Growth and nutrition of Douglas fir, Scots pine and pedunculate oak in relation to soil acidification

Promotoren: Dr. Ir. N. van Breemen,
hoogleraar in de Bodemvorming en Ecopedologie.

Dr. G.R. Findenegg,
hoogleraar in de Bodemvruchtbaarheid en
Plantevoeding.

Co-promotor: Dr. Ir. W.G. Keltjens,
universitair hoofddocent in de Bodemvruchtbaarheid en
Plantevoeding.

P.H.B. de Visser

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STELLINGEN

1. De "optimal nutrition" methode om de maximale boomgroei te bereiken met optimale benutting van nutriënten, kan in Nederlandse bossen beter benaderd worden op basis van het meestal gebrekkige fosfor dan van stikstof, gezien de overmaat van de laatste.
Dit proefschrift.
T. Ingestad, 1988. Scan. J. For. Res. 3, 157-173.

2. De overmatige stikstofvoeding van bomen wordt aangetoond door groeiverdunning van de stikstofconcentratie in de naalden, volgend op het opheffen van een groeibeperking, zoals watertekort.
Dit proefschrift.
E.-D. Schulze, 1989. Science 244, 776-783.

3. Toediening van basische kationen, met nitraat of sulfaat als begeleidend anion, aan een zure bosbodem ten behoeve van een verhoogde nutriëntenvoorziening van de bomen, heeft als ongunstig neveneffect dat veel aluminium en zuur door kationenomwisseling van bodemcomplex in oplossing gaat.
Dit proefschrift.
E.E. Hildebrand, 1986. Forstwissenschaftliches Centralblatt 105, 60-76.

4. De suggestie van Zwiazek en Blake, dat ophoping van suikers in de plantecel een actief proces is ter vermijding van droogteschade, verhult dat een aantal passieve processen tijdens het watertekort minstens zo belangrijk zijn voor de ophoping.
J.J. Zwiazek and T.J. Blake, 1990. Can. J. For. Res. 20, 108-112.

5. Het model voor de lineaire relatie tussen groei en lichtintensiteit op basis van orgaan-specifieke groei en phyllotaxis is niet strijdig met de exponentiële relatie volgens Ingestad, maar vormt hierop juist een goede functionele aanvulling voor de groeifase na de exponentiële groei.
T. Ingestad, 1982. Plant Cell Environ. 5, 443-453.
G.A. Pieters en M.E. van den Noort, 1990. Developments in Plant and Soil Sciences 41, 61-68.

6. De zeer zware storm in januari 1990 vormde een natuurlijk experiment ter bepaling van zowel de meest geschikte spruit/wortel verhouding van bomen, als van de bodemgeschiktheid voor beworteling.
Dit proefschrift.

7. Soms heeft experimenteel veldwerk veel weg van rampenbestrijding.

8. De enorme verzuring van de Nederlandse bosbodems is terug te voeren op de absurd grote import van gereduceerde stikstof via veevoer, welke aan het eind van de keten als ammonium in de bosbodem wordt geoxideerd.

NN08201, 1813

9. Het aanleggen van uitgebreide onderzoeksfaciliteiten in een bos is, naast wetenschappelijk zeer waardevol, ook bevorderlijk voor de sociale contacten tussen onderzoekers.

10. De hypothese dat het lachen een bijprodukt is van de evolutionaire ontwikkeling van onze hersenen, is wel komisch.
Daniel Dennett in het VPRO-programma "Een schitterend ongeluk".

11. Mooie scheppingen in de popmuziek zijn vaak ontstaan als orde uit chaos tijdens dampende jamsessies.

12. Gezien zijn positieve werking op de "esprit" van mensen, hoort koffie thuis in de categorie geestrijk vocht.

13. Voor het beklimmen van zowel sparrebomen als bergen dient men over een masochistische aard te beschikken.

Stellingen behorende bij het proefschrift "Growth and nutrition of Douglas fir, Scots pine and pedunculate oak in relation to soil acidification". Pieter de Visser, Wageningen, 6 september 1994.

Abstract

De Visser, P.H.B., 1994. Growth and nutrition of Douglas fir, Scots pine and pedunculate oak in relation to soil acidification.

Doctoral thesis, Wageningen Agricultural University, Wageningen, Netherlands, 185 pp.

In a Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and in a Scots pine (*Pinus sylvestris* L.) stand on sandy soil in the Netherlands, inputs of water, nutrients and acid loads were changed for four years. Effects of soil changes on growth and nutrition were compared with similar foreign experiments, and with some soil-tree relationships in an oak (*Quercus robur* L.) stand, which had different soil types within the site. Water limitations in the stands were demonstrated by a 40% to 50% increase in tree basal area growth from water additions of 3 mm d^{-1} or more. Needle N and K contents were depressed and needle shedding was retarded in autumn by irrigation in the Douglas fir stand. In both coniferous stands mineralization and nitrate leaching were enhanced by the moister soil conditions. The modest growth response to nutrient applications in addition to irrigation, proved that no nutrient deficiencies were present at the sites, although foliar P and K increased instantly. The application of dissolved K, Mg and Ca to both acid forest soils increased Al dissolution and decreased Ca/Al ratios in soil solution. This soil reaction was even stronger when applying dissolved $(NH_4)_2SO_4$ and was explained by the combined effect of soil exchange processes and root uptake of the applied cations, both increasing soil acidification. The applied $(NH_4)_2SO_4$ initially enhanced tree growth, later followed by growth reduction in the forest stand and tree death in a pot trial at similar NH_4 supply rates.

Douglas fir growth was higher at optimal water and nutrient applications when atmospheric loads were excluded. The reduced NH_4 inputs resulted in a decrease of NO_3 leaching, in a lower needle N concentration and tended to decrease Al concentrations and Al/Ca ratios in soil solution relative to the treatment with atmospheric loads.

Transpiration of Douglas fir, as measured from sapflow, was drastically reduced during summer drought. Irrigated trees showed optimal transpiration rates and were found to absorb water more readily after rain events relative to previously water-stressed trees. NH_4 applications in a pot trial initially increased shoot growth and transpiration of juvenile Douglas fir, but strong soil acidification later impaired root functioning and water uptake.

Additional index words: acid deposition, drought, irrigation, fertilization, nutrient cycling, *Pinus sylvestris*, *Pseudotsuga menziesii*, *Quercus robur*

Aan mijn vader, die dit graag had willen meemaken

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CHAPTER 1

General introduction

General introduction

Forest dieback

In the beginning of the 1980s in Central Europe an alarming forest dieback was observed. In the Netherlands the first country wide inventory in 1984 revealed that almost 50% of the forest had a reduced vitality (Den Boer and Van den Tweel, 1985). One to two years earlier, more than half of the trees in Germany showed severe crown-thinning (Anonymous, 1984). In later years the inventories also revealed other decline symptoms like needle-yellowing or -reddening, insect infestations and frost damages. Firstly only silver fir (*Abies alba* Miller) seemed affected, later also Norway spruce (*Picea abies* Karst.), Scots pine (*Pinus sylvestris*) and beech (*Fagus sylvatica*) showed decline symptoms. In the Netherlands the damage consisted of a high loss of needles or severe discolouration of needles or leaves. At the first inventory in 1984 Scots pine showed the lowest percentage of vital trees (34%), but recovered to 62% in 1992 (Smits, 1992). Vitality of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) decreased considerably from 50% in 1984 to 9% in 1992. The most abundant decidous species, pedunculate oak (*Quercus robur*), also showed a strong dieback from 57% vital trees in 1984 to 14% in 1992, with 45% non- or low-vital trees.

Air pollution and soil acidification

Most scientists related the dieback symptoms to the deleterious effects of air pollution on tree functioning. The decreased tree vitality would result from (1) direct effects on leaves and needles of SO_2, NO_x, O_3, NH_y gasses and wet acidic deposition, and (2) indirect effects of increased S and N loads, causing unfavourable soil conditions.

In the Netherlands only O_3 air concentrations occassionally exceed critical levels (Heij and Schneider, 1991) which may affect photosynthesis, stomatal control and dark respiration (Smeets *et al.*, 1990). The moderately low air concentrations of NH_3 in forests are absorbed and assimilated in biomass, thus acting as a fertilizer (Van der Eerden, 1992), but may have deleterious effects on trees in the longer term (Heij and Schneider, 1991).

The air pollution indirectly affects the condition of the soil. In the Netherlands this is mainly mediated by the high N deposition, with a national mean of approximately 47 kg ha^{-1} y^{-1} (in the year 1989, see Erisman, 1993) one of the highest in Europe, especially with regard to NH_4 originating from intensive husbandry (Asman, 1990). After entering the soil, NH_4 is nitrified or absorbed by trees, both causing soil acidification (Van Breemen *et al.*, 1982). Additionally, NO_x and SO_2 are transformed to nitric and sulfuric acid, which subsequently acidify the soil. Many studies have shown the consequences of increased soil acidification: low pH, leaching of base cations from the soil, increases in concentrations of toxic, monomeric Al and decreased availability of P (Johnson, 1987; Hallbacken and Tamm, 1986; Van Breemen *et al.*, 1982). Especially in poor, sandy soils, where most Dutch forests are located, base saturation of less than 10% and pH-values down to 3.0 have been observed frequently (*cf.* Kleijn *et al.*, 1989). This study will primarily deal with the effect of these unfavourable soil conditions on tree growth.

Apart from soil acidification, the forest ecosystem has been eutrofied due to atmospheric deposition of N. The enrichment of N in organic matter (Tietema, 1992) or on soil exchange sites by NH_4 adsorption has caused a complete shift in nutrient availability towards lower C/N and lower element/N ratios. How much of the antropogenic N is ultimately retained in the soil organic matter strongly depends on the capacity of biota to assimilate N. This capacity is depressed in a non-vital forest (Van Breemen *et al.*, 1986), creating a risk of high N losses to groundwater. In this study the soil has to be taken into account as a source and sink for nutrients.

Soil-mediated effects of atmospheric deposition on trees

Adverse soil chemical conditions due to air pollution, as described above, have negative effects on the tree condition. Tree roots may be affected by an increase in Al concentrations (Marschner, 1991) and by a decrease in Ca/Al ratios in the soil solution (Ulrich, 1983; Eldhuset *et al.*, 1987). Root length growth is hampered which may result in a lower water and nutrient uptake capacity.

Increased atmospheric deposition of N during the 1950s initially enhanced tree growth, but after 10 years or more tree growth often detiorated (De Kort, 1986). Forest stands that used to be N limited before, showed a growth increase up to levels where other nutrients like P become limiting (Mohren *et al.*, 1986). If growth responds to increased N supply on a Mg poor soil, it was shown that a growth dilution of Mg takes place, resulting in Mg retranslocation from, and yellowing of older needles (Oren *et al.*, 1988). In the Netherlands in most forests a nutritional imbalance is evident (Mohren *et al.*, 1986; Van den Burg and Kiewiet, 1989; Van Dijk and Roelofs, 1988). Greenhouse experiments suggest that this imbalance increases the vulnerability to natural stresses like drought (Dueck, 1990) and insect/fungi attack (De Kam *et al.*, 1991). Another drawback of the increased N supply relates to the increase in shoot biomass relative to that of roots (*cf.* Brix, 1981; Linder and Axelsson, 1982). In aggrading forests the

canopy can enlarge at the expense of the root system, and will demand more water of the same, small root system, thereby increasing drought sensitivity. The most alarming and frequent observations of forest decline in Central Europe coincided with the rather dry years of 1982 and 1983 (Innes, 1993). The vulnerability of trees to drought also may have increased in two other ways:
a) the increased soil acidity has thickened and shortened tree roots (Marschner, 1991; Olsthoorn *et al.*(1991));
b) stomatal control (Cornic, 1987; Van der Eerden and Pérez-Soba, 1992) and, as a result, drought tolerance (Larsen, 1983), have decreased due to a combination of air pollution and disturbed nutrition, *cf.* K and P.

Tree dieback is seldomly caused by one single stress factor, and probably a combination of the stresses, mentioned above, is the most harmful for tree functioning.

Until the present day, our knowledge about the response of trees to the different growth factors in combination with antropogenic stresses is merely descriptive. The clear relations between exposition to acidity and effects on seedlings, found in water cultures (*cf.* Eldhuset *et al.*, 1987; Keltjens and Van Loenen, 1989; Ryan *et al.*, 1986; Van den Driessche, 1978), do not hold in mature stands. Yet seedling trials may give a good insight in the mechanisms of tree dieback. If one of the above-mentioned stress factors would affect tree growth in a given stand, the response of the trees to the experimental elimination of the stress would increase our understanding of its importance in tree functioning. In Germany Mg fertilizer trials gave outspoken evidence of the relation between tree dieback and the poor Mg supply from acid soils (Evers and Hüttl, 1990/91; Feger *et al.*, 1991; Zöttl, 1985). Also in Germany, the assumed effect of Al on root growth, was confirmed by measurements following a lime application, which resulted in an increased root longevity (Murach and Wiedemann, 1988). In the Netherlands, there is an urgent need to verify the assumptions made about tree damage, related to excess N, soil acidification and concomitant shortage of other nutrients. Explanations of the observed decline were often hypothetical (Nihlgård, 1985; Mathy, 1988) because they were related to interaction mechanisms that were hard to verify. The results about trials with seedlings on the relation between soil acidity and root growth or fungal diseases (De Kam *et al.*, 1991), and the purely correlative field evidence of effects of atmospheric deposition on tree vitality (Evers, 1991; Van Dijk and Roelofs, 1988), should all be verified by field experiments.

Approach

In the research described in this thesis soil conditions in the forest stands have been changed experimentally and the responseviness of trees to these changes was examined. Until now, only few studies dealt with the effects on trees of a change in soil acidification rate or related stress factors (Kreutzer and Göttlein, 1991; Stuanes *et al.*, 1988). Most studies focused on mitigation of the effects, but were very valuable for understanding the causes of forest dieback (*cf.* Evers and Hüttl, 1990/91). Lack of hard data on the effects of acidification rates implies that the reaction of trees on acid, sandy soil to either emmission reductions or further increases of acid deposition, cannot be predicted. The stress effects on growth are best checked by exposure of whole stands to different levels of soil stress during several years. Similar experiments in the greenhouse could than give further evidence on mechanisms observed. The soil changes should be achieved experimentally. The use of controlled field conditions is a common practice in agricultural research, but was adopted in forestry only in the seventies (Tamm, 1991). In the following, five questions will be adressed, and the answers that will follow from the study presented here, may shed some light on the assumptions, mentioned above, about the causes of forest dieback. The field experiments and additional seedling trials, conducted in this investigation and reported in this thesis, are than shortly introduced and related to the raised question.

Decreasing or increasing soil acidification is a possibility to modify the exposition of trees. The response of trees might be better understood if different degrees of soil acidification are created within the same stand. The rate of soil acidification can be decreased by interception of acid inputs by a roof cover (Wright *et al.*, 1988) and can be increased by application of extra acid loads (Stuanes *et al.*, 1988; Tamm, 1991). The question that will be adressed is:

(i) Are growth and nutrition of trees influenced by ongoing soil acidification due to ammoniumsulphate inputs ?

Two Dutch sites and two foreign sites have been subjected to changes in atmospheric loads of $(NH_4)_2SO_4$. These changes cause different rates of soil acidification by changed rates of tree uptake of NH_4 or nitrification, of SO_4 retention, and subsequent change of pH and dissolution of Al. The objective is to determine the influence of either prolonged high rates of soil acidification, or decrease of acid loads, on the growth of trees and their nutrition. The experimental NH_4 loads range from 17 to 120 kg N ha^{-1} per year.

Another approach is to eliminate presumed nutrient shortages that have probably been aggravated by acid deposition. An improved supply of all nutrients can improve the nutritional balance of trees and, consequently, growth and vitality. The question is:

(ii) What is the effect on growth of an improvement of the nutritional balance of trees at the present deposition rates ?

The optimal nutrition approach (Ingestad, 1988) can be used to increase the nutrient supply of P and base cations in a subtle way. It consists of application of all nutrients necessary for the annual gross growth in optimal proportion to the estimated annual N uptake. Optimal proportions between nutrients were determined in seedling experiments in Sweden by Torsten Ingestad and coworkers (*cf.* Ingestad, 1979).

One of the major concerns is the impact of atmospheric deposition on tree water relations. Drought sensitivity may have been increased by changes in shoot/root ratio, by root damage or by stomatal disturbances, raising the following question:

(iii) To what extent tree growth is limited by drought, and are there interactions between water stress and soil acidification ?

On soils without groundwater recharge, irrigation that is tuned on the evaporative demand can eliminate water stress. Irrigation combined with decreased soil acidity may clarify the role of the latter in the water economy of the tree.

In all the experiments discussed so far, applications of NH_4, nutrients or water are varied to study tree response. However, other parts of the ecosystem like understorey vegetation or forest floor, can respond as well and may influence the fate and recovery of the applied nutrients, including N. On the other hand, nutrients like N may be released by drastic manipulations, given the large pools of N in forest floor and soil organic matter. Additions of lime, but also of K and P, have been shown to enhance mineralization (Arnold *et al.*, 1993). So the nutrient flows should be studied:

(iv) What is the effect of an increased supply of water and nutrients on the nutrient cycling in the forest ecosystem?

Ingestad (1988) referred to the increased cycling resulting from fertilizer applications as an increase in "nutrient flux density". This increased internal cycling may also apply to N, but whether the ecosystem will retain more N should be tested experimentally. Strongly aggrading forests take up more N and will have a higher critical load (Schulze *et al.*, 1989) than slowly growing forests.

Some questions might be raised when interpreting results from field experiments. A certain tree response may not be fully explained or the assumption made may need further evidence. In the presented nutrition experiments it is, for instance, assumed that the applied nutrients are readily available to trees and not bound to soil, but this should be tested in a more controlled manner. Pot trials may provide the conditions necessary for a more detailed study on mechanisms of nutrient allocation and root functioning. The following issue may be discussed:

(v) To what extent presumed mechanisms on growth and nutrition of the forest stand can be verified in a pot trial ?

The NH_4 supply should be varied to detect at what level and duration growth and nutrition are affected. The same holds for the application level of nutrients that should eliminate shortages. Transpiration rates of seedlings are much easier quantified and root studies are more controlled.

Methodology: Selection of the tree species was done on basis of their abundance in Dutch forests (Scots pine, oak), on basis of their alarming decrease in vitality in the five most recent years (Douglas fir, oak) and/or because it was the subject of the common Dutch research effort on acidification (Douglas fir). Soil conditions were manipulated in a Scots pine (*Pinus sylvestris* L.) and in a Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand. A study on the effect of soil type on growth and nutrition of pedunculate oak (*Quercus robur* L.) was carried out in a mixed oak stand, previously subject of a detailed biogeochemical monitoring (Van Breemen *et al.*, 1986). Atmospheric inputs of N and S ranged from moderate (42 kg N and 32 kg S ha^{-1} y^{-1}) in the Scots pine and Douglas fir stand, to average (52 kg N and 46 kg S ha^{-1} y^{-1}) in the oak stand, according to Dutch standards. It was assumed that the direct effects of air pollutants (NH_3, NO_x, O_3 and SO_2) on trees are uniform within a studied stand, and thus among the experimental soil units. The treatments were not replicated for logistic and financial reasons. However, tree growth was examined in replicated subplots within most treatments, and the results of four succeeding experimental years can be treated as replicates. The root system of individual trees is assumed to integrate the exposition to differences in soil solution concentrations, and the soil differences between the root systems are assumed negligible after several years of treatment. Some treatments were repeated in replicated greenhouse experiments under more controlled conditions to verify the treatment effects.

The chemistry of the soil solution is assumed to be the best reflection of the exposure of the tree roots to acidification and nutrient stress. The soil solution is the intermediate between soil solid phase and tree roots and its composition partly reflects the intensity of nutrient limitation or ion toxicity.

Outline of this thesis

Subsequent to the Introductory Chapter, in Chapter 2 the differences in soil conditions are related to growth and element contents in oak trees. At this site (Hackfort estate, near Vorden) soil solution chemistry was already investigated in detail (*cf.* Van Breemen *et al.*, 1986). The study can be seen as an inventory on the dependence of the element concentrations in tree parts on those in soil solution, with special attention to annual rings.

In Chapter 3 the results of the experimental soil changes in five coniferous forests in Europe are presented. The sites differed in deposition regime, but some manipulation treatments were similar. The effects on trees, litterfall and understorey vegetation are described in terms of biomass and plant nutrient composition. The effects of the treatment on soil conditions have been described elsewhere (Farrell *et al.*, 1994).

Chapter 4 and 5 deal in more detail with the results of the applications of water, nutrients and NH_4 at the Dutch sites. Also experiments are described where acid deposition was counteracted or further aggravated. Effects of the soil condition on trees and on the nutrient cycle are reported. The tree parameters examined are growth of diameter, height growth (occassionally), needle nutrient status and needle fall. The fate of applied nutrients is described by an input/output budget.

