It expresses the fact that these elements are not minimum factors for growth. However, the possible nutrient imbalance caused by heavy loads of nitrogen from both fertilization or atmospheric N-deposition has been focused in many investigations in the U.S. and Europe (Aronsson, 1985; Heinsdorf et al., 1988; Hüttl, 1990; Mohren et al., 1986; Rehfuess et al., 1983; Weissen et al., 1990; Zöttl, 1990).

In addition to the dilution effect in this experiment, a drop as in potassium, magnesium and calcium levels with increasing water strain integral was faced. The decrease was pronounced, although it levelled out for values exceeding 100 MPa-days. Boron and potassium reached very low levels. Symptoms such as needle- and needle tip yellowing were observed on some of the trees. A decrease in nutrient concentrations has been observed under field conditions during hard droughts, both in spruce and pine (Christiansen, 1992; Wehrmann, 1961), and from nurseries (Will, 1961). Drought stress on Norway spruce trees brought about a decrease in sap concentration of calcium, magnesium and potassium and also a decrease in needle concentration of these elements (Dambrine et al., 1993). The phenomenon is well known from agricultural crops (Dunham and Nye, 1976; Viets, 1972). All elements seem to be affected by drought, but potassium and phosphorus have been reported to have a more restricted uptake during drought than other elements (Dunham and Nye, 1976). However, the phosphorus concentration was little affected by the drought treatments in the present study. Boron concentrations are known to be significantly reduced during droughts, both in agricultural crops and in forest trees on drained peatland (Brække, 1977, 1979; Hobbs and Bertramson, 1950; Russel, 1973). One explanation is that most of the available boron is bound in the organic matter, and that the availability drops during soil drying because of reduced microbial decomposition activity. The reason for the rather low boron concentration in the present investigation could be an antagonistic effect with nitrate (Wikner, 1983). It has also been shown that an abundance of ammonium increases the coprecepitation of boron with iron and aluminium in the range of pH 5-6 in the soil water (Wikner, 1983). This could also have influenced the uptake of boron in the present study when the ammonium concentration in soil water probably increased.

A negative feedback of decreased potassium concentration due to drought can possibly occur due to the well known effect of this element in the stomatal regulating mechanism (Levitt, 1976).

Photosynthesis and transpiration correlated well to pre-dawn water potential during summer. A strong reduction of photosynthetic rates and transpiration was first attained after more than 2 months, as was the case for the pre-dawn water potential. The relatively fast recovery of photosynthesis after rewatering is in agreement with investigation on Scots pine (Bengtson, 1980), where small after-effects of drought upon photosynthesis were found in a five day period after rewatering. The small positive, but not significant effect of drought and increased N upon WUE in this investigation is supported by other investigations (Sands and Mulligan, 1990). They refer literature showing an increase in WUE due to increased soil water-deficit and also due to fertilization with N and P. A better WUE caused by a better nitrogen nutrition could be beneficial for trees during periods with restricted water availability, although a quantitative estimation of this is not possible.

### *Concluding remarks*

The results show a very clear effect of increased nitrogen availability on drought strain in the trees. Changes in drought resistance are probably of minor importance for the trees compared to the effect of increased transpiration, resulting in decreases in water potential, growth and nutrient uptake during droughts. The high N-deposition in many areas has implications not only as a possible triggering factor for nutrient imbalances, but also on nutrient uptake during droughts and occurrence of discolouration and needle loss. Therefore a larger periodic variation in growth patterns due to both positive and negative effects of nitrogen are likely in combination with fluctuations in weather conditions in the future.

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