Chapter 6 and 7 report about two pot experiments, with full control of supply of N, macronutrients and water to Douglas fir seedlings to study the interaction between NH_4 availability and water stress. Response in growth, nutrient uptake, transpiration and vitality is quantified in relation to ammonium supply and acidity. One of the treatments is similar to that applied to Douglas firs in the field and the results are used to predict the recovery of applied nutrients in the field trial.

Chapter 8 focuses on the water relations in Douglas fir in the summer of 1992. The flexibility of the tree to respond to a pronounced drought period is studied. Xylem sapflow and a number of other physiological entities in water-stressed and irrigated trees are described. A carbon based simulation model is used to estimate potential and actual transpiration. Water supply as major growth-limiting factor is discussed.

In Chapter 9 the questions put forward above, will be answered and discussed on basis of the experimental evidence, obtained in this research.

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CHAPTER 2

The relations between chemical composition of oak tree rings, leaf, bark, and soil solution in a partly mixed stand

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The relations between chemical composition of oak tree rings, leaf, bark, and soil solution in a partly mixed stand

Abstract: Elemental composition of tree rings of oak (*Quercus robur* L.) was studied along a vertical gradient in the trees situated on three different soils. High concentrations of N, P, K, Mg, S and Mn were observed in the last 15 annual rings relative to older rings and were related to transition from sapwood to heartwood. In the sapwood, a strong gradient for N, P, S and Mn was observed and was partly related to high concentrations of Mn^{2+}, NH_4^+ and NO_3^- in the soil solution. No significant changes in concentration of other elements within the sapwood occurred. Manganese content in wood and leaves corresponded to concentrations of Mn^{2+} in the soil solution for the five years examined. Differences in soil availability of Al and Ca were not reflected in stemwood composition, yet in branches and leaves Ca content was influenced.

Introduction

In recent years, chemical analysis of tree rings has been used to detect historical evidence of effects of air pollution on trees. Effects of Pb and other trace-metal pollution on wood composition have been reported (Ashby and Fritts, 1972; Rolfe, 1974; Ward *et al.*, 1974; Baes and McLaughlin, 1984). On a more regional scale, combustion of fossil fuels and emmissions of ammonia, originating from animal husbandry, result in acid deposition. Soil acidification is enhanced by inputs of ammonium sulfate followed by rapid nitrification (Van Breemen *et al.*, 1982). In acidified forest soils, concentrations of Al^{3+}, Fe^{2+} and Mn^{2+} are high (Van Breemen *et al.*, 1982; Ulrich, 1983), and base cation concentrations are relatively low. Low cation to Al ratios in the soil solution may decrease root uptake of cations by ion antagonism (Foy *et al.*, 1978). Under very acid conditions, Al and H are directly toxic (McCormick and Steiner, 1978; Ryan *et al.*, 1986). Deficiencies of Mg and Ca in trees on soils subjected to high acidic deposition are explained by decreased availability of base cations in the soil (Zöttl and Hüttl, 1989; Matzner, 1989). Only a few studies show a direct relation between the availability of elements in the soil and element contents in tree rings (Bondietti *et al.*, 1989; Guyette and McGinnes, 1987; Legge *et al.*, 1984; McClenahen *et al.*, 1989; Arp and Manasc, 1988). To obtain historical evidence for chemical changes in the soil conditions as a result of acid deposition, dendrochemistry could be a valuable tool (Baes and McLaughlin, 1984; Berish and Ragsdale, 1985). McClenahen *et al.* (1989) suggested that heavy metal xylem concentrations could be useful biomonitors of soil chemical changes. Tree ring composition could point out in which years an increased soil acidification and a concomitant higher availability of toxic elements like Al and Mn took place.

In the three oak woodland sites studied here, different soil types occur close to each other, but plant species differ only slightly (van Breemen *et al.*, 1988). Acid loads are high and similar at the three sites. Differences in nitrification rate, uptake rate of the trees and acid neutralizing capacity result in different concentrations of elements in the soil solution. The objective of this paper is to examine the relation between soil solution composition (Al, Mn, Fe and nitrate), tree growth and nutrient contents in trees. Apart from site differences, changes in tree ring content may indicate past changes in soil solution concentrations. For example, increases of Al contents in tree rings could be related to increased Al availability due to higher soil acidification rates. Possible links between growth and tree-ring contents are discussed.

Study site

The oak woodland (3.2 ha) is situated in the natural "Oude Maat" reserve in the eastern part of the Netherlands. The stand was coppiced until 1939 and was left largely undisturbed since then except for occasional thinnings. The dominant tree species is *Quercus robur* L., with some admixture of *Betula pendula* Roth. The undergrowth consists mainly of *Pteridium aquilinum* Kuhn, *Maianthemum bifolium* F. W. Schm., *Holcus mollis* L., *Rubus idaeus* L. and *Anemona nemorosa* L. The soil parent material consists of sandy to loamy Pleistocene sediments of the river Rhine. Soil properties strongly vary within short distances because of differences in topography, soil processes and human influences. There are three different soil types represented by the study site A (Aeric Haplaquept), B (Umbric Dystochrept) and C (Typic Haplaquoll) (USDA 1976; van Breemen *et al.*, 1988).

Methods

At the borders of a 10 x 20 m^2 plot in each of sites A, B and C, five oak trees of mean basal area were felled. The trees were selected on the basis of dominant or codominant position in the stand. In January 1985 the bole of each felled tree was immediately divided into 2-meter sections from 1-m height onwards. Two discs were sampled from each section; one disc of 10 cm thick for chemical analysis, another disc was stored in 96 % alcohol for ring-width measurements. From each tree, two discs were sampled at different heights, and stored in closed plastic bags at -20 °C. The frozen discs were divided in small blocks to determine fresh and dry weight after heating to 70 °C for 48 h. From this, water content and specific gravity for intervals of 10 tree rings along four radii were calculated. Of the same discs, phloem and outer bark were sampled. Tree ring samples of 5-year intervals were cut off in duplicate from the 10 cm discs derived from each bole section, by chisel and band-saw. Each younger set of 5 rings was taken 2 m higher in the tree (see Fig. 1). Given a rather constant height growth of 2 m in five years from 1940 to 1980, each set of 5 annual rings had an equal cambial age of approximately 6 to 10 years (Fritts, 1976). Twigs ($\phi < 1.5$ cm) and branches ($\phi > 1.5$ cm) of each felled tree were weighted, and subsamples were taken for analysis. All samples were dried (70 °C) and ground. The samples were analyzed for N (by colorimetry with sodium-salisylic acid), P (by colorimetry with aluminium-molybdate), Na, K, Ca (by way of atomic emmission spectrometry), Mg (by way of atomic adsorption spectrometry) and the stem samples also for S, Fe, Al and Mn (by way of inductively coupled plasma spectrometry). For analytical details see Houba *et al.* (1985).

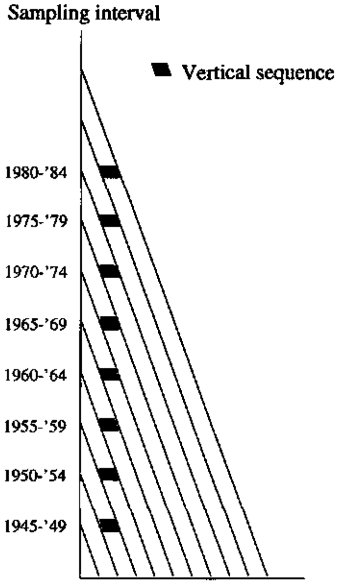

Figure 1. Schematic overview of sampling points in the tree stem. Each sample contains five annual rings and was duplicated.

Annual ring width was measured within 0.01 mm along four radii of a disc taken from each 2 m-bole section. Cross-dating was done by eye. Volume growth of the sample trees was calculated with the tree-ring data. On each of the three sites, hydrogeochemical monitoring included the collection of rainwater, throughfall, and litter fall and measurements on soil water contents (see Van Breemen *et al.*, 1988).

Soil solutions were sampled and analyzed chemically every two weeks during the period 1981-1987. At each plot, soil solutions were sampled at depths of 0 (litter percolate), 10, 20, 40, 60 and 90 cm, with duplicates at 10, 40 and 90 cm, using Soil Moisture Equipment Type 1910 high-flow porous ceramic cups connected to evacuated bottles.

Chemical analysis was done by ion chromatography (NO_3^-, SO_4^{2-} and Cl^{-1}), spectrophotometry (NH_4^+, $H_2PO_4^-$, Al^{3+} and SiO_2), atomic absorption spectrophotometry (Ca^{2+}, Mg^{2+}, Mn^{2+} and Fe^{2+}), and flame emission (Na^+ and

K^+). Further details on sampling are given by Van Breemen *et al* (1988). For analytical procedures, see Begheyn (1980).

Statistics were carried out with STATGRAPHICS version 2.1 (1986). Analysis of variance was performed on chemical composition data of tree rings of each 5-year sampling interval separately, with the number of observations equal to the number of felled trees (*i.e.* 15), to determine the effect of the site. Between-site differences were further examined with a multiple range test, based on 95% confidence limits. Difference in elemental contents between heartwood and sapwood was studied by analysis of variance of the analyses of tree rings of all trees of the period 1950-1960 and 1970-1980 respectively. Differences between 5-year periods within the sapwood were examined with a two-sided *t*-test. The effect of the site on elemental contents of twigs, branches and bark, as well as on volume growth of the sample trees, was studied by analysis of variance and followed by the two-sided *t*-test. In case of correspondance between soil and biomass chemical composition, data were further analyzed by simple linear regression.

Results

Tree growth

Diameter and volume growth (Fig. 2) of the sampled oaks at site A decreased drastically in the last 20 years. Growth at A was lower than at sites B and C ($p < 0.05$) according to the *t*-test on annual increments. Annual ring width at B and C decreased in time according to a negative exponential growth curve (De Visser, 1986) and volume growth per tree remained rather constant. Before 1968 volume growth was higher for the sampled trees at site B relative to C ($p < 0.05$), but growth remained equal since. Trees at site B are higher than at the other sites (see Table 1).

Birch has a basal area of 9.53 $m^2\ ha^{-1}$ at site A, but showed a high mortality rate, probably because of age (45 years). The oaks of this study were not supressed by birch.

Elemental contents of tree rings

The average stemwood composition is rather equal between the sites (Table 2); except Mn contents appears to be higher at site A and Na at site B, relative to the other sites. The difference in elemental content between sites was tested by one-way analysis of variance of each sample set of five tree rings separately. Results are given only for $p < 0.20$ (Table 3) and show a major difference for Mn contents. An additional multiple range test showed that Mn increases in the samples of the period 1970-1984 in the order B < C < A (see table 4 for *p*-values). Sodium content is different for the 1975-1980 sampling period (Table

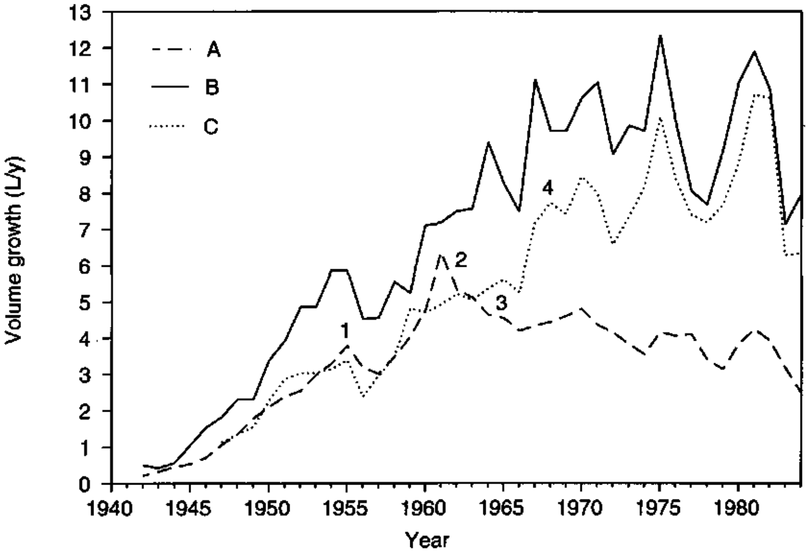

Figure 1. Oak volume growth at the three sites (*n*=5). Growth for all trees started in 1939. From 1955 (1) to 1962 (2) growth at sites A and B was equal, then growth at site A started to decrease and became lower than at site C (3). Growth at sites B and C was equal from 1966 onwards (4).

Table 1. Growth characteristics of oak and birch at the study sites.

	Site A		Site B	Site C
	Birch	Oak	Oak	Oak
Mean DBH (cm)	19.62±2.83	17.07±2.18	21.97±4.53	20.44±1.58
Mean height (m)	19.13±1.89	16.42±1.83	18.33±0.65	16.72±1.22
Mean basal area (m^2/ha)	9.50±5.3	13.90±4.6	27.70±8.1	25.00±5.7
Annual growth ('80-'84):				
Ring width (mm/year)	1.60±1.0	0.61±0.07	1.38±0.41	1.43±0.13
Height (m/year)	ca. 0.4	0.16±0.08	0.28±0.08	0.21±0.12
Volume (m^3 ha^{-1} $year^{-1}$)	ca. 1.1	3.30±2.7	8.90±2.1	8.70±3.1

3) and is found higher at site B than at sites A and C, according to the multiple range test. Magnesium and Ca contents seem to be higher in sapwood at site A, but are not significant (*n* = 10 per site).

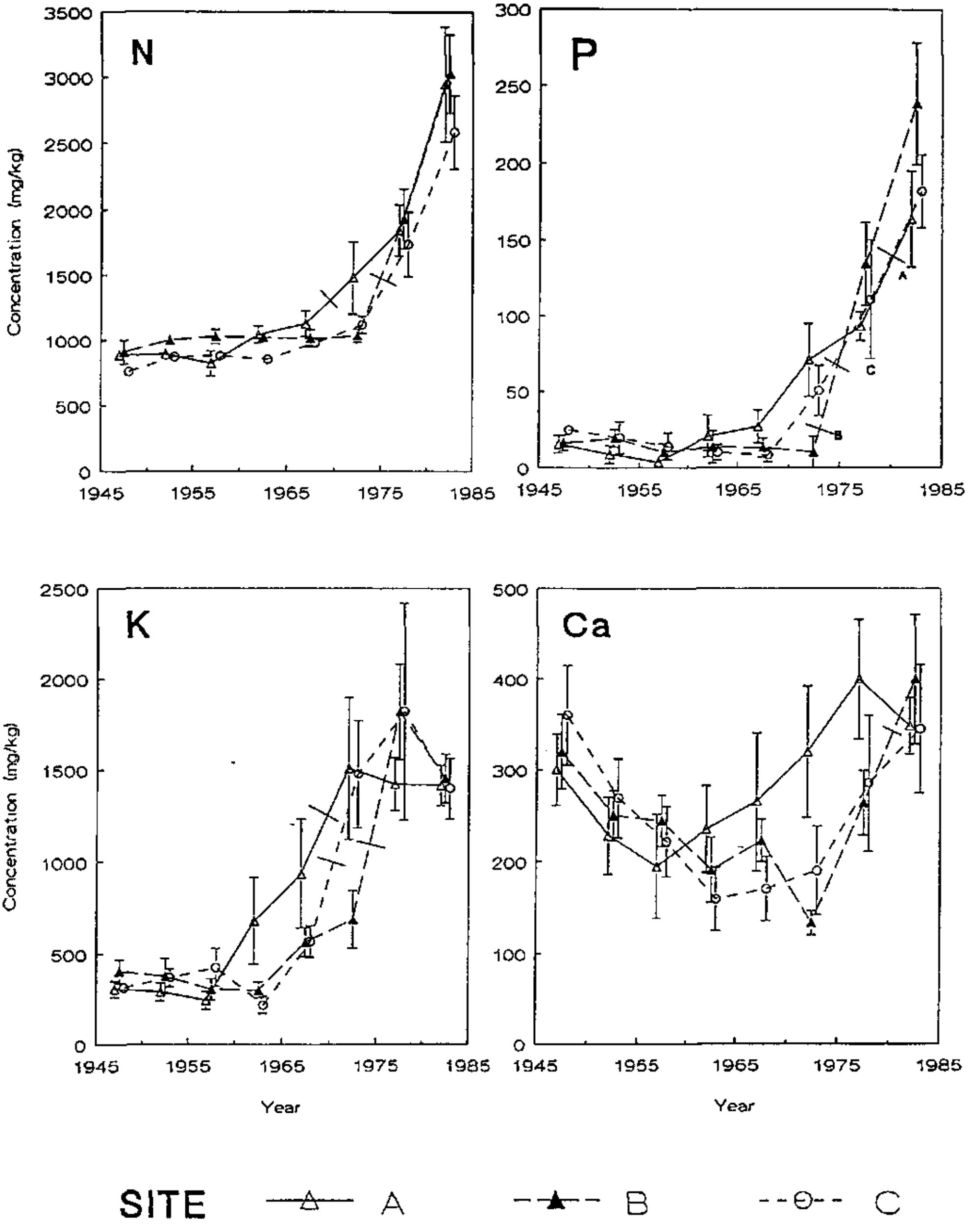

Figure 3. Element contents in sets of five annual rings, sampled at increasing height in the stem. Values are means of duplicate samples of five trees per site. The error bars represent ± 1 SE. A rise in concentration ($p < 0.05$) is indicated with a bar at right angles to the plot curve.

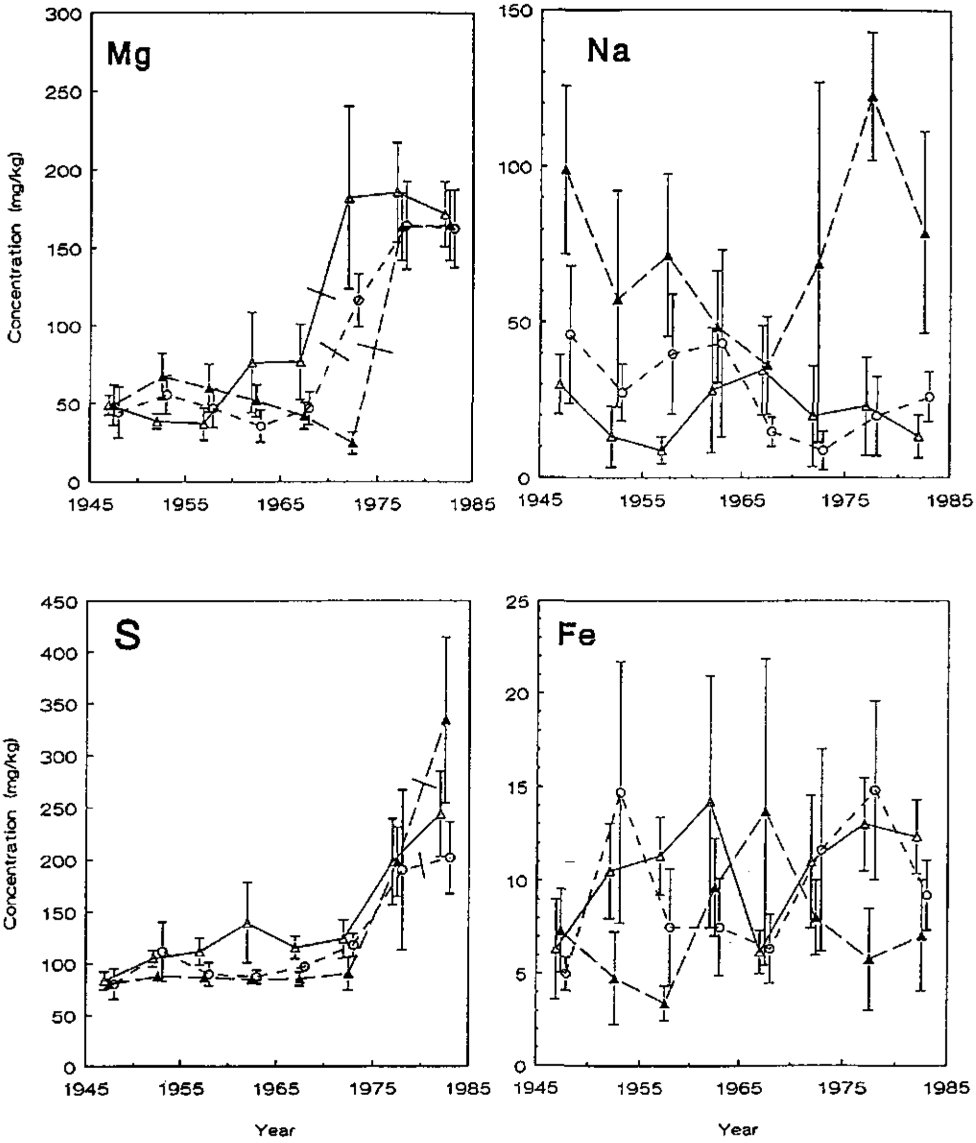

Figure 3. (continued)

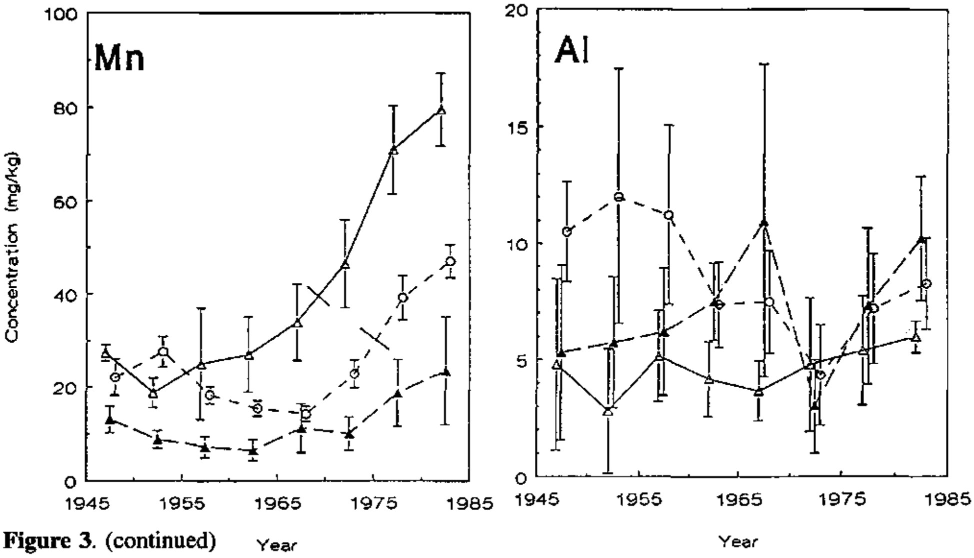

Figure 3. (continued)

Table 2. Mean element concentrations and standard deviations (mg kg^{-1}) in oak wood, including heartwood and sapwood (n = 60).

	N	P	Na	K	Ca	Mg	S	Fe	Mn	Al
Site A										
Mean	1420	52	20	906	281	106	149	11	43	4.6
SD	862	68	38	759	165	100	80	7	29	4.2
Site B										
Mean	1385	56	63	652	250	77	153	11	11	7.4
SD	808	94	76	558	122	61	143	20	12	6.1
Site C										
Mean	1226	49	26	811	231	82	140	12	25	9.1
SD	670	75	47	837	151	68	144	22	14	11.2

The rise in concentration of N, P, K, Mn, S, Ca and Mg (Fig. 3) within the tree corresponds to the change from heartwood to sapwood. This was found by analysis of variance of four samples of heartwood as well as sapwood per tree, and combined for the 15 sample trees ($p < 0.001$ for these elements). The border between heartwood and sapwood was determined for every sample tree, and lies, on average, at a distance of 10 (site B) to 15 (sites A and C) annual rings from the bark. Differences among the 5-year sampling intervals were studied with a t-test and are significant for the mentioned elements (indicated for $p < 0.05$ in Fig. 3) during the change from heart-wood to sapwood. The t-test showed a further increase of the contents of N (all sites), P (sites B and C), and Mn (site C) within the sapwood ($p < 0.05$). For most tree species Mn remains equal

Table 3. One-way analysis of variance results for the effect of soil type on the element contents in samples of five tree rings for 7 5-year periods. For all elements except Mn, results are given only for $p < 0.20$. p, Probability that the level of the F-ratio is significant; df, degrees of freedom; MS, mean squares; F-ratio, quotient of the two MS values

		Between groups		Within groups			
Element	Period	df	MS	df	MS	F-ratio	p
Mn	1950-1955	2	216.87	10	42.60	50.91	0.0299
Mn	1955-1960	2	404.63	11	272.07	1.49	0.2681
Mn	1960-1965	2	287.56	12	117.77	2.44	0.1289
Mn	1965-1970	2	355.43	9	163.26	2.18	0.1693
Mn	1970-1975	2	1310.48	8	218.49	6.00	0.0256
Mn	1975-1980	2	3065.67	8	271.60	11.29	0.0047
Mn	1980-1984	2	2605.41	10	349.83	7.44	0.0105
Al	1960-1965	2	41.87	12	22.50	0.86	0.1978
Na	1965-1970	2	122.80	11	60.12	2.04	0.1760
Na	1970-1975	2	276.32	8	128.52	2.15	0.1789
Na	1975-1980	2	647.45	9	16.91	38.29	<0.0001
Na	1980-1984	2	395.69	11	150.44	2.63	0.1165
S	1980-1984	2	1107.62	10	337.02	3.29	0.0800

between heartwood and sapwood (Berish and Ragsdale, 1985; Frelich *et al.*, 1988; McClenahen *et al.*, 1989), but Wardell and Hart (1973) showed a gradient for Mn in *Quercus alba* L. Aluminium ($p = 0.5819$), Fe ($p = 0.7753$) and Na ($p = 0.6313$) did not show any concentration changes between heartwood and sapwood.

Table 4. Between-site comparisons of mean Mn contents: t-test p-values.

Period	A > B	A > C	B < C
1955-1960	0.1830	0.4972	0.0032
1960-1965	0.0346	0.1310	0.0070
1965-1970	0.0733	0.0186	0.5237
1970-1975	0.0357	0.0151	0.0076
1975-1980	0.0086	0.0112	0.0457
1980-1984	0.0030	0.0021	0.0376

Element concentrations in other tree parts

Nutrient composition of leaves, twigs, branches, living bark, and roots are given in Table 5. Most pronounced differences between sites found were for Ca, which is relatively high in leaves, branches and twigs at site A, and is low in

Table 5. Element composition (*g/kg* dry weight, only Al in mg/kg) of various tree parts (*n*=5, *for Mn* and Al *in bark n*= 2 and *not* analysed for branches and twigs) at the three sites. Significant differences (P<0.05) between sites are indicated by different letters behind the mean value.

	N	P	K	Ca	Mg	Mn	Al
Leaves							
A	26.46±0.15a	1.88±0.33	9.88±1.41	6.52±1.12a	1.62±0.35	1.18±0.49a	72± 1
B	28.90±1.77b	1.76±0.18	9.58±1.06	4.78±0.86b	2.22±0.41	0.18±0.05b	61± 4
C	26.88±3.00a	1.84±0.18	9.74±0.86	4.04±0.71b	1.96±1.22	0.42±0.08c	76±21
Bark							
A	6.54±0.67	0.29±0.05	3.25±0.51	15.36±0.72a	1.15±0.37	0.52±0.13	13±10
B	6.92±1.47	0.37±0.10	3.37±0.47	15.72±5.06a	1.03±0.24	0.24±0.09	25±17
C	6.26±0.31	0.36±0.74	3.52±0.92	11.48±1.48b	0.98±0.19	0.51±0.14	39±21
Branches (1.5 < diam. < 4 cm)							
A	5.46±1.11	0.31±0.09a	1.96±0.23	2.60±0.29a	0.47±0.05a	-	-
B	5.73±0.51	0.40±0.07a	1.93±0.30	1.84±0.52b	0.39±0.06ab	-	-
C	5.59±0.61	0.47±0.07b	2.25±0.28	1.96±0.50b	0.59±0.11c	-	-
Twigs (diam. < 1.5 cm)							
A	9.73±1.19	0.65±0.14	2.71±0.23	3.24±0.33	0.76±0.06	0.18±0.01	19±0.02
B	10.22±1.33	0.81±0.08	2.57±0.30	2.40±0.72	0.69±0.06	-	-
C	10.07±1.56	0.81±0.90	2.81±0.28	2.64±0.50	0.88±0.10	-	-
Roots (diam. < 5 mm)							
A	11.44±1.55	0.70±0.14	1.38±0.88	1.68±0.56	0.34±0.17	0.09±0.06	2137±1328
B	14.92±0.88	1.35±0.59	5.19±1.23	2.85±1.22	0.60±0.18	0.09±0.01	8125± 725
C	11.93±2.47	0.96±0.27	3.33±2.07	2.28±1.09	0.77±0.14	0.15±0.02	>10000

leaves and bark at site C. Foliar Mn increases in the order B < C < A. This order seems to be present in roots and bark also. Nevertheless, these differences are not significant (there were only 2 to 4 replicates for root and bark). Nitrogen ($p = 0.0486$) and possibly Mg contents ($p = 0.0568$) in leaves is higher at site B than at site A. Aluminium concentrations in roots are high at all sites, and cannot be attributed to incorporation of sand particles in the sample because samples were rinsed intensively. By rinsing, however, K and Mg could have been leached from the root samples, so the concentration of these elements could have been underestimated.

Table 6. Mean and coefficient of variation (CV in % of mean) of ionic equivalent concentrations ($mmol_c\ m^{-3}$) *in soil solutions at six depths at the three sites.* Values are means of all data between April 1981 and April 1984. Data from Van Breemen et al (1988).

	Site A		Site B		Site C	
	Mean	CV	Mean	CV	Mean	CV
pH	3.55	6	3.51	11	3.82	9
K^+	207	61	292	38	230	47
Na^+	318	35	230	38	211	37
Ca^{2+}	968	46	453	43	292	44
Mg^{2+}	424	47	217	44	272	43
Al^{3+}	860	55	987	49	515	46
Fe^{2+}	15	98	21	77	21	75
Mn^{2+}	81	47	19	64	26	56
NH_4^+	154	27	323	143	284	157
NO_3^{-1}	615	50	1378	53	803	66
SO_4^{2-}	1048	33	809	39	680	35
$H_2PO_4^{2-}$	8	359	16	137	12	207

Nutrients in the soil solution and relation to wood composition

Table 6 contains the mean ionic concentrations of the soil solutions sampled upto 60-cm depth during the period 1981-1984 and includes the average of the coefficients of variation, which were first calculated for each depth. Detailed description of the soil properties is presented elsewhere (Van Breemen *et al.*, 1988); here the most obvious site differences are summarized. At all sites, the soil solution is dominated by dissolved aluminium and nitrate. Although nitrate concentrations are high in all soils (above 0.8 mmol L^{-1}), the average (1.7 mmol L^{-1}) and peak concentration (8 mmol L^{-1}) are highest at site A. Nitrate concentrations show large seasonal fluctuations, with the highest values observed in autumn (Fig. 4a). In the soils of site A (20- to 40-cm depth) and B (below 40 cm depth), very high concentrations of free Al^{3+} are found (2 $mmol_c\ L^{-1}$). At site C Al concentrations are ca. 1 $\text{mmol}_c\ \text{L}^{-1}$. Manganese concentrations are more than twice as high at site A than at the other sites (Fig. 4b). Calcium concentrations are higher in the whole profile at site A (see also Fig. 4c). This is caused by a calcareous subsoil beneath 75-cm depth. Mean ionic equivalent Ca^{2+} concentrations at 60-cm depth are as high as 2.4 mmol L^{-1} at site A, 0.5 mmol L^{-1} at site B and 0.3 mmol L^{-1} at site C.

A linear regression of Ca and Mn contents in biomass on average soil solution concentrations proved valid ($p < 0.05$) for three variables:
(*i*) Mn-contents in wood of 1980-1984 vs. $[\text{Mn}^{2+}]$ in soil ($R^2 = 0.631$), (*ii*) Mn-contents in leaf of 1987 vs. $[\text{Mn}^{2+}]$ in soil ($R^2 = 0.680$), (*iii*) Ca-contents in leaf of 1987 vs. $[\text{Ca}^{2+}]$ in soil ($R^2 = 0.563$). The *F*-ratios were 47.85, 27.57 and 16.74, with probabilities of 0.0001 ($n = 29$), 0.00016 ($n = 14$) and 0.0127 ($n = 14$) for cases 1, 2 and 3 respectively.

Discussion and conclusions

Tree ring elemental composition along a time gradient in oak is mainly influenced by its position in heartwood or sapwood. An increase in concentrations of N, P, K, Mg and Mn is observed from heartwood to sapwood and from inner to outer sapwood. This concentration gradient was also found by others, who observed that the concentration of those elements depends on the amount of living ray cells (Merrill and Cowling, 1966; Wardell and Hart, 1973). Migration of elements during transition from sapwood to heartwood may also be related to the element mobility. In this study no concentration gradients are found for less mobile elements such as Al, Ca, and Fe, but concentrations show large standard errors. A decreasing trend in Ca content, as was found for trees on soils with recently increased soil acidification (Momoshima and Bondietti, 1990) could not be confirmed, although Ca content seemed to decrease with age in the heartwood samples.

In analogy to the vertical ring width chronology (Fritts, 1976), it is important to study dendrochemistry on samples that were formed by cambium of the same age and thus situated at more or less the same distance of the tree crown when constant height growth is assumed. Heartwood formation changes the content of mobile elements, so only samples in the same stage of senescence should be compared, preferentially only heartwood samples. Also, dendrochemistry along a vertical gradient can be influenced by height because xylem tissue acts as a strong ion exchanger for certain cations (Bondietti *et al.*, 1989*a*). This may cause vertical chromatographic fractionation in the stem, resulting in ratios of Ca to Fe or Al that decrease with increasing sampling height (Aleksakhin and Ravikovich, 1966; Momoshima and Bondietti, 1990).

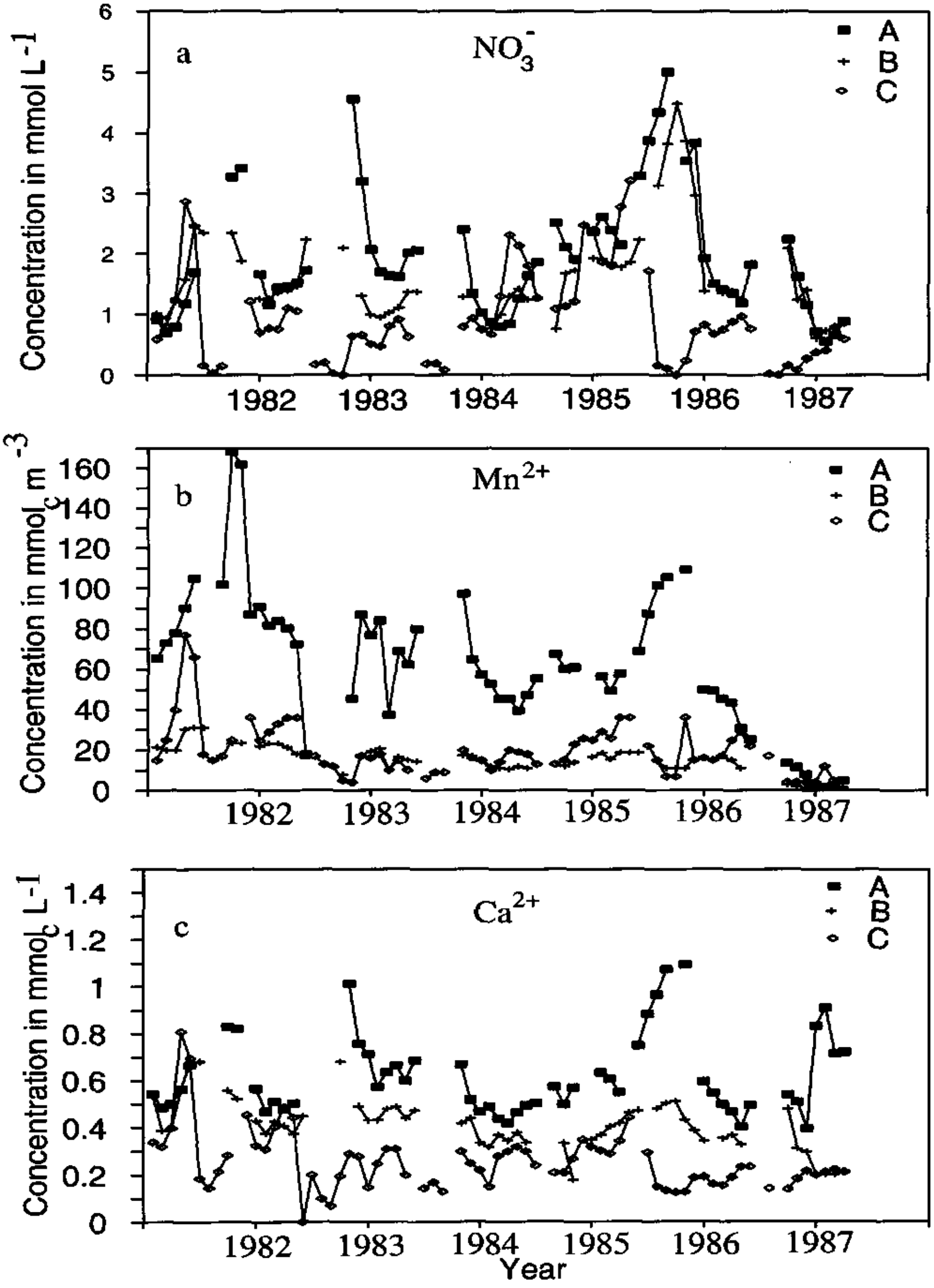

Figure 4. Concentration of NO_3^- (a), Mn^{2+} (b), and Ca^{2+} (c) at 40-cm depth at the three sites from 1981 to 1987.

No large differences in tree-ring element contents are found among the three study sites. Manganese contents at plot A was higher in the last 20 years. This is related to high Mn^{2+} concentrations in the soil solution, which is also reflected in leaf chemistry. Apparently the Mn content in living stemwood can indicate Mn availability in the soil, as was shown for needle analyses by Kazda and Zvacek (1989). High concentrations of Mn in soil and vegetation at site A suggest that Mn toxicity may be the reason for the growth decline at site A in the last 20 years. However, growth reduction of oak seedlings on water culture was only observed at Mn levels that were at least an order of magnitude higher than those in the soil solution at site A (Van Leeuwen, 1988). Despite significant differences in soil solution chemistry between the sites for Al^{3+}, Ca^{2+} and Mg^{2+}, no differences occur in the tree rings. Nevertheless, Ca and Mg contents in leaves did correspond to site differences. Stark *et al.* (1984) found a response of xylem sap chemistry of *Pseudotsuga menziesii* (Mirb.) Franco on differences in soil conditions that were more distinct than in the present study. In most research on xylem sap analysis poor growth was always related to low Ca availability (Stark *et al.*, 1984; Bondietti *et al.*, 1990). At site A however, poor growth of oak is accompanied by high Ca concentrations in soil and leaves. The better availability of Al in the soil at site B is not reflected in Al contents in leaves and branches. Although Al^{3+} concentrations in soil solution of all plots are very high, Al content in wood never exceeds 12 mg kg^{-1}, which is not considered high (Legge *et al.*, 1984; McClenahen *et al.*, 1989). Ratios of Al to Ca in trees are relatively high compared with those observed in *Picea abies* Sarg. by Bondietti *et al.* (1989*b*) and may hamper radial growth. Although chemical analyses were done on a limited number of samples, Al:Ca ratio in oak wood is not expected to be a good predictor of Al and Ca availability in the studied soils; there is a general lack of correspondence between soil solution concentrations and wood contents.

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CHAPTER 3

Biological response of five forest ecosystems to input changes of water, nutrients and atmospheric loads

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Co-authors: C. Beier, L. Rasmussen, K. Kreutzer, N. Steinberg, M. Bredemeier, K. Blanck, E.P. Farrell, and T. Cummins

Biological response of five forest ecosystems to input changes of water, nutrients and atmospheric loads.

Abstract: In five coniferous forest ecosystems in Europe water and nutrient supply, as well as atmospheric loads, were manipulated for three or more years. Water supply was optimized and nutrients were added according to tree demand in optimal proportions relative to the ambient N supply. Tree growth was strongly enhanced by optimal water supply but not further enhanced by nutrient additions. The nutritional balance in trees was improved for P and K. The increased water and nutrient supply retarded needle shedding in autumn and diminished root production. The manipulated decrease in N input to the soil decreased the N content in needles in one stand so far. Water additions tended to lower N contents at two sites. Large applications of N increased N content in needles even though the N nutrition was already optimal. Liming with dolomite has stimulated tree growth only in the nutrient-poor stand, but has generally increased Ca content in needles. Number of species and cover of understorey vegetation has increased considerably by liming and, in some cases, by water additions.

Ecosystem manipulation experiments are shown to be a useful tool for the quantification of the growth effects of traditionally limiting factors. Additionally they give indications of the effects on forest ecosystem processes of future changes in atmospheric loads.

1. Introduction

Deposition of air pollutants in forest ecosystems may accelerate the rate of soil acidification (Van Breemen *et al.*, 1982) and result in decreased ratios of Ca:Al (Ulrich and Pankrath, 1983) and cation:ammonium (Roelofs, 1986) in the soil solution. In forest ecosystems, the soil-mediated effects of atmospheric deposition can be modified by experimental manipulation. The response of trees might be better understood if different degrees of soil acidification are created within the same stand. The rate of soil acidification can be altered by interception of acid inputs by a roof cover (Beier and Rasmussen, 1993, Wright *et al.*, 1988), acid irrigation or by liming (Kreutzer and Göttlein, 1991, Stuanes *et al.*, 1988).

Apart from soil acidification, prolonged atmospheric deposition in N.W. Europe has resulted in excessive supply of N and S to trees. The new supply rates can induce temporarily higher growth rates. However, additional growth may be limited by other nutrients or by water and so restrict extra N uptake. Water and nutrient additions can help restore the balance of nutrients (Ingestad, 1988). This balanced fertilization can be applied on the basis of optimal nutrient proportions derived from seedling trials (Ingestad, 1979). Optimal nutrient supply can be combined with the removal of atmospheric pollutants by roof interception to control all the water and element fluxes to the soil.

The study reported here involves six sites in the EXMAN project (Beier and Rasmussen, 1993). The sites vary in degree of continentality and pollution load (Farrell *et al.*, 1993). Five of the sites have been subjected to a variety of treatments with the object of changing the intensity of acidification and/or restoring the nutritional balance of the ecosystem. The object of this paper is to report the influence of these treatments on the biomass and floristic component of the forest ecosystems during the period 1989-1991, and to consider the implications of the results for the revitalization of ecosystems damaged by atmospheric pollution.

2. Material and methods

Experimental manipulations were carried out at 5 coniferous forest stands in NW Europe (Table 1). One other stand, Ballyhooly (IE), with low atmospheric inputs of S and N, serves as a reference station. The manipulations consisted of addition of water and/or solutes to the soil in supplement to the existing input, or the removal of atmospheric input by the construction of large (100 to $1200m^2$) roofs beneath the canopy. The combination of roof and irrigation system makes it possible to control the inputs to the soil. The manipulations, which are summarized in Table 1, were as follows:

Control: each site had a control plot where no treatment was applied, and monitoring similar to that on the treatment plots was done. The levels of atmospheric inputs found and their fate on passage through the forest ecosystem are reported in an accompanying paper (Farrell *et al.*, 1993).

Drought: summer drought was induced for 2 months (July-August) in 1990 and again in 1991, under the roof at Klosterhede. Throughout the rest of the year the stand was irrigated under the roof by a sprinkler system, using stored throughfall water.

Irrigation: demineralized water, but with seasalts in equivalent amounts as measured in throughfall included, was added by a sprinkler system under the roof (Klosterhede) or in supplement to the existing throughfall (Kootwijk, Harderwijk and Höglwald) to arrive at optimal water supply (3 to 4 mm day^{-1}) for tree growth. Irrigation commenced at Klosterhede, Kootwijk and Harderwijk in July 1989 and at Höglwald in 1984.

Fertigation: the use of fertilizer applied dissolved in the irrigation water is referred to as fertigation hereafter. Water was added as described for the irrigation treatment. The water contained macro and micro nutrients in optimal

Table 1. Sites, geographic position, dominant tree species, plot size and treatments (*n* = 1)

Individual plot size	Plot	Treatment	Roof
Klosterhede, Denmark	8°24'E, 56°29'N	Norway spruce	
450m^2	1: Control		-
	2: Irrigation	Demineralized water	+
	3: Fertigation	Optimal nutrition	+
	4: Summer drought	Throughfall in winter	+
Kootwijk, Netherlands	5°50'E, 52°10'N	Douglas fir	
900m^2	1: Control		
	2: Irrigation	Demineralized water	-
	3: Fertigation	Nutrition	-
	4: Fertigation	Optimal nutrition (100m^2)	+
Harderwijk, Netherlands	5°40E, 52°20'N	Scots pine	
900 m^2	1: Control		-
	2: Irrigation	Demineralized water	-
	3: Fertigation	Nutrition	-
	4: Fertilization	$(NH_4)_2SO_4$ (130m^2)	-
Höglwald, Germany	11°10'E, 48°30'N	Norway spruce	
2500m^2	A1: Control		-
	B1: Irrigation	Acidic water	-
	C1: Irrigation	Deacidified water	-
	A2: Liming	Liming	-
	B2: Irrigation + liming	Liming + acidic water	-
	C2: Irrigation + liming	Liming + deacid. water	-
Solling, Germany	9°34'E, 51°38'N	Norway spruce	
1ha	1: Control F1		-
	2: Fertilization FD	N + K + Mg + liming	-

ratios (Ingestad, 1979) to the N input to the soil. The N was added according to tree demand, estimated from growth in the previous years. In the plots without a roof the ambient atmospheric N input was subtracted from the estimated N demand (Table 2). Fertigation has been carried out at Klosterhede, Kootwijk and Harderwijk since July 1989.

Fertilization: at Harderwijk ammonia was supplied in excess of requirements by weekly additions of dissolved $(NH_4)_2SO_4$ amounting to an annual dose of 120kg N ha^{-1}. The treatment started in July 1989. At Solling a combination of nutrient additions (in 1973) and liming was carried out (both in 1975 and 1980).

Total nutrient additions were 300kg N ha^{-1}, 205kg K ha^{-1}, 820kg Mg ha^{-1} and 2075kg Ca ha^{-1}.

Table 2. Nutrient additions (kg ha^{-1} $year^{-1}$) to the fertigation plots. The N input to the soil due to atmospheric deposition is indicated in parentheses.

Site	N		P	K	Ca	Mg	Fe	Mn	B	Mo	Zn	Cu
Klosterhede	30	(0)	32	40	43	36	1.2	2.3	0.2	0.04	0.03	0.03
Harderwijk	31	(42)	13	65	7	8.5	0.7	0.4	0.6	0.007	0.03	0.03
Kootwijk	39[a]	(40)	36	60	4.8	6	0.8	0.5	0.7	0.008	0.04	0.04

[a] Average of 78, 39 and 19 kg N ha^{-1} applied in the years 1989, 1990 and 1991 respectively.

Liming: at Höglwald, dolomitic limestone was applied at 4t ha^{-1} (880kg Ca ha^{-1}, 490kg Mg ha^{-1}) in 1984. Dolomitic limestone was applied at Solling, in combination with other nutrients and is further referred to as fertilization (see above).

Acid irrigation: in addition to throughfall, a solution of sulphuric acid at a pH of 2.7 was sprinkled on the soil surface at Höglwald. From 1984 to 1990 the yearly irrigation was between 170 and 183mm (15 to 18 events of 10 to 12mm each). The yearly proton input was about 4kmol H^+ ha^{-1}. In 7 years a total of 27.7kg H^+ ha^{-1} and 1194kg SO_4^{2-} ha^{-1} were added.

Stem diameters at breast height (DBH) were measured in all plots every winter in order to calculate diameter and basal area (BA) increment. Needles from different age-classes were sampled from ten trees from the 7th whorl in autumn each year in each treatment and analyzed for N, P, K, Ca, Mg and Mn. N was determined with the Kjeldahl method or colorimetrically (the Netherlands). After wet destruction P was determined colorimetrically, K by atomic emission spectrophotometry and Ca and Mg by atomic absorption spectrophotometry (Denmark, Netherlands, Ireland), whereas in Germany P, K, Ca and Mg were determined by inductively-coupled plasma spectrophotometry (ICP).

Biomass of living and dead roots (sample size ≥ 12) was determined with a root auger (diam. 8 cm) in all organic and mineral soil horizons all plots in Klosterhede (1991), Kootwijk (1990) and Höglwald (1991). Litter fall was collected monthly from litter traps (n ≥ 6) and dry weight and element content were determined. Vegetation cover of each plot was extrapolated from measurements on 5 (Klosterhede, Harderwijk) to 21 $1m^2$ quadrats. Tree seedling density was determined for the whole treatment area.

3. Results

3.1. Effects of the manipulations on diameter growth

Some basic characteristics of the study sites are shown in Table 3. Comparisons between the control plots are described in an earlier paper (Farrell *et al.*, 1993). Basal area is considered the best parameter of growth response in forest stands and accordingly emphasis is placed upon it here. Treatment effects on growth and nutrients are summarized in Table 4, in Tables 5 and 6 data are presented in more detail.

Table 3. Soil and tree characteristics of the research sites. Dbh is diameter at 1.3 m height. CAI is current annual increment of bole volume. Biometric calculations according to La Bastide and Faber (1971).

Site	Soil		Trees			
	Type	Texture	Age (years)	Dbh (cm)	Height (m)	CAI (m^3 ha^{-1} y^{-1})
Klosterhede	Haplorthod	Sand	72	22	20	11[a]
Kootwijk	Dystrochrept	Sand	41	20	18	22
Harderwijk	Udipsamment	Sand	41	14	10	9
Höglwald	Hapludult	Clay loam	84	36	37	25
Solling	Dystrochrept	Loam	105	34	26	13
Ballyhooly	Haplorthod	Sandy loam	52	29	24	25[a]

[a] Height growth was calculated from age and current tree height.

3.1.1. Drought

Drought was induced at only one site, Klosterhede. Surprisingly, the basal area increment in the drought plot is significantly higher than in the control plot for the period 1988-1990 (Table 5). However, measurements from 1991 show a rapid decrease in tree growth from 1990 to 1991, but no conclusions can be drawn so far.

3.1.2. Irrigation

The most pronounced growth response to irrigation was observed at Klosterhede, where the basal area growth was 2.4 times that of the control. A clear response to irrigation was also recorded at Kootwijk, with a smaller positive response at Harderwijk. At Höglwald responses were never significant.

3.1.3. Fertigation

While at all sites a marked response to fertigation was observed in basal area increment, there was little, if any, additional response to fertigation over the observed effect of irrigation alone. On the basis of these results, there is little evidence of nutrient deficiency at any of the fertigated sites. In the fertigated plots, the improved current annual basal area increments are of the same order as the control increment at Ballyhooly.

3.1.4. Fertilization

The effect on growth of the N additions was small in both fertilized stands. The response at Solling was measured ten years after the N and K fertilization and two years after the last dolomitic limestone application.

3.1.5. Liming

The effect of liming and fertilization on growth at Solling is reported above. At the only other site where dolomite was applied, Höglwald, growth was slightly negative.

Table 4. Growth response to treatments and effects of applied nutrients on the nutrient content of current-year needles; +, - and n indicate positive, negative or no significant change ($p < 0.05$), respectively

	Treatment[a]				Applied nutrient				
	I	IF	Lime	Fert	N	P	K	Mg	Ca
Klosterhede	+	n			n	+	n	n	n
Kootwijk	+	n			n	+	+	n	n
Harderwijk	+	n			n	+	+	n	n
Harderwijk-NH_4				n	+				
Solling FD			+	+	+		-	+	+
Höglwald A2	n		n					n	+

[a] I, irrigation; IF, fertigation; Fert, fertilization

3.2. Effects on nutrient concentrations of needles

The evidence of foliar analysis from the control plots suggests a deficiency of nitrogen in the stands at Klosterhede and Solling, and phosphorus deficiency also at Solling, Kootwijk and Harderwijk (see table 6 and Farrell *et al.*, 1993).

Table 5. Stand biomass at the start of the manipulations (1989 in all sites except Höglwald (1983) and Solling (1973)) and growth (average of 5 (Höglwald), 10 (Solling) or 3 years from the start) in all the EXMAN treatments; [a]Number of trees (ha^{-1}); [b]Diameter (cm) at 1.30 m height; [c]Basal area (m^2 ha^{-1}); [d]Estimates (data not present)

Site	N[a]	DBH[b]	Δ DBH	BA[c]	Δ BA	% ΔBA of control
			Control			
Klosterhede	601	21.5	0.48	31.4	0.87	
Kootwijk	995	19.8	0.48	32.1	1.57	
Harderwijk	1886	13.5	0.29	19.7	1.23	
Höglwald A1	603	36.0	0.34	68.8	1.2	
Solling F1	538	33.5	0.32	47.3	0.73	
Ballyhooly	632	29	0.5	44	2	
			Drought			
Klosterhede	800	21.0	0.49	31.4	1.44	166
			Irrigation			
Klosterhede	933	20.4	0.64	31.5	2.08	239
Kootwijk	1100	19.4	0.60	35.07	2.49	159
Harderwijk	1444	15.5	0.50	30.5	1.57	128
Höglwald B1	611	40.4	0.34	78.8	0.91	76
Höglwald C1	589	40.6	0.40	76.8	1.58	132
			Fertigation			
Klosterhede	933	21.7	0.64	35.8	2.19	252
Kootwijk	1044	19.7	0.63	34.0	2.15	137
Kootwijk-roof	1100	21.7	0.78	38.7	2.78	177
Harderwijk	1789	13.7	0.50	29.3	1.79	146
			Fertilization			
Harderwijk NH_4	1600	15.5	0.36	32.0	1.44	117
Solling FD	538[d]	34.6[d]	0.40	50.5	0.81	111
			Liming			
Höglwald A2	567	44.3	0.34	87.4	0.72	60
Höglwald B2	600	41.0	0.37	79.0	0.95	79
Höglwald C2	644	37.7	0.31	71.9	0.97	81

Both German sites (Höglwald and Solling) and Harderwijk show evidence of potassium deficiency. The Solling stand shows a pronounced deficiency of Mg.

3.2.1. Drought

P and K concentrations at Klosterhede are slightly, but not significantly, different between drought and control treatment.

3.2.2. Irrigation

The obviously high concentration of foliar N in the Dutch forests (Kootwijk and Harderwijk) (Table 6) was reduced to a small extent ($p < 0.05$) as a result of water additions. A similar decrease seems to result from acid irrigation at Höglwald. The considerable decrease of N inputs in the roof plot at Klosterhede and Kootwijk did not result in a change in N concentration. The irrigation treatment slightly lowered the K concentration in the needles at some sites and raised it at others. This response was very obvious for the irrigated trees at the covered plot at Klosterhede in 1989 (Beier and Rasmussen, 1993), where during the first year K deficiency was reported. This situation was a result of irrigation with demineralised water with only seasalts added, but without addition of extra K equivalent to replenish the natural leaching from the canopy. From the second treatment year onwards more K was added in order to restore the K cycle.

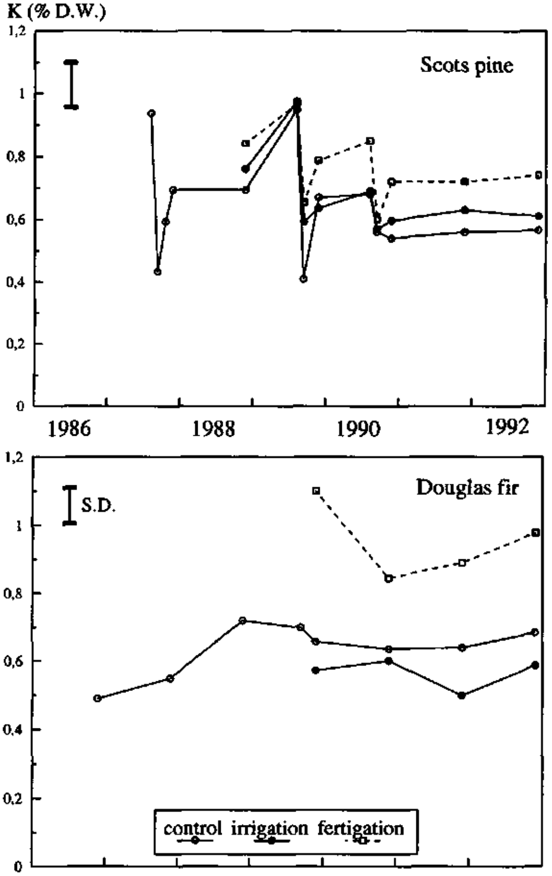

Figure 1. Response of K concentration in current year needles to fertigation, started in 1989, at the Dutch sites.

3.2.3. Fertigation

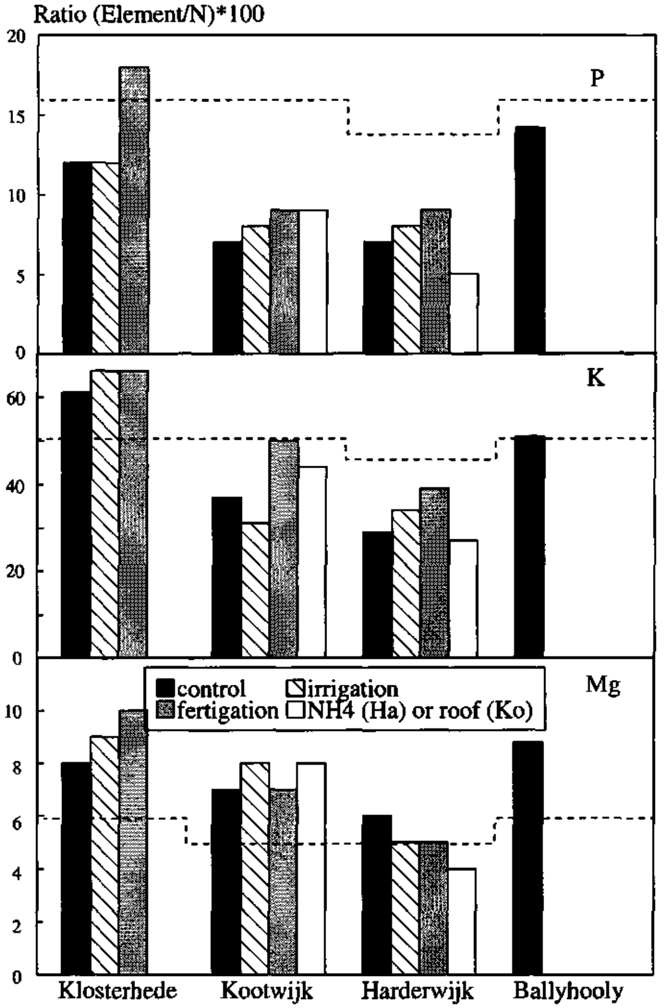

Figure 2. Nutrient contents of current year needles relative to N for all treatments in four stands. The dashed line indicates the optimal ratio (Ingestad, 1979) for each tree species.

Needle concentration of phosphorus was improved by fertigation at Klosterhede and at Kootwijk (Tables 4 and 6). At Harderwijk a small, but yet significant response was observed for P. The addition of K resulted in increased K concentrations in needles at both Dutch sites. The K concentrations in the current-year needles responded immediately in the first season of fertigation (1989/90) (Fig. 1). Since P concentration has been raised to 2.1 mg g^{-1} and 1.7 mg g^{-1} in the fertigated trees at Klosterhede and Kootwijk, respectively and K concentration is 7.2 mg g^{-1} and 8.9 mg g^{-1} at Harderwijk and Kootwijk, respectively, these nutrients are at optimal supply (Anon., 1990). Nutrient ratios in the control plots (Fig. 2) show distinct differences between the sites. According to Ingestad's (1979) optimal ratios for Scots pine and Norway spruce, the supply of P and K relative to N was insufficient at the Dutch sites; at Klosterhede only the supply of P was insufficient. K/N ratios in the needles have responded to the extra K application in the irrigation treatment at Klosterhede, and as well in the fertigation plots at Klosterhede and Kootwijk. P/N ratios improved considerably at Klosterhede by fertigation. Despite the improved

Table 6. Nutrient concentrations (mg g^{-1}) in current year needles (n=10) in the control and change as a percentage of the concentration of the control trees (% of mg g^{-1}) in the treatments in 1991, except for Solling (1983) and Höglwald (1989). n.d. is not determined

Site	N	P	K	Ca	Mg	Mn
	Control		mg g^{-1}			
Klosterhede	12.1	1.5	7.4	1.9	1.0	0.09
Kootwijk	17.4	1.2	6.4	1.6	1.3	0.04
Harderwijk	19.2	1.4	5.6	2.1	1.1	0.09
Höglwald	14.2	1.5	4.3	3.3	1.1	2.30
Solling F1	11.7	1.0	5.2	3.4	0.3	1.70
Ballyhooly	14.7	2.1	7.5	2.3	1.3	n.d.
	Drought		**change as % of control**			
Klosterhede	6	-13	16	-5	0	33
	Irrigation					
Klosterhede	-2	-7	7	32	10	44
Kootwijk	-9	0	-22	6	-8	1150
Harderwijk	-4	7	13	-5	-18	-30
Höglwald B1	-10	13	-9	-18	-9	-17
Höglwald C1	-4	13	21	-9	-9	n.d.
	Fertigation					
Klosterhede	-2	40	5	32	20	89
Kootwijk	3	42	39	-6	-8	650
Kootwijk-R	-10	17	8	-6	-8	650
Harderwijk	-3	14	29	5	-9	-11
	Fertilization					
Harderw NH_4	7	-21	-2	0	-27	233
Solling FD	4	0	-15	35	33	0
	Liming					
Höglwald A2	1	7	19	42	18	-48
Höglwald B2	-3	13	2	15	0	35
Höglwald C2	-6	27	-2	-3	-9	-22

P nutrition in the fertigated trees at the Dutch sites, the ratios are far from the high optimal ratio of 0.3 (Ingestad, 1979). The fertigated trees at Klosterhede have the highest availability of P, K and Mg relative to N of all EXMAN plots, but the absolute N concentration is low (approximately 1.2%). The ratios are even higher than at the Ballyhooly reference site, where ratios are equal or close to optimum.

3.2.4. Fertilization

At Harderwijk needle concentrations of N increased within one year after the start of ammoniumsulphate applications. The needle concentrations of P and K decreased considerably. At Solling a higher concentration of N, Ca and Mg in the current year needles was observed eight years after the first application. The shortage of Mg and to a certain degree N is alleviated in the treated trees (for more details see Matzner, 1985).

3.2.5. Liming

At Höglwald liming without irrigation (A2 plot, see Tables 4 and 6) and with acid irrigation (B2) resulted in higher Ca concentration in the needles. The small response of Mg concentration following dolomite application was not significant.

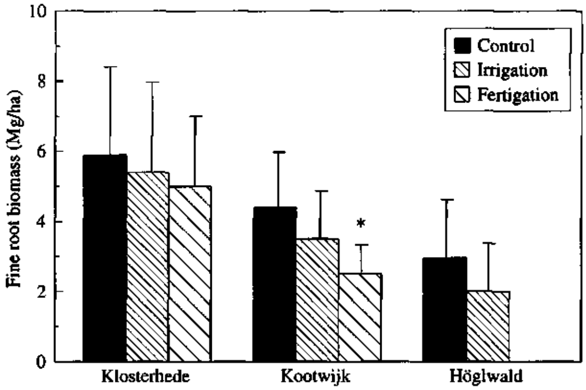

Figure 3. Fine root biomass (Mg ha^{-1}) at three manipulated sites. The standard deviation is also indicated.

3.3. Root development

Increased water supply tended to diminish fine root biomass at Klosterhede, Kootwijk and Höglwald (Fig. 3), although the effect was less marked at Klosterhede. Fertigation decreased root biomass further, but only at Kootwijk was the effect of this treatment significant ($p < 0.05$). The reduction in fine root biomass was particularly marked in the upper 20cm of the soil at Kootwijk. At Kootwijk, specific root length (SRL) was low in the roof plot from 0 to 10cm depth and high below 20cm depth under all treatments (Table 7). The formation of longer, thinner roots indicates the improvement of growth conditions, *e.g.* of root penetration, higher water supply or decreased concentrations of NH_4^+ or Al.

Fertilization and liming at Solling resulted in a decreased fine root turnover and less fluctuations of the fine root biomass relative to the control. Bauch *et al.* (1985) reported an increase of Ca and Mg concentrations in fine roots in both humus layer and mineral soil, while Al concentrations decreased.

3.4. Litter and cone fall

From 1988 to 1990 a trend towards higher litter production was observed at Klosterhede. The litter production differed among the manipulated plots at the start of the experiment. The drought plot was not drought-treated until 1989, and

Table 7. Specific fine root length of Douglas fir (Kootwijk) in 1990 (m g^{-1}).

Depth (cm)	Control	Irrigation	Fertigation	Roof
0-10	11.25a	9.80ab	11.93ab	8.99b
10-20	10.42a	10.27a	10.15a	10.18a
20-40	6.31a	10.89b	10.16b	8.94b
40-60	6.59a	9.07a	8.58a	6.33a

Within each depth means with the same letter are not significantly different ($p<0.05$).

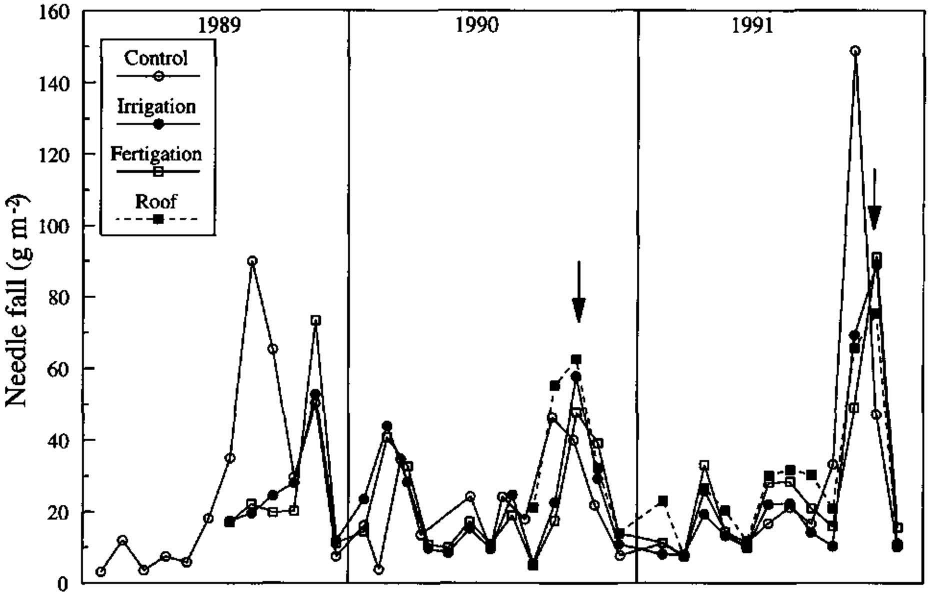

Figure 4. Needle fall (g m^{-2}) in the treatments in Douglas fir. The arrows indicate the maximum monthly needle fall in the treatments.

so it received equal amounts of water as the control plot in 1988. Nevertheless, in that period litterfall was significantly lower. During the second year of manipulated drought (1990), litter production exceeded the control values by 13%, which mainly resulted from a 90% increase in cone fall (Table 8). Cone fall in the irrigated and fertigated plot decreased considerably. The high variation in annual litterfall in each plot at Klosterhede (7 to 40%, $n = 5$) did not allow any conclusions on treatment responses.

At Kootwijk in the dry years 1989 and 1991 litter production was reduced ($p < 0.05$) to the same extent in both the irrigated and fertigated plot. In the optimal nutrition plot under the roof, litterfall was equal to the control. The improved water supply resulted in a delay of needle fall by one month (Fig. 4). The same delay was observed for pine at Harderwijk, but total annual litter fall was equal for all plots. Cone production in irrigated and fertigated plots was more than 20% lower than at the control site over the period 1989-1991. At Höglwald all treatments had the same amount of annual litterfall.

Table 8. Annual litterfall and average cone fall (g m^{-2}) in the control and a percentage thereof for all years in the treated plots. n.d.= not determined

	Control g m^{-2}	Treatment (% of control)		
		Irrigation	Fertigation	Others
Litterfall				
Klosterhede				Drought
1988	211.7	128	99	79
1989	389.5	104	96	68
1990	402.4	120	121	113
Kootwijk				Roof
1989	381.8	54	55	115
1990	341.9	110	110	94
1991	381.9	82	88	105
Harderwijk				
1989	561.8	116	122	
1990	250.5	113	113	
1991	392.9	75	84	
Höglwald	Control	Irrigation	Acid irrigation	Lime+irrigation
1986	605.4	102	101	102
1987	458.9	99	94	100
1988	427.0	119	108	104
1989	428.3	108	108	101
Cone fall				Drought
Klosterhede	n.d.	32	24	190
Harderwijk	101.8	79	75	
Kootwijk	23.4	117	99	

3.5. Vegetation changes

At Harderwijk the fern *Dryopteris dilatata* and the nitrophilic *Rubus idaeus* and *Epilobium angustifolium* have increased in cover in the irrigated plot as a result of the improved water supply (Table 9). At Höglwald the water addition itself did not influence the vegetation cover. However, lime clearly stimulated the abundance of *Oxalis acetosella*. At Klosterhede the most obvious change with time is the appearance of *Epilobium angustifolium* and *Senecio vulgaris* in the fertigation plot, and the development of *Dryopteris carthusiana* in both manipulated plots (3% cover). The cover of *Deschampsia flexuosa* increased from 1988 to 1990 in control and irrigation plot and even doubled in the fertigated plot. Nevertheless, difference in plant cover relative to the control was still small at Klosterhede and data are therefore not presented.

Table 9. Average soil cover (%) of a number of plant species and number of juvenile trees (ha^{-1}) at two sites. [a]Treatment at Harderwijk is fertigation, lime+irrigation at Höglwald.

	Year	Control	Treatment	
			Irrigation	Other[a]
Harderwijk			soil cover (%)	
Dryopteris dilatata	1992	1	42	12
Deschampsia flexuosa	1992	80	42	56
Rubus idaeus	1992	0	25	9
Epilobium angustifolium	1992	0	8	1
			N seedlings	
Betula pendula	1992	370	1970	1860
Sorbus aucuparius	1992	330	910	590
Quercus robur	1992	90	180	70
Sambucus nigra	1992	0	110	140
Höglwald			soil cover (%)	
Rubus idaeus	1983	0	80	9.1
	1989	4.8	0	22.7
Oxalis acetosella	1983	1	3	2
	1989	16	19	83
			N seedlings	
Fraxinus excelsior	1983	0	-	0
	1989	0	-	310
Sambucus nigra	1983	0	-	0
	1989	0	-	300

In both the irrigated and fertigated plots at Harderwijk an enormous increase in a number of nitrophilic, woody plants was observed since the start of treatment (Table 9). Also the presence of oak increased. At Höglwald liming let to drastic changes in the forest floor vegetation in three different ways; (i) improved Ca supply stimulated the growth of *Oxalis acetosella* (ii) pH increase (see Beier and Rasmussen, 1993) enhanced the presence of species of the class *Querco-Fagetea*, e.g. *Fraxinus excelsior* and (iii) a group of nitrophilic species appeared (Rodenkirchen, 1991).

4. Discussion

4.1. Irrigation

Diameter growth at Klosterhede, Kootwijk and Harderwijk was enhanced by water additions. At all three sites poor, sandy soils with low water-holding capacities are present. This growth difference between control and irrigation treatment is likely a consequence of the poor water supply from the soil in combination with the rather dry experimental years. In the Skogaby research project basal area growth responded somewhat less to optimal irrigation (+25%) during the same treatment years (Nilsson and Wiklund, 1992). It is not clear to what extent the water limitation originates from drought susceptibility caused by malfunctioning roots related to high concentrations of free Al^{3+} (0.5 - 1.5 $mmol_c\ L^{-1}$, see Farrell *et al.*, 1993)(Marschner, 1989). At the Höglwald site no water shortage was observed under the prevailing weather, so irrigation did not benefit growth. Linder and Flower-Ellis (1992) also found that response to irrigation depends on site conditions. Water additions have diminished annual needle fall in the Douglas fir stand at Kootwijk only. Drought stress at the control site resulted in a higher rate of needle shedding, as was found for *Pinus radiata* by Cromer *et al.* (1984).

4.2. Fertigation

At Klosterhede, at Harderwijk and in the non-roofed plots at Kootwijk no growth difference has been found yet between the irrigation and the fertigation treatments. For each site, different circumstances presumably let to this result.

At Klosterhede only P concentrations increased significantly, but P nutrition was never growth limiting according to Dutch standards (Anon., 1990). Soil solution (Beier and Rasmussen, 1993) and needle composition did not respond to the addition of the base cations. The increased nutrient uptake by a more abundant understorey vegetation may be too small to account for the disappearance of the applied nutrients. Most of the nutrients were probably retained in the organic and mineral soil. Feger *et al.* (1991) applied 130 kg Mg ha^{-1} as solid Mg_2SO_4 to an iron-humus podzol and found 77% retention in the soil and only 3% recovery in the needles of Norway spruce.

The manipulated change in N supply, from nitrate and ammonium under ambient conditions, to 100% nitrate under the roof may decrease rhizosphere acidification but should not necessarily lead to higher growth (Gijsman and Van Noordwijk, 1990). Similar to Klosterhede, the cover of fern increased at Harderwijk as a result of water addition. The enormous increase in nitrophilic species at Harderwijk indicates a high N availability when combined with non-limiting water supply. This did not occur at Klosterhede, where still N limitations were present. The concentrations of K and to some extent P in the needles increased and resulted in an improved nutritional balance relative to N. Although K/N ratios did not reach optimal levels (Ingestad, 1979), the lack of growth response to K increase in the fertigated plot at Harderwijk indicates that not K, but other limitations should be eliminated, like Mg relative to N. At the Norrliden experiment Tamm (1991) also found that addition of P and K to N fertilizer did not result in growth of Scots pine above additional inorganic N alone. Further growth increase might as well be limited by soil physical properties and provenance.

At Kootwijk the fertigation improved K and P nutrition, but Ca nutrition remained insufficient. The low application rate of Ca at Kootwijk, and of Mg at Harderwijk, were obviously not enough to enhance tree growth relative to the irrigation treatment. The lack of growth response could be due to non-beneficial secondary effects of the fertigation on soil: higher rates of soil acidification and higher soil solution concentrations of Al^{3+} were observed (Beier and Rasmussen, 1993). Also at the Solling site an increase in soil solution acidity was found in the first year after fertilization due to the exchange of H^+ and Al^{3+} with added K^+ and Mg^{2+} (Matzner *et al.*, 1985). Tamm (1991) also found lower pH values in plots receiving P and K solely. The improved site conditions could result in a higher crown density and a subsequently higher needle fall rate at steady-state. The results on litter fall of all three fertigation plots do not univocally point at an increase or decrease of needle biomass and needle fall with time. In the Swedish optimal nutrition experiments (Linder, 1987; Tamm, 1991) biomass allocation to above-ground parts was increased and it was related to improved N nutrition. Nilsson and Wiklund (1992) observed an enormous increase in needle biomass in fertigated Norway spruce, that caused higher rates of needle fall, despite the higher needle retention resulting from improved water supply. Only at Klosterhede above-ground growth could in theory benefit from increased N nutrition, but this was not aimed at.

Nutrient cycling between soil and understorey vegetation has probably been increased in proportion to the increased biomass of fern (Klosterhede) and other species (Harderwijk). So the ground vegetation profits from the enhanced N mineralization (Beier and Rasmussen, 1993) to a larger extent than do the trees.

4.3. Liming and fertilization

Liming plus fertilization with N and K at Solling increased tree growth and in needles of the added elements. Although one can not strictly separate the beneficial effects of N, Mg and lime additions, the very poor Mg nutrition is probably the main growth-limiting factor. A number of studies showed the positive effect of Mg applications on Mg nutrition and tree health in South Germany (Evers and Hüttl, 1990; Feger *et al.*, 1991), France (Ranger and Mohammed Ahmed, 1993) and Austria (Katzensteiner *et al.*, 1992). The carbonate in the lime clearly eliminated the acidifying effects of the fertilizer additions from the second year onwards (Matzner *et al.*, 1985). The Ca/K antagonism led to a decrease in K concentrations in needles. The growth at Solling is probably favoured by the combination lime+fertilizer, as was found for spruce (Spiecker, 1991) and pine (Rehfuess *et al.* 1991).

Liming slightly depressed diameter increment in the Norway spruce stand at Höglwald. On poor forest sites a growth decrease for many years can be expected after liming (Persson *et al.*, 1990). However, at Höglwald a fertile soil is present and after liming no nutrient limitations in the needles were observed. Liming resulted in higher soil availability of Ca, Mg and NO_3 (Kreutzer and Göttlein, 1991). Only Ca and to a small extent Mg concentration in needles increased due to passive uptake.

Acid irrigation did not affect tree growth and vitality, although a decrease of the number of mycorrhizal and non-mycorrhizal root tips was found in the upper soil layers (Blaschke, 1986). In lower parts of the root zone soil chemical conditions were still beneficial for growth (Kreutzer and Göttlein, 1991).

Ammonium sulphate applications at Harderwijk did not hamper growth of Scots pine yet, despite the fairly large decrease of needle concentrations of P and Mg. The observed increase in N concentrations and the widening of the N/Mg ratio in the needles has also been found in the ARINUS project in SW Germany after ammonium sulphate application (Feger, 1992).

Our nutrition treatments are not comparable to the optimum nutrition experiments at Jädraås and Stråsan in Sweden (Linder, 1987; Tamm, 1991). The goal of these Swedish experiments was mainly to find the maximum level of wood production, and they were dealing with N nutrition as the main limiting factor. Our sites received moderate to high loads of N, so our treatments focused more on the limitations of other macro nutrients. Following this approach, it is shown in this paper that biological response of the ecosystem to nutritional changes is not restricted to wood yield alone.

5. Conclusions

The conclusions can be summarised as follows.

(1) Irrigation is a good tool to quantify the water limitation of the site for

tree growth.

(2) The lack of growth response to nutrient applications in addition to irrigation is related to the low application rate of the nutrients that were short in supply.

(3) Fertigation results in a quick response of K needle concentrations, but the recovery of other added nutrients is small and site-specific.

(4) Nitrogen fertilization increases N needle concentrations even beyond optimal values.

(5) A single limestone application can increase Ca nutrition for at least eight years.

(6) Dolomitic limestone application increases growth and Mg nutrition drastically at the Solling site.

(7) Fertigation can decrease the amount of fine roots.

(8) Improved water supply in most cases decreases cone production and delays needle shedding.

(9) Irrigation promotes the growth of understorey vegetation under conditions of high N availability, and this is further enhanced by liming.

Acknowledgements

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CHAPTER 4

Effects of water and nutrient applications in a Scots pine stand to tree growth and nutrient cycling

Submitted to Plant and Soil

Co-author: N. van Breemen

Effects of water and nutrient applications in a Scots pine stand to tree growth and nutrient cycling

Abstract: In a Scots pine forest stand, demineralized water, a complete set of nutrients with water and dissolved $(NH_4)_2SO_4$ were applied to the soil by means of frequent irrigation for four years. Effect of treatments on tree growth and chemical composition of soil water and vegetation were monitored. Diameter growth responded positively to the increased water supply from the first year onwards. Nutrient applications increased K and P concentrations in pine needles immediately, but growth was enhanced only in the fourth treatment year and coincided with an improved K supply. Most of the applied P and K was retained in the soil, and only 6 % was recovered in the vegetation. Tree nutrient status did not respond on Ca and Mg applications, whereas Ca and Mg leaching losses were increased. The applied NH_4 was mostly retained in the 0 - 20 cm surface soil and caused an increase of Al in soil solution. Tree growth was stimulated initially by extra NH_4, but was hampered after three years due to a decreased P supply. We discuss whether nutrient applications are profitable for trees when cation absorption to roots and soil both enhance acidification of the root environment.

Keywords: atmospheric deposition, excess NH_4, balanced nutrition, *Pinus sylvestris* L., soil acidification

Introduction

In the last decades atmospheric N deposition in Northwestern Europe has increased and has caused nutritional imbalances in trees. In soils that initially had a poor availability of N and base cations, the N supply increased while the base cation supply remained low or decreased (Van Breemen and Van Dijk, 1988). Antagonism between NH_4 and K or Mg in root uptake (Nihlgård, 1985) and direct uptake of NH_3 through the stomata (Van der Eerden and Pérez-Soba, 1992) can aggravate nutritional imbalances. Apart of this nutritional problem, N deposition increases soil acidification. This is due to nitrification of NH_4 (Van Breemen *et al.*, 1982) or to proton excretion by roots when NH_4 uptake dominates over NO_3 (Arnold, 1993; Chapter 6 of this thesis). The increased proton production has led to high concentrations of H and free Al, that were shown harmful to roots of tree seedlings (Eldhuset *et al.*, 1987; Keltjens and Van Loenen, 1989). Growth (Waring, 1985) and needle nutrient status (Hüttl, 1986) can be used as estimators of the vigor of the forest stand.

In this study the effects of the recent high atmospheric N inputs on growth and nutrition of trees have been studied. The nutritional balance was experimentally changed by varying the supply of either N or other nutrients to trees. In one treatment, supply of nutrients other than N was increased, in another treatment only the supply of NH_4 was increased. Most attention has been paid to the relation between the availability of N versus that of P and K, since that was found to mostly influence growth in Scots pine stands (Tamm, 1991), but the balance of N with other nutrients was studied as well. Apart from initially positive, nutritional effect of NH_4 applications on growth, secondary effects that may follow, *i.e.* increase of soil acidification rate (Van Breemen *et al.*, 1983) and detiorated tree growth (Nihlgård, 1985) have been monitored. The effects on tree growth of an improved water supply has been studied too, because an imbalance of K to N can increase drought sensitivity (Larsen, 1983) and was shown to be enhanced by $(NH_4)_2SO_4$ deposition in case of *Calluna vulgaris* (Dueck et al., 1990). This study deals with the effects on soil and trees of: 1) improved nutritional balance according to optimal nutrient ratios (Ingestad, 1979, 1988); 2) disturbed nutritional balance by excess NH_4; 3) improved water supply.

Nutrient budgets for the soil-vegetation system were calculated for each treatment to estimate the proportion of incoming N and applied nutrients that have actually been taken up by the vegetation. The possible amelioration of the soil with nutrient applications and the effects of prolonged high rates of atmospheric deposition are discussed.

Material and methods

The forest stand (0.9 ha) is located near Harderwijk (52°20'N, 5°40'E) in the central part of the Netherlands, and consists of even-aged Scots pine (*Pinus sylvestris* L.) trees, sowed in 1952. Stand density is 1886 trees ha^{-1}. Bole volume growth was 9.4 m^3 ha^{-1} y^{-1} in 1987 and 1988. A nitrofilic ground vegetation is present, consisting of *Deschampsia flexuosa* and some *Corydalis claviculata* and *Dryopteris dilatata*, and an open shrub layer of *Sorbus aucuparius*. The coarse sandy soil is a typic Udipsamment (Soil Survey Staff, 1975) on fluvioglacial deposits. Chemical properties of the first 10 cm of the A_h horizon (0 - 23 cm) are: pH (H_2O) 4.3; pH (1M KCl) 3.3; organic carbon 1.63 %; total N 0.065 %; CEC (0.01 M $BaCl_2$) 2.9 cmol(+) kg^{-1} soil, exchangeable cations (0.01 M $BaCl_2$): 0.15 Na, 0.43 Ca, 0.11 Mg, 0.10 K cmol(+) kg^{-1} soil; exchangeable acidity (1M KCl) 2.1 cmol(+) kg^{-1} soil. A 7 cm thick organic surface horizon (O_h) contains (mass fraction in % of dry weight) 1.6 N, 0.6 P, 0.7 K, 1.6 Ca and 0.5 % Mg and has a C/N ratio of 33.

From May 1989 to October 1992 four treatments were carried out, of which one (N+S) was continued until January 1994:

(**C**) control (530 m^2); (**I**) irrigation (plot size 900 m^2): addition of 6 to 8 mm of demineralized water every second day during the growing season; (**IF**) fertigation (plot size 900 m^2): irrigation, as described before in (**I**), and application of the following nutrients, required for an estimated annual gross uptake of 100 kg N ha^{-1}: N 30 (*ie.* 100 kg minus 40 kg N deposition and minus 30 kg estimated N mineralization), P 13, K 60, Ca 7, Mg 8 kg ha^{-1} and micronutrients Mn 0.43, Fe 0.8, B 0.22, Zn and Cu 0.04 and Mo 0.007 kg ha^{-1}. Potassium, P, Na, Mo and B were given as K_2HPO_4, K_2SO_4, Na_2MoO_4, H_3BO_3, the others as nitrates. All nutrients were dissolved in the irrigation water. The nutrient application rate was computer-controlled and varied over the growing season according to mineralization rate, as described by Ingestad (1988); (**N+S**) Ammonium excess (plot size 120 m^2): weekly applications of dissolved $(NH_4)_2SO_4$ in all seasons, amounting to 120 kg N ha^{-1} y^{-1}.

Precipitation and throughfall were collected in two and ten funnels (ϕ 24 cm) respectively, placed 1.20 m above the land surface and sampled every fortnight, starting June 1987. The soil solution was sampled every fortnight (1989-1990) or every four weeks (1991-1992), using ceramic lysimeter plates for the "0" cm depth between litter layer and mineral soil (n=4) at a continuous suction (-0.05 MPa) or by ceramic cups (Soil Moisture Equipment) at 20, 40 and 90 cm depth (n=4) in all treatments, except **N+S** (n=2), connected to suction (-0.05 MPa) bottles every sampling event. On all water samples pH and Ec was determined and were analysed for K and Na by flame emission, Ca and Mg by AAS, total Al, NH_4, H_2PO_4 by spectrophotometry, NO_3, SO_4, Cl by ion chromatography, total carbon (C_t) and soluble organic anions (SOA) by IR spectophotometry. The analytical procedures have been described by Velthorst (1993).

Stem diameters at breast height (DBH) were measured in all plots every winter in order to calculate diameter growth and basal area (BA) increment. Height measurements were done in 1988 and 1989 on all trees in each treatment with an extendable pole. Stem volume increment (V) was calculated from the formula:

$$V = DBH^{1.82} * H^{1.07} * e^{-2.88} \quad (1).$$

Branch, needle and root biomass were estimated from DBH using the regression data on 10 felled trees of small (n=5) and mean (n=5) basal area. The annual element uptake was estimated from growth and composition of biomass components. Biomass and chemical composition of the understorey vegetation was determined in August 1991 and 1992 on 10 randomly selected subplots (0.25 m^2 each) in every treatment. Needles from two age-classes were sampled from ten trees from the 7th whorl in autumn each year. Needle and vegetation samples were dried at 70°C for 48 hours, weighed and ground to pass a 0.5-mm sieve and then digested in a mixture of sulphuric and salicylic acid, H_2O_2 and selenium. In the digests total N and P were determined colorimetrically, K and

Ca by atomic emission spectrometry and Mg by atomic absorption spectrometry. Litter fall was collected monthly from litter traps of 1 m^2 (n=4 in treatment plots, n=11 in the control) in **C**, **I** and **IF** plot and dry weight and element content were determined.

Soil water fluxes were calculated with a dynamic model for water transport in the unsaturated zone SWIF (Tiktak and Bouten, 1992), based on the Darcy flow equation and evapotranspiration estimated from daily radiation and temperature data. The model input of daily values of throughfall and interception were calculated from 14-day funnel samples and daily precipitation at a weather station at 5 km distance. This was done by distributing the funnel values over the 14 days proportionally to the weather station values and by assuming a constant interception within each period. Radiation and temperature data were taken from weather station De Bilt, at 35 km distance. Crop factor and measured soil hydraulic properties were calibrated by fitting simulated to measured values of soil moisture, registered on 11 occassions at 6 depths (10 cm intervals) with 5 replicates in summer 1991. A horizontally homogeneous water transport was assumed. Element fluxes were calculated from the product of water flux and chemical composition on a monthly basis. Calculated annual means were corrected so as to obtain equal in- and output fluxes of Cl.

Treatment effects were tested with analysis of variance, followed by a LSD test (STATGRAPHICS 6.0).

Results and interpretation

Open field precipitation and throughfall inputs

Table 1 presents mean annual inputs of all major solutes in bulk open field precipitation collectors and in throughfall collectors (mol_c ha^{-1} y^{-1}). The nitrogen and sulphur throughfall inputs to the soil amounted to about 45 and 32 kg ha^{-1} y^{-1} respectively (Table 1). Hydrogen ions derived from deposition of sulphuric and nitric acid were largely buffered in the tree canopy. Leaching of K from the tree canopy was considerable. The higher flux of NH_4 in throughfall than in open field precipitation could be accounted for by higher throughfall fluxes of NO_3 + SO_4 (*i.e.* codeposition). If SO_4 and NO_3 did not interact with the canopy and NH_4 was deposited mainly as their counter ion, no substantial further NH_4 deposition could be calculated, suggesting that no NH_4 absorption in the canopy took place. In order to estimate nutrient leaching from the canopy, Cl was assumed chemically inert and the ion proportions of seasalts relative to Cl in interception deposition were assumed equal to those in seawater (Weast, 1974). The leaching losses of base cations (mainly foliar K) balanced the high input of H from bulk open field and possibly some interception deposition of HCl. No temporal trend was observed in the deposition of N and S during the observation

Table 1. Chemical fluxes of bulk open field deposition and throughfall in mol_c ha^{-1} y^{-1}, in the period 1-1-1990 to 1-1-1993. Cl was assumed not to interact with the canopy. Interception deposition of seasalt elements was calculated from the value Cl interception deposition (932 mol), according to their concentration ratios in seawater. * bulk deposition of H, Al and H_2PO_4 was calculated assuming equal ratios (total deposition)/(open field) as Cl (=2.13). Leaching from the canopy (+) equals (throughfall flux) - (bulk open field) - (interception deposition).

Ion	Open field	Throughfall	Interception deposition	Canopy leaching
H	135	30	288*	-258
K	40	340	37	263
Na	588	1332	792	-48
Ca	218	389	19	152
Mg	165	372	177	30
Cl	824	1756	932	0
SO_4	808	1987	98	
NH_4	873	2357		
NO_3	467	885		
Al	50	25	107*	-25
H_2PO_4	11	8	23*	-15
Σ -	2110	4844		
Σ +	2069	4637		
Waterflux (mm)	820	630		

period of 1988 to 1993.

Soil solution composition

Irrigation effects: Mean ion concentrations in the soil solution of the third treatment year 1991 are presented in Table 2. The pH was generally close to 4, and Al, Cl and SO_4 were the dominant ionic solutes. Dissolved Na, Cl and SO_4 were depressed by irrigation. Such dilution effects due to irrigation became visible in 1990, one year after the start of the experiment. Concentrations of Ca and K decreased with time. Mean NO_3 concentrations were higher in the irrigated **I** than in the **C** plot. This was due to high summer concentrations of nitrate in the **I** plot, as can be seen from plots of NO_3/Cl-ratios with time (Fig.

Table 2. Mean flux-weighted pH and solute concentrations (mmol$_c$ m^{-3}) in the soil solution at 20 cm depth in 1991. Coefficient of variation (standard deviation as % of mean) between the individual samplers is given between brackets. For details on treatments see text.

	Treatments							
	Control		Irrigation		Fertigation		$(NH_4)_2SO_4$	
	C		**I**		**IF**		**N+S**	
Element								
pH	4.24	(0.05)	4.21	(0.03)	4.08	(0.15)	3.88	(0.03)
Al	655	(7)	641	(6)	1066	(27)	2662	(53)
K	8	(8)	8	(54)	199	(17)	23	(44)
H	57	(6)	62	(4)	84	(27)	132	(9)
Ca	99	(73)	58	(26)	142	(21)	160	(17)
Mg	118	(20)	127	(43)	216	(23)	282	(11)
Na	481	(11)	340	(38)	360	(4)	457	(4)
NH_4^+	8	(6)	5	(4)	24	(97)	137	(29)
NO_3^-	173	(84)	398	(24)	816	(54)	318	(39)
$H_2PO_4^-$	0	(43)	0.09	(100)	0.22	(16)	0.14	(39)
SO_4^{2-}	527	(6)	256	(25)	483	(1)	2710	(7)
Cl	634	(5)	475	(41)	598	(1)	698	(22)

1). In the control plot the ratio NO_3/Cl was always close to zero: the low NO_3 concentrations fluctuated in correspondance with changes in soil water storage, resulting from transpiration. In the **I** plot, NO_3 dominated over SO_4, while in the **C** plot the reverse was true. Al and NO_3 concentrations in **I** were correlated, giving an R^2 (linear regression) of 0.56. In the **C** plot Al was correlated to SO_4 (R^2=0.35) but not to NO_3 (R^2=0.01). Al concentrations were higher in the **I** plot than in **C** before summer 1990, but than became similar to those in the **C** plot (Fig. 2). K concentrations in the litter percolate showed a strong seasonal pattern of low summer and high winter concentrations (Fig. 3).

Fertigation effects: To evaluate the effects of fertigation, the soil solution chemistry of the fertigated plot should be compared with that from the irrigated plot, which received the same amount of water. In 1991 concentrations of all elements except Na were higher in the **IF** than in the **I** plot (Table 2). Fertigation caused a significant decrease in pH and a strong increase in

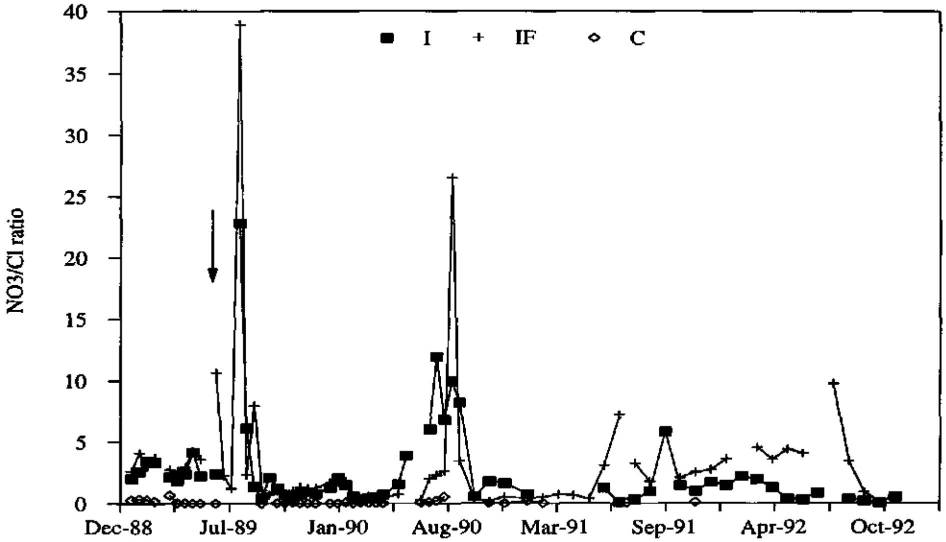

Figure 1. Ratios of NO_3 to Cl soil solution concentrations at 20 cm depth. Start of the treatments is indicated by an arrow. C, control; I, irrigation; IF, fertigation.

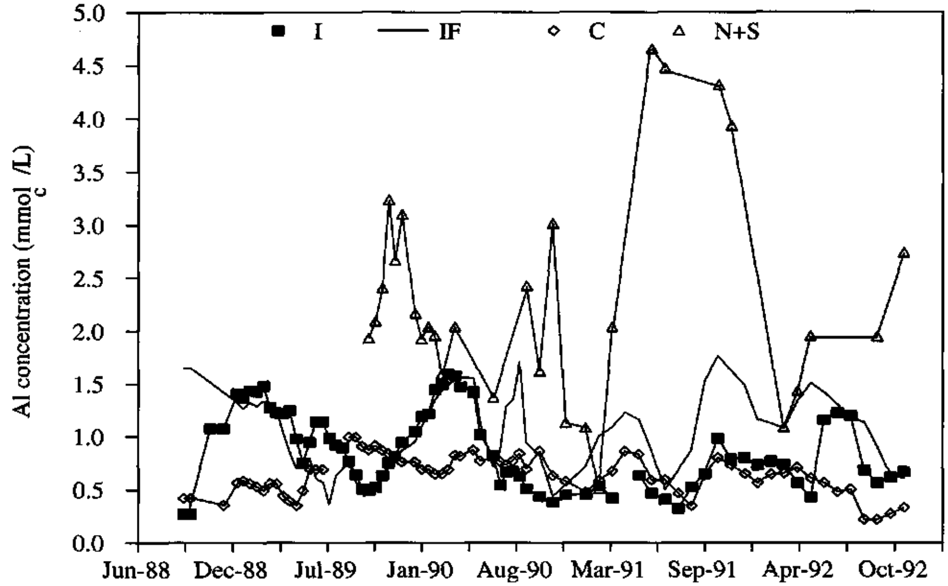

Figure 2. Time course of Al^{3+} concentration ($mmol_c\ L^{-1}$) at 20 cm depth. C, control; I, irrigation; IF, fertigation; N+S, ammoniumsulphate application.

dissolved K (Fig. 3) and SO_4. Even below the rooting zone K concentrations more than doubled. Al concentrations in **I** and **IF** plot were equal in winter

88/89 and 89/90 (Fig. 2). Thereupon Al concentrations remained high in the **IF** plot, while they decreased in the **I** plot. From 1990 onwards, also NO_3 concentrations were higher in **IF** than in **I**, and differences between the plots for Al and NO_3 were more pronounced in summer (Figs. 1 and 2). NO_3 and Al concentrations were more correlated in the **IF** plot (R^2=0.71) than in the **I** plot. Phosphate concentrations gradually increased upon fertigation, but only in the litter percolate. Concentrations of NH_4, Mg, Ca and Cl gradually increased at all depths.

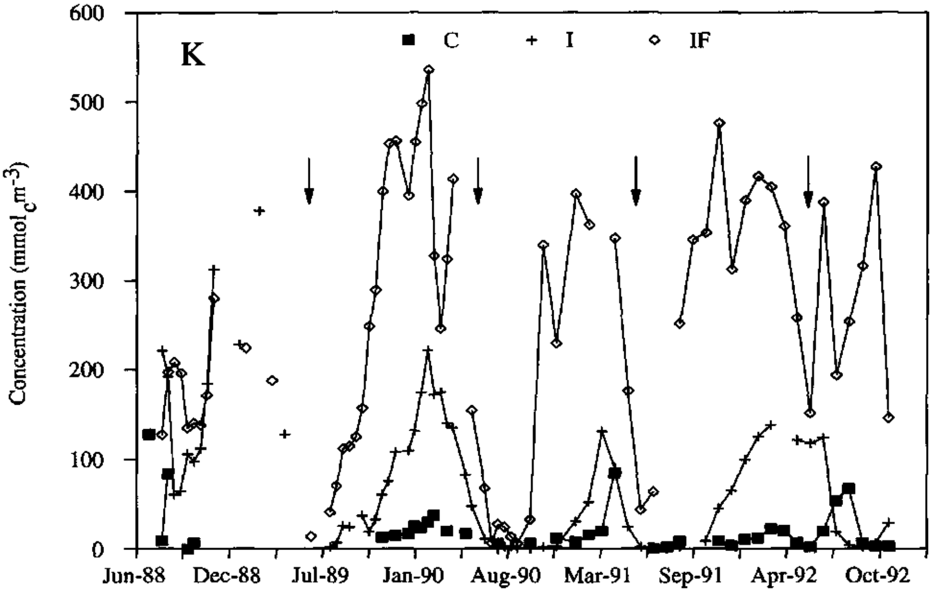

Figure 3. Time course of K concentration (mmol$_c$ m^{-3}) in the litter percolate in three treatment plots. Arrows indicate annual start of treatments; C, control; I, irrigation; IF, fertigation.

(NH_4)$_2$$SO_4$ application: Application of (NH_4)$_2$$SO_4$ caused an increase in concentration of all ions relative to those in the control except for Na and Cl (Table 2). At 20 cm depth the soil solution in the N+S plot became completely dominated by Al and SO_4. NH_4 concentrations at 20 cm depth in the N+S treatment were high too, but had decreased by a factor of five to ten relative to those just below the forest floor. The increase in concentrations of base cations, H and Al preceded that of NH_4 at every sampling point, apparently due to exchange processes. In summer 1991 Al concentrations reached high values of 5 (20 cm) to 11 (40 cm depth) mmol$_c$ L^{-1}. Nitrate concentrations at 20 cm depth increased steadily from the start of ammonium application and became higher than those in the fertigated soil from the middle of 1992 onwards. At all depths

pH, Ca/Al and K/NH_4 ratios decreased with time. The total flux of NH_4 over three years in the litter percolate (4280 mol_c ha^{-1} y^{-1} after Cl correction) is almost equivalent to the amount Al mobilized from the mineral soil over the same period (4820 mol_c ha^{-1} y^{-1}) (Fig. 4). The temporal pattern of NH_4 influx at the soil surface is mirrored closely by the Al outflux at 40 cm depth, indicating rapid Al mobilization by a combination of ion exchange and dissolution by HNO_3 from nitrified NH_4 (Fig. 4).

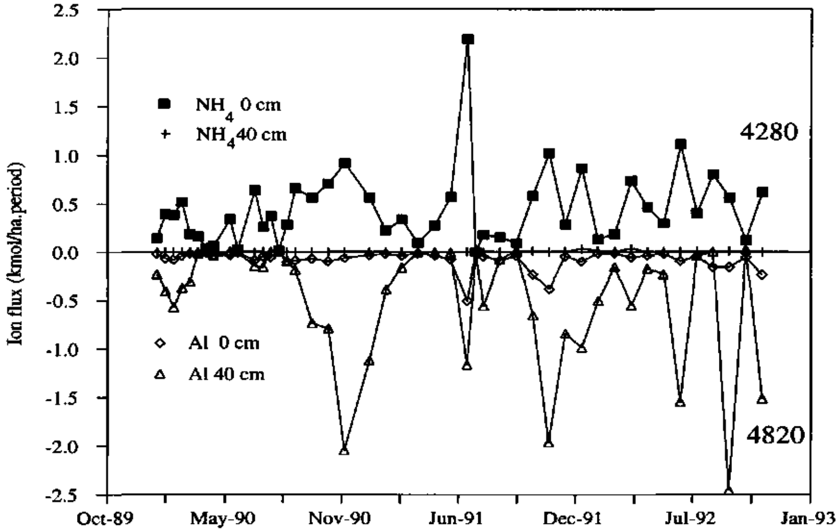

Figure 4. NH_4 and Al fluxes (mol_c ha^{-1}) per sampling period in the ammoniumsulphate treatment in the litter percolate (0 cm depth) and at 40 cm depth. Cumulative amounts (adjusted for Cl) for NH_4 beneath the litter layer and for Al^{3+} at 40 cm are indicated.

Tree growth

The mean annual tree diameter increment was 3.1 mm y^{-1} in the period 1983-1988, moderate but normal for Scots pine in the Netherlands on these poor sandy soils. A moderate height growth of *ca.* 30 cm y^{-1} was measured in the two years before the treatment started. In all plots equal growth of DBH (diameter at breast height) and BA (basal area) (30.4±1.2 m^2 ha^{-1} y^{-1} at the end of 1988) was observed at the start of the experiment. However, a storm in January 1990 felled trees unequally over the plots (Table 3). Therefore, BA values of surviving trees were dealt with and were calculated backwards to the starting year.

In the first treatment year, 1989, DBH growth was higher in the **I** plot (Table

4). BA increment was not significantly different between plots. Diameter increment in the control plot was smaller in 1990 and 1991 than in 1989, while growth remained high in treatments **I** and **IF**. In both years water additions significantly increased DBH and BA growth. In 1992 growth in all plots was higher than in the two years before. Again water additions enhanced tree growth. Nutrient additions significantly increased DBH growth ($p<0.05$) and, to a lesser extent, BA growth ($p<0.1$). In the extremely wet year after abondment of treatment, 1993, growth in **C**, **I** and **IF** plot was equal.

Table 3. Basal area (BA in m^2 ha^{-1}) before and after the experimental period, BA growth (m^2 ha^{-1} y^{-1}) in the treatments. BA growth, including that due to trees that were windthrown in 1990, are given between brackets. Level of significance of difference between two columns: ***, $p<0.001$; **, $p<0.01$; *, $p<0.05$; (*), $p<0.10$

	$(NH_4)_2SO_4$		Control		Irrigation		Fertigation
	N+S		**C**		**I**		**IF**
BA 1988	29.96		23.84		20.95		18.01
BA 1992	34.74		28.49		27.11		24.01
BA growth							
1988	1.53 (id)	-	1.16 (1.53)	-	0.96 (1.52)	-	0.78 (1.49)
1989	1.87 (id)	*	1.52 (1.93)	-	1.77 (2.05)	-	1.55 (2.37)
1990	1.05	*	0.88	***	1.24	-	1.52
1991	0.98	-	0.98	***	1.41	-	1.49
1992	1.32	-	1.47	*	1.80	(*)	2.25
1993	1.14	*	1.78	-	1.54	-	1.47
mean '90-'92	1.12	-	1.11	*	1.48	*	1.75
% of 1988	73		96		154		224

High loads of NH_4 initially stimulated BA growth for two years, followed by a rapid decrease to levels lower than before. Ammoniumsulphate additions had a negative effect on DBH growth in 1993, the last treatment year of the **N+S** plot.

Element contents in needles

In general nitrogen contents of pine needles were high (Table 5) and increased with needle age (data not shown). Nutrient contents generally mostly exceeded

Table 4. Stem diameter at breast height (DBH in cm) before and after the experimental period (1989-1992) and annual DBH growth. Level of significance of difference between two columns: ***, $p<0.001$; **, $p<0.01$; *, $p<0.05$; (*), $p<0.10$

	$(NH_4)_2SO_4$ N+S		Control C		Irrigation I		Fertigation IF
				cm			
DBH 1988	15.30		13.54		15.45		13.21
DBH 1992	16.52		14.97		17.54		15.37
diameter growth							
1988	0.41		0.32		0.34		0.30
1989	0.51	*	0.39	*	0.62		0.52
1990	0.30		0.24	**	0.42		0.51
1991	0.27		0.24	**	0.46		0.45
1992	0.38		0.35	***	0.58	***	0.73
1993	0.28	*	0.43		0.46		0.44
mean '90-'92	0.32		0.28	**	0.49		0.56
% of 1988	78		88		144		187

those considered normal ("N") in the Netherlands, but P and Ca concentrations were low ("L") in some years. The mass ratios between P and K on the one hand, and N on the other, can be considered normal for Dutch standards (Anon., 1990), but much lower than the ratios considered optimal for whole seedlings (Ingestad, 1979). The Mg/N mass ratio is variable but is mostly too low (< 0.05) for Dutch circumstances.

In 1990 and 1991 N concentrations tended to decrease as a result of irrigation and fertigation (Table 5). In 1989 P and K concentrations in needles were higher in the **IF** plot than in **C** and **I** plot. In later years the highest K contents were always observed in the **IF** trees. The P/N and K/N mass ratios increased by fertigation and were near the optimal values of 0.1 and 0.5 respectively (Anon., 1990) in 1992. Phosphorus concentrations tended to increase in the order **N+S** < **C** < **I** < **IF**. From 1991 onwards, P in the **N+S** trees dropped below the treshold value, and Mg became almost limiting. The trees did not show any visual damage.

Within a growing season, needle element concentrations changed during shoot extension (Table 6). Nitrogen concentrations decreased during shoot growth and increased again in August and September, when growth had ceased. Mid summer values were lowest, and rather similar for all treatments, despite

Table 5. Element concentrations (% of dry weight) in current year needles before (1988) and during the treatment. Significant differences ($p<0.05$) between treatments are indicated by a different letter behind the mean (tested for the years 1990, 1991 and 1992). In the right column Dutch criteria for nutrient supply are given: L=low, N=normal, H=high (Anon., 1990).

Treatment	1988	1989	1990	1991	1992	
	N					
Control	2.16	1.95	1.96ab	1.92	1.60b	L:<1.4
Irrigation	2.32	2.00	1.78b	1.85	1.66b	N:1.4-1.8
Fertigation	2.19	1.92	1.83b	1.87	1.60b	H:>1.8
$(NH_4)_2SO_4$		2.08	2.09a	2.05	2.03a	
	P					
Control	0.16	0.13	0.16ab	0.14ab	0.11	L:<0.14
Irrigation	0.19	0.16	0.15ab	0.15a	0.14	N:0.14-0.17
Fertigation	0.20	0.18	0.18a	0.16a	0.15	H:>0.17
$(NH_4)_2SO_4$		0.14	0.13b	0.11b	0.11	
	K					
Control	0.53	0.67	0.61	0.56	0.57b	L:<0.5
Irrigation	0.70	0.63	0.60	0.63	0.61b	N:0.5-0.7
Fertigation	0.68	0.79	0.74	0.72	0.74a	H:>0.7
$(NH_4)_2SO_4$		0.65	0.55	0.55	0.53b	
	Ca					
Control	0.20	0.19	0.21	0.21	0.17	L:(0.2)
Irrigation	0.26	0.16	0.22	0.20	0.20	N:(≥0.2)
Fertigation	0.30	0.22	0.23	0.22	0.22	
$(NH_4)_2SO_4$		0.20	0.23	0.21	0.20	
	Mg					
Control	0.13	0.10	0.10	0.11	0.10	L:<0.07
Irrigation	0.09	0.09	0.09	0.09	0.09	N:0.07-0.1
Fertigation	0.14	0.09	0.10	0.10	0.10	H:>0.1
$(NH_4)_2SO_4$		0.09	0.09	0.08	0.08	

large differences in soil solution concentration. In early-summer P was highest in **IF** and lowest in **N+S**. In autumn K and Mg were low in **C** and **N+S** respectively. For **C** these data of three selected trees are in agreement with the data of the trees from the annual inventory (Table 5).

Table 6. Element concentrations in current year needles of three trees at three moments in 1990. Significant differences ($p<0.05$) between concentrations per sampling date are indicated by a different letter behind the mean.

Treatment	N	P	K	Ca	Mg
	June 6				
Control	2.19	0.20ab	0.68	0.12	0.10
Irrigation	2.06	0.21ab	0.69	0.10	0.10
Fertigation	2.14	0.23a	0.85	0.14	0.10
$(NH_4)_2SO_4$	2.03	0.17b	0.80	0.10	0.09
	July 27				
Control	1.39	0.10	0.56	0.12	0.06
Irrigation	1.56	0.14	0.57	0.13	0.07
Fertigation	1.40	0.11	0.60	0.14	0.06
$(NH_4)_2SO_4$	1.46	0.11	0.60	0.13	0.06
	October 10				
Control	1.82	0.11	0.54b	0.18	0.08
Irrigation	1.78#	0.15#	0.60ab#	0.22#	0.09#
Fertigation	1.67	0.15	0.72a	0.20	0.09
$(NH_4)_2SO_4$	2.09#	0.13#	0.55b#	0.23#	0.09#

analysis from annual inventory (Table 5).

Element fluxes in the soil

Ion fluxes in the soil system were calculated per soil water sampling period on basis of simulated water fluxes and soil solution composition. Only data of the year 1991 were used, in other years not enough replicated water samples of all soil layers could be collected due to soil drought. Calculated annual means were adjusted so as to obtain equal in- and outputs of Cl. This had little effect on the chemical fluxes (±10%), except in the **I** plot, where fluxes at 40 cm depth increased by 60% relative to those computed on the basis of estimated water fluxes. In the Figures 5a to 5d the throughfall input (litter input was omitted in the graph), the downward fluxes and the net annual uptake in biomass of the main elements except Na and Cl are shown. Uptake of NH_4 and NO_3 were assumed to be equal.

In the control plot NH_4 from deposition was fully depleted in the first 20 cm of soil (Fig. 5b), and the NO_3 efflux below the root zone was very small. The decrease of NH_4 flux along passage of the litter layer was balanced by a proton release and Al mobilization, probably due to nitrification and cation uptake by roots. The protons were buffered in the mineral soil by Al mobilization.

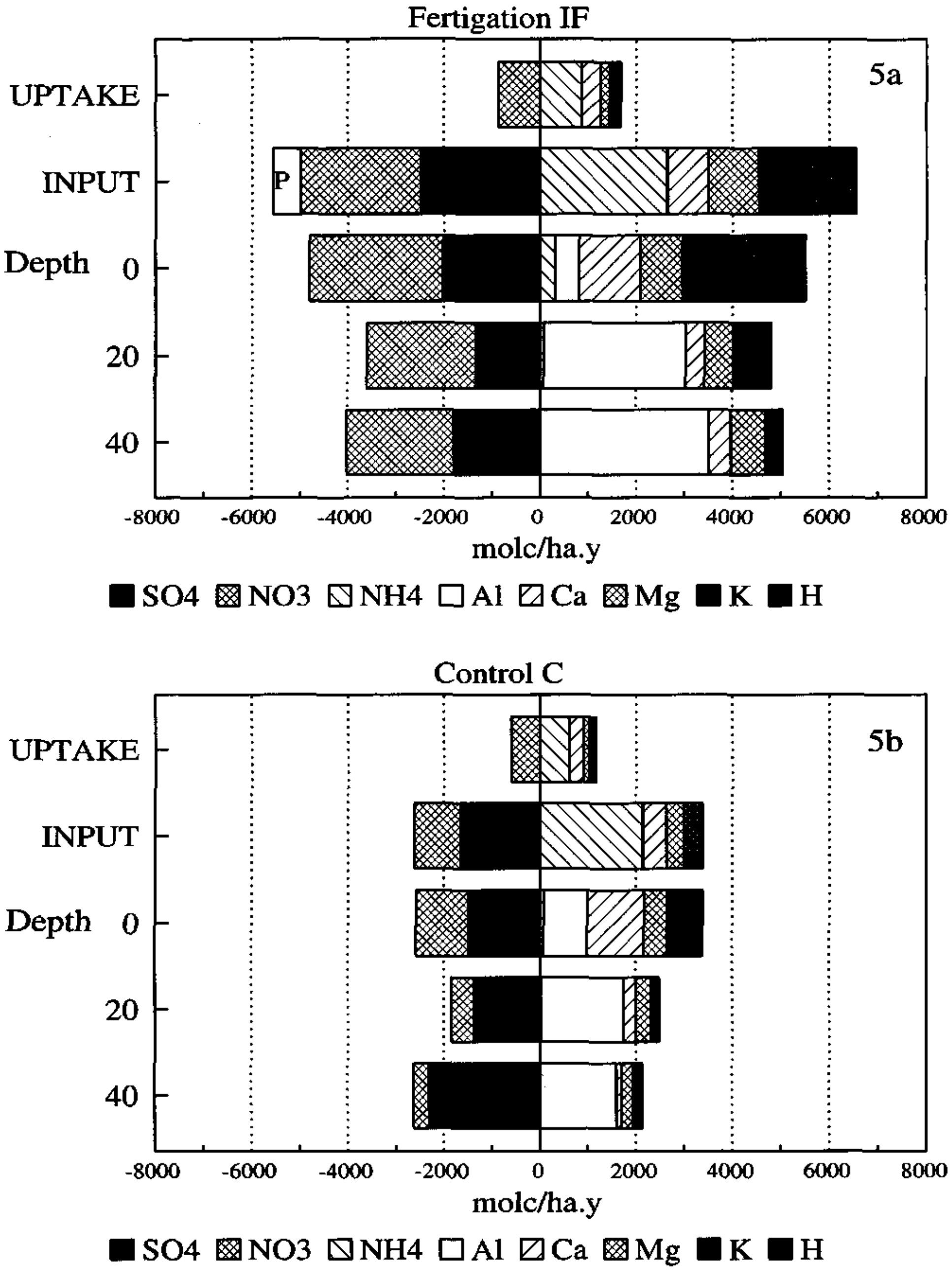

Figure 5. Fluxes (mol$_c$ ha^{-1} y^{-1}) of the most dominant ion species, except Na and Cl, in all plots in 1991. The applied P is indicated by a separate box.

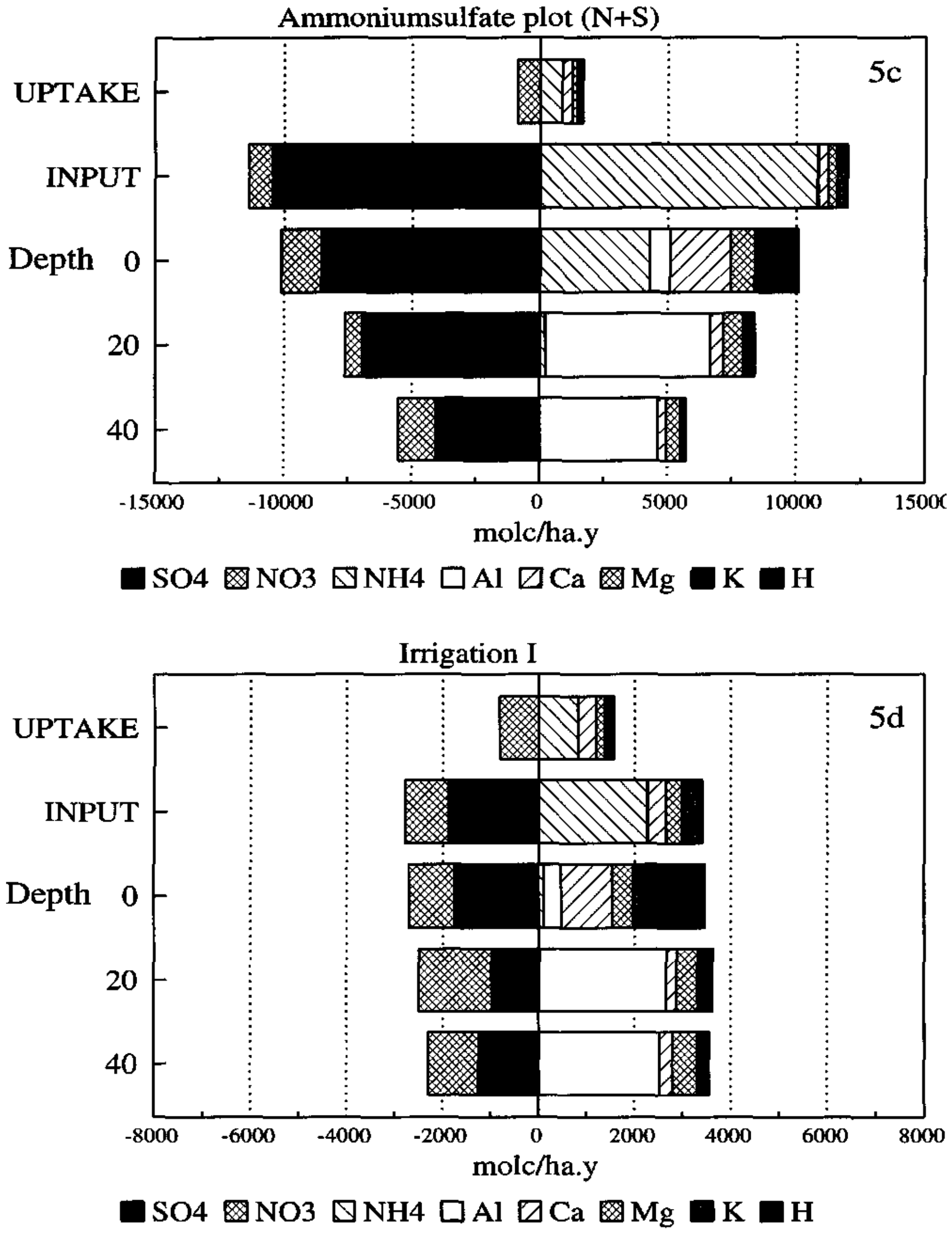

Figure 5 (continued). Uptake is net accumulation in biomass, input is throughfall+fertilizer. Anions at the left, cations at the right. Please note the difference in scale for Figure 5c.

In the irrigated **I** plot, the input of NH_4 equalled the output of Al (Fig. 5d). In the litter layer protons were produced and the flux of Ca and Mg increased, presumably by mineralization. In- and efflux of NO_3 in soil were almost similar, whereas SO_4 fluxes slightly decreased with depth. A small net loss of Mg was calculated.

In the **IF** plot 90 % of the input of NO_3 and SO_4 was leached (Fig. 5a). Aluminium leaching increased relative to the control, buffering the proton production by the extra nitrification from added NH_4, and exchange for applied base cations at the soil adsorption complex. Fertigation also increased the leaching of base cations, by an amount equivalent to 20% (K) to 50% (Mg) of added fertilizer amounts.

In the **N+S** treatment most of the added NH_4-N disappeared from the percolating water, presumably mostly by immobilization. About 15 kg N ha^{-1} extra NO_3 leached in 1991 relative to the control plot, which is 13% of added N. Almost half of the added S appeared to be retained in the soil in 1991 (Fig. 5c). Concentrations of dissolved SO_4 and NO_3 further increased in 1992 and SO_4 concentrations became almost equal at all depths. The mean SO_4/Cl ratios in 1992 decreased with depth from 10 (0 cm) to 6 (90 cm), indicating that the saturation of soil exchange sites for SO_4 was still proceeding.

Nutrient budget of soil and vegetation

Total deposition and fertilizer applications represent the nutrient inputs to the stands (Table 7). We assumed that canopy uptake of NH_4 could be neglected, as we did in estimating losses from and to the canopy. The balance of input, output and net uptake represent net nutrient additions to or removals from the soil, under the assumption that litterfall and mineralization fluxes of nutrients are equal, and that gaseous losses of N were negligible. The balance was negative for K, Mg and P in the **C**, **I** and **N+S** treatment. By contrast, part of the N input was retained in the soil under all treatments.

Enhanced growth of trees in both **I** and **IF** resulted in concomitant higher net nutrient uptake (Table 7). Uptake of K and P was slightly higher in **IF**. The increase in needle K concentrations also resulted in increases of the K flux with litter fall in the fertigated plot. The N uptake increased in the order C < I < IF < N+S. Most of the applied K, P and NH_4 was retained in the soil-vegetation system, and only a small part was incorporated in woody biomass. Net uptake in understorey vegetation was assumed negligible, but gross uptake was considerable, amounting annually to 18 kg N, 12 kg K and 0.8 kg P in the **I** plot and further increasing by fertigation with 4 kg N, 6 kg K and 2 kg P ha^{-1} approximately. In the **C** plot a much lower nutrient uptake was found, mainly by grasses. The cycling of the added nutrients with litterfall was not significantly enhanced by fertigation, except in case of K.

Table 7. Nutrient input to the soil, output at 90 cm depth, net nutrient uptake by trees, the balance, retained in (+) or extracted from (-) the soil (kg ha^{-1} y^{-1}) and litterfall (not measured in the $(NH_4)_2SO_4$ plot). All measured data are mean annual values for the period 1989-1992, except output, which was quantified only in 1991.

Treatment	N	P	K	Ca	Mg
	Input				
Control	43.2	0.2	2.8	11.1	4.3
Irrigation	43.2	0.2	2.8	11.1	4.3
Fertigation	72.5	13.2	62.8	18.1	12.8
$(NH_4)_2SO_4$	163.2	0.2	2.8	11.1	4.3
	Output				
Control	4.3	0.0	2.6	3.3	5.7
Irrigation	15.8	0.0	1.8	4.8	5.8
Fertigation	28.2	0.0	15.8	8.9	9.2
$(NH_4)_2SO_4$	20.4	0.0	1.5	6.7	6.9
	Net uptake				
Control	16.9	0.9	5.6	5.5	1.6
Irrigation	22.7	1.3	7.8	7.6	2.1
Fertigation	24.2	1.5	9.3	7.9	2.2
$(NH_4)_2SO_4$	26.2	1.2	7.9	7.7	2.1
	Balance (Input - Output - Net uptake)				
Control	22.0	-0.7	-5.4	2.3	-3.0
Irrigation	4.7	-1.2	-6.8	-1.3	-3.7
Fertigation	20.1	11.6	37.7	1.3	1.4
$(NH_4)_2SO_4$	116.6	-1.0	-6.6	-3.3	-4.7
	Litterfall				
Control	26.4	1.1	3.8	11.8	2.2
Irrigation	24.1	1.3	4.1	11.2	1.8
Fertigation	25.2	1.3	5.3	10.9	1.9

Soil acidification

In proportion to total anion losses, plots **C** and **N+S** had the highest leaching of SO_4, while **I** and **IF** showed predominantly NO_3 losses.

The net retention of base cations in biomass and soil was equivalent to a release of H^+ amounting to 0.4 (**C**), 0.1(**I**), 2.4 (**IF**) and 0.3 (**N+S**) kmol H^+ ha^{-1} y^{-1}. This retention increased the alkalinity of the soil+vegetation system, but was associated with a concomitant increase in the acidity of the soil solution, especially in the **IF** plot (*e.g.* Table 2). Enhanced growth caused extra root H excretion. The exchange of base cations resulted in an increased Al seepage of *ca.* 1 kmol_c in the **IF** relative to the **I** plot. The higher net uptake in biomass of K, Ca and Mg minus P in **IF** trees relative to **I** trees, produced negligible extra protons (0.06 kmol_c in Table 8). The rate of soil acidification, based on the proton budget (Table 8), was 2.1, 3.6, 2.6 and 11.5 kmol H^+ ha^{-1} y^{-1} for the **C**, **I**, **IF** and **N+S** plot respectively. The high value for **N+S** resulted for 60% from net retention of SO_4.

Table 8. Proton budgets of the four plots in the year 1991. Values are in kmol_c ha^{-1} y^{-1}. Lower boundaries were 90 cm for plots C and N+S and 40 cm depth for I and IF. C, control; I, irrigation; IF, fertigation; N+S, $(NH_4)_2SO_4$; ANC, Acid Neutralizing Capacity.

Plot	***H source***						
	external		internal			SUM	
	free H	Ntrans	Org.acids	Base cations biomass	Base cation precip.		
C	0.18	1.57	0.09	0.54	0	2.35	
I	0.18	2.19	0.12	0.74	0	3.19	
IF	0.18	2.33	0.12	0.80	1.55	4.98	
N+S	0.18	10.74	0.09	0.75	0	11.72	
	H sink						
	Weathering					SUM	ΔANC
	Anion precip.	Al dissol.	Base cation dissol.	H output			
C	0.28	1.70	0.16	0.01		2.15	2.14
I	0.41	2.50	0.65	0.06		3.61	3.55
IF	0.68	3.49	0	0.07		4.24	2.62
N+S	7.34	3.72	0.45	0.06		11.57	11.51

Discussion

That tree growth was enhanced by irrigation indicates that the Scots pine is water-limited at least in dry periods. Strong drought may decrease the vitality of Scots pine, and was suggested to be the main reason for its recent dieback (Innes, 1993). Water+nutrient applications improved the nutrient status of K and P relative to N, which is present in excessive amounts in the control, but this did not further promote growth over the effect of irrigation alone in three out of four years. In the last treatment year growth was enhanced in the fertigated plot, most probably because the K/N ratio had increased close to the optimal value of 0.5 (Anon., 1990; Ingestad, 1979). The rather poor response on K is in conflict with the positive growth response to K application observed in a neighbouring stand with an equal needle K status of 0.6% of dry matter (Arnold and Van Diest, 1993). However in that stand growth response was apparent only after two years. There, growth also responded much less (6%) than to our irrigation applications (30%), and the latter may have masked the effect of K. Equal but high growth rates between previously fertigated trees and others in 1993 were probably induced by the very wet soil conditions observed in summer, again hiding the effect of a difference in K status, which was probably still present. The benefits of the higher needle K status of fertigated trees may be manifest during periods of drought (Larsen, 1983) or extreme frost, thus primarily increasing vitality and only indirectly causing a growth advantage.

Fertigation had some negative side effects. Exchange of applied base cations, predominantly K, with solved Al and H persisted during all the years, causing a lower pH of the soil solution and high concentrations of dissolved Al. A similar exchange with Al and H was observed after application of K salts on acid soil (Matzner *et al.*, 1983; Tamm, 1991). Continued fertigation would finally result in lower Al concentrations, if a maximum adsorption of bases both by tree roots and soil could be reached in steady-state with fertilizer input. The loss of the exchanged acidity, currently present in soil solution, can be quite slow. This was shown by Rasmussen (pers. comm.), who observed that dissolution of Al started to decrease slowly two years after the start of a "clean rain" treatment that consisted of base cation applications with Cl as counter-ion. The elevated acidity in solution due to nutrient applications may have deleterious effects on roots.

The total estimated proton production of 2.35 kmol H^+ ha^{-1} y^{-1} is low relative to other Dutch forest stands (Heij and Schneider, 1991), and this is mainly a result of the rather low estimate of NO_3 leaching. The calculated values are particulary sensitive to spatial variability in the N transformations and differed by 0.6 in **I** to 1.7 kmol H^+ ha^{-1} y^{-1} in **IF** between replicates. Atmospheric loads and proton production might have been underestimated due to the omission of stemflow measurements, that can contribute by about 5% (Van Dobben *et al.*, 1992).

The initial positive growth response to extra NH_4 additions in the **N+S** treatment showed that Scots pine can assimilate considerable amounts of N for growth (Hoffmann *et al.*, 1990; Pérez-Soba and De Visser, 1994). Yet after two years growth started to decrease slightly and declined below control levels in the fifth treatment year. Keltjens and Van Loenen (1989) showed Scots pine to be very tolerant of Al, so growth decrease might not be related to the observed high Al concentrations (upto 70 mg L^{-1}). However Al could have induced P stress by formation of $AlPO_4$ precipitates in roots (Cumming *et al.*, 1986). This is corroborated by strongly reduced contents of P as well as P/N ratios in needles after two years of added extra $(NH_4)_2SO_4$. De Kam *et al.* (1991) hypothesized that a combination of high needle N contents and summer drought might stimulate the development of the fungus *Sphaeropsis sapinea*, but no apparent fungus attacks were observed.

Nutrient budget calculations showed the amount of fertilizer nutrients taken up in vegetation was very small, relative to the amounts retained in the soil, esp. for K and P in **IF** and N in **N+S**, and relative to seepage, esp. for N and Mg. Feger *et al.* (1991) also observed a small recovery (3%) of applied Mg in Norway spruce needles on sandy soils. Yet the utilization of fertilizer nutrients might take several years, as was demonstrated for K by Shepard and Mitchell (1990). Also retranslocation of nutrients from older tissue might still play a dominant role (>55%) in the nutrition of the new tissue (Lim and Cousens, 1986). Mid summer element concentrations of current-year needles were rather similar for all treatments, despite large differences in soil solution concentration of P and K. Extra K uptake in the **IF** trees probably took place after July. The high retention rates of P and K in plot **IF** can not be attributed to higher nutrient allocation to needle biomass, since stand density and canopy biomass decreased after a storm in 1990. Possibly some K leaching occurred due to preferential water flow, not recovered in the lysimeters.

The N budget and flux data suggest high N storage, predominantly in the litter layer. The N retention in plots **C** and **IF**, amounting to 90% of the N flux from current litter fall (Table 7), would be consistent with an aggradation of N in the litter layer by a slow rate of N mineralization (12% in two years), as observed by Tietema (1993) for Scots pine needle litter in a similar forest. A slow decomposition of pine litter is very probable, because the litter layer studied here contained *c.* 2 Mg N, suggesting a mean annual accumulation of 50 kg N ha^{-1} since sowing, 42 years ago. This is comparable to the N flux from litterfall, that fluctuated between 44 and 74 kg N ha^{-1} y^{-1} in the three years before the storm event. N accumulation was also found in other forests subjected to increased N loads (Arnold, 1993; Van Breemen *et al.*, 1986). Denitrification might also have contributed to the N depletion within the soil, especially in stagnant water layers in the thick O_h layer.

The increased NO_3 formation upon irrigation was probably caused by enhanced mineralization and nitrification due to higher soil water availability.

Although enhanced NO_3 leaching was mainly observed in the mineral soil (Fig. 5d), enhanced growth of the ground floor vegetation (Chapter 3) may have contributed to the increased mineralization by addition of more easily decomposable litter. The effect on cycling of the vegetation in plot I relative to plot C was shown for K by increased concentrations (Fig. 3) and fluxes (Fig. 5d) between forest floor and mineral soil. The resulting NO_3 leaching indicates that the forest ecosystem is not able to retain the extra NO_3 formed during warm and wet summers. Increased leaching of NO_3, accompanied by Al, was also observed in a similar irrigation treatment in a Douglas fir forest (Chapter 5). Since N supply to trees is already optimal in most Dutch forests, this extra NO_3 production increases soil acidification by NO_3 leaching and accompanying base cation loss (Van Breemen et al., 1983), and affects ground water quality.

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CHAPTER 5

Effects of irrigation and balanced fertilization on nutrient cycling in a Douglas fir stand

Plant and Soil (in press)

Effects of irrigation and balanced fertilization on nutrient cycling in a Douglas fir stand

Abstract: The effects of optimal supply of water and nutrients on tree growth and nutrient dynamics were studied in a 40 year old Douglas fir stand. Macro- and micronutrients were applied during four growing seasons and were in fixed, optimal proportions to the estimated annual uptake of N. The nutrients were dissolved in irrigation water, that was applied daily according to evaporative demand. Also irrigation without nutrients was carried out. The nutrients and water were also applied at a lower NH_4 load, realized by withdrawal of throughfall water by a roof construction.

Nitrogen nutrition was optimal under ambient conditions due to atmospheric N inputs of almost 50 kg ha^{-1} y^{-1}. Nutrition of P, K and in some years Ca seemed critical. In all four growing seasons water additions enhanced tree growth, with a mean increase of basal area growth of 40 %. Needle fall rates decreased by irrigation, but when balanced fertilization was included, needle fall seemed to increase over the years. Irrigation decreased the concentration of most elements in the soil solution and depressed K and N contents in Douglas fir needles. Mineralization and nitrate leaching were enhanced by moister soil conditions. Nutrient applications increased the needle concentrations of P and K considerably, but this did not result in a growth enhancement relative to irrigation. Fertilization also increased K and P in shedded needles. Only minor leaching losses were calculated. The recovery in trees of fertilizer K and P was maximally 15%. Input-output budgets suggested that P was strongly retained in the soil. Tree growth response to nutrient applications at reduced NH_4 loads was highest of all treatments. The decrease in NH_4 load depressed needle N concentrations and decreased nitrate leaching, but soil solution acidity was only slightly diminished.

Key words: acidification, leaching losses, nitrogen saturation, needlefall, *Pseudotsuga menziesii* (Mirb.) Franco, throughfall

Introduction

The last decades in NW Europe high loads of N and S, originating from intensive animal husbandry and fossile fuel burning, are present in atmospheric deposition. The widespread forest damage has frequently been related to the negative effects of atmospheric deposition on the soil chemical conditions. In some countries the increased NH_4 deposition has proved to be the major reason for increased soil acidification (Van Breemen *et al.*, 1982), nutrient imbalance

(Hüttl, 1990; Nihlgård, 1985) and vulnerability of trees to drought (Pérez-Soba and Van der Eerden, 1993) and pathogens (De Kam *et al*, 1991; Flückiger and Braun, 1992).

The nitrification of the external NH_4 input (Van Breemen *et al.*, 1982) as well as root uptake of NH_4 and concomitant H^+ excretion (*cf.* Smiley, 1974; Runge, 1983) are responsible for soil acidification. Therefore the damage of a too high NH_4 supply is intimately connected to the effect of soil acidification. In weekly-buffered soils the increase of free Al might hamper Ca and Mg uptake (Foy *et al.*, 1978), but also NH_4 limits uptake of other cations (Flaig and Mohr, 1992; Runge, 1983; Schulze and Freer-Smith, 1990). Aluminium, and not NH_4, decreases root vitality (Marschner, 1991) and causes P stress by formation of insoluble Al-phosphates in the soil and in the root cortex (Cumming *et al.*, 1986).

The increased N availability itself creates an unbalanced nutrient uptake in trees on soils that were poor in both N and other nutrients some decades ago (Van Breemen and Van Dijk, 1988). The strong affinity of trees for NH_4 (*cf.* Runge, 1983) might further aggravate this unbalance. If the unbalance would be the sole cause of tree dieback, judicious applications of the limiting nutrients (Evers and Hüttl, 1990) should have to improve nutrient status and growth. This might be helpful to Douglas fir in the Netherlands, that has been judged P limited as a result of increased N deposition. A recent monitoring found much lower P/N ratio in needles than 30 years ago (Mohren *et al.*, 1986). Whether this decrease caused the recent decrease in vitality of Douglas (Smits, 1992) is not yet clear.

The impact on growth of a restoration of the mineral balance has been adressed in this paper. The fate of the applied macronutrients in the mineral cycling of the stand has been studied. A balanced nutrient supply according to optimal nutrient ratios (Ingestad, 1979) was aimed at.

The first goal was to realize an improved status of all nutrients under the circumstances of an ambient N load. The aim was to test whether Douglas fir increases growth and needle retention if only the symptoms of unbalanced nutrition are eliminated by balanced fertilization.

The second goal was to decrease the NH_4 load in combination with optimal nutrient supply, to study the detrimental effects of excess NH_4 on cation uptake and acidification. An increased cation uptake relative to the first approach is expected when NH_4 antagonism plays a role in nutrient shortages.

The Douglas fir stand, selected for this experiment, had been examined on tree growth, air quality and hydrochemistry in the period 1986-1989 as a part of the Dutch Programme on Acidification Research (Evers *et al.*, 1991; Olsthoorn and Tiktak, 1991; see Heij and Schneider (1991) for further references). In the balanced fertilization experiment, all nutrients were applied continuously and according to tree demand. The treatments were combined with optimal water supply to optimize nutrient transport to tree roots and to determine the impact of water limitation on stand growth. The higher N availability can increase needle biomass (*cf.* Binkley and Reid, 1984; Linder and Axelsson, 1982) and the resulting higher transpiration demand might not be met by root uptake in dry periods. The magnitude of growth response on water applications might be indicative for this higher demand.

The response of the stand to the soil ameliorations was studied in terms of growth, needle retention, nutrient status and mineral cycling. Growth reduction can be related to the impact of stress (Landmann, 1988; Waring, 1985) and may thus give an indication of tree vitality.

Material and methods

The forest stand (1.2 ha) is located near Kootwijk (52°11'N, 5°46'E) in the central part of the Netherlands, and consists of even-aged Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), planted in 1953 as two year old seedlings. Stand density is 992 trees ha^{-1}. No understorey vegetation is present. The fine sandy soil is a Plaggic Dystrochrept (Soil Survey Staff, 1975) on eolian deposits. Chemical properties of the A_p horizon were: pH (H_2O) 3.8; pH (1M KCl) 3.1; organic carbon 3.1%; total N 0.1%; total P 255 mg kg^{-1} soil; extractable Al (1M KCl) 286 mg kg^{-1} soil; CEC (0.01M $BaCl_2$) 2.8 cmol(+) kg^{-1} soil, exchangeable cations (0.01 M $BaCl_2$): 0.10 Na, 0.20 Ca, 0.03 Mg, 0.06 K cmol(+) kg^{-1} soil.

Starting June 1989 four treatments (n=1), named C, I, IF and IF+R, were carried out for four years:
(C) control (1200 m^2); **(I)** irrigation (plot size 900 m^2) of 6 to 8 mm of demineralized water every second day during the growing season, based on model estimates (Tiktak and Bouten, 1992) of water demand and assumed optimal for tree growth at a pressure head of 0.01 MPa ; **(IF)** fertigation (plot size 900 m^2), that consisted of irrigation, as described in (2), and application of the following nutrients, required for growth at an estimated annual gross uptake of 120 kg N ha^{-1}: N 34 (as average, decreasing from 78, 39, 19 to 0 from 1989 to 1992 respectively, with the first years' supply = 78 kg N = gross uptake minus atmospheric deposition), P 36, K 60, Ca 4.8, Mg 6 kg ha^{-1} and micronutrients Mn 0.52, Fe 0.9, B 0.26, Zn and Cu 0.04 and Mo 0.008 kg ha^{-1}. The nutrients N, K, P, Na, Mo and B were given as NH_4NO_3, K_2HPO_4, Na_2MoO_4, H_3BO_3 respectively, the others as nitrate salts, and were dissolved in the irrigation water. Nutrient application rate was computer controlled and followed an addition curve during the growing season, as described by Ingestad (1988); **(IF+R)** Fertigation under a roof (plot size 100 m^2), in summer equal to

treatment IF, except that throughfall was withdrawn by a roof cover (100 m^2), placed two meters above the soil surface. In winter, the irrigation amounts were equal to the measured throughfall, and seasalts were added in amounts that corresponded to measured Cl and Na fluxes. Litter was collected from the roof each month and distributed over the soil evenly.

Precipitation (n=2) and throughfall (n=12) were collected in funnels and sampled every fortnight, starting June 1987. The soil solution was sampled every fortnight (1989-1990) or every four weeks (1991-1992), using ceramic lysimeter plates underneath the litter layer (n=4) at continuous suction (-0.05 MPa) or by ceramic cups (Soil Moisture Equipment) at discontinuous suction (-0.05 MPa) at 20 (n=10), 40 (n=4) and 90 (n=4) cm depth in all treatments. On all water samples pH and Ec was determined and were analysed for K and Na by flame emission, Ca and Mg by AAS, total Al, NH_4, H_2PO_4 by spectrophotometry, NO_3, SO_4, Cl by ion chromatography, total carbon (C_t) and soluble organic anions (SOA) by IR spectophotometry. The analytical procedures have been described by Velthorst (1993). Duplicate tensiometers were installed at the same depths as the ceramic cups and hydraulic heads were measured every fortnight.

Stem diameters at breast height (DBH in cm) were measured in all plots every winter in order to calculate diameter and basal area (BA) increment. Height measurements (H in m) were done each year on 50 - 100% of the trees in each treatment with an extendable pole. Stem volume increment (V in L) was calculated from the formula:

$$V = DBH^{1.90} * H^{0.81} * e^{-2.43} \qquad (1).$$

Branch, needle and root biomass were estimated from DBH using biometric data of Evers *et al.* (1991). The annual element uptake was estimated from growth increments of tree compartments and their chemical composition. Fine root biomass was not included in the estimate, because their turnover occurred within one year (Olsthoorn and Tiktak, 1991). Needle biomass increment was assumed to be 400 kg ha^{-1} kg^{-1} higher than average needle fall, according to calculations with the model FORGRO (*cf.* Mohren *et al.*, 1992) and irrespective of treatment. Branch increment was fixed at 2 Mg ha^{-1} y^{-1}, as was derived from Evers *et al.* (1991). In the last treatment year Leaf area index (LAI) was measured with a LICOR device in all plots. Litter fall was collected monthly from litter traps of 1 m^2 (n=6 except n=2 on the roof) in each treatment and dry weight and element content were determined.

Needles from different age-classes were sampled from ten trees from the 7th whorl in autumn each year. After the experiment twig and stemwood biomass in each plot was sampled (n=2). Plant samples were dried at 70°C for 48 hours, weighed and ground to pass a 0.5-mm sieve and then digested in a mixture of sulphuric and salicylic acid, H_2O_2 and selenium. In the digests total N and P were determined colorimetrically, K and Ca by atomic emission spectrometry and Mg by atomic absorption spectrometry (see Walinga *et al.*, 1989).

Water fluxes were calculated with a dynamic model for water transport in the unsaturated zone SWIF (Tiktak and Bouten, 1992), that was already validated for the site. The model is based on the Darcy flow equation and calculation of evapotranspiration with daily radiation and temperature data. Daily values of throughfall and interception were calculated from biweekly funnel samples and daily precipitation at a nearby weather station. A horizontally homogeneous water transport was assumed. The product of element concentration and water flux was used to estimate the downward element flux at each sampling depth.

Results

Soil solution composition

The soil solution chemistry only gradually changed during the experimental period. In winter '89/'90, seven months after start of applications, solute concentrations were similar in all plots under moist conditions. In Table 1 the mean soil solution concentrations before and during the experiment are shown. Concentrations for Cl and Na slightly increased in the control plot between the two periods, and points at a somewhat drier soil after 1989. In the irrigation plot the concentrations of mobile ions K, Na, SO_4 and Cl at 20 cm depth were lowered. The NO_3 and Al concentrations seemed to have increased in the first 40 cm soil and showed similar seasonal variations (correlation coefficient of 0.90 with R^2 80.66). The NH_4 concentrations at irrigation seemed to decrease in the topsoil relative to the control plot, but there is a lack of evidence because NH_4 data were most stochastic of all substances. Below a depth of 20 cm NH_4 rarely occurred.

In the soil of the fertigation treatment without roof (**IF**), a strong increase in K and P concentration was observed in all summers in the litter percolate. At 20 cm depth in the first two treatment seasons short peaks of K were observed (Fig. 1). From 1991 onwards K and P concentrations at 20 cm depth were continuously higher than in the untreated soil. Fertigation, both with and without roof cover, decreased the concentrations of Cl, Na and SO_4 similarly to the irrigated plot. The mean Al and NO_3 concentrations were slightly higher than in the irrigated plot. In most summers strongly elevated Al concentrations were found (Fig. 2) and high amounts of NO_3 were present also in deeper soil layers (Fig. 3). In the growing season of 1992 no NH_4NO_3 was applied and soil solution concentrations of Al and NO_3 at 20 cm depth were not elevated.

In winter Al (Fig. 2) and NO_3 soil solution concentrations in the roofed plot (**IF+R**) always strongly decreased. In summer NO_3 concentrations were higher than in the control, and this led to the rather high three-year average (Table 1).

Table 1. Mean soil solution concentrations (mmol$_c$ m^{-3}) and pH from 1-1-1989 to 15-5-1989 (control) and from 1-1-1990 to 15-11-1992 at 20 cm depth. Coefficient of variation = σ/μ_n; *n*: sample size; C, control; I, irrigation; IF, fertigation; R, roof.

	Mean					Coefficient of variation				
	1989	1990-1992				1989	1990-1992			
Element	C	C	I	IF	IF+R	C	C	I	IF	IF+R
pH	3.54	3.46	3.67	3.56	3.67	0.06	0.12	0.04	0.05	0.04
Al^{3+}	1260	1174	1363	1504	971	0.12	0.35	0.52	0.58	0.38
Ca^{2+}	184	149	185	165	167	0.41	0.55	0.67	0.60	0.23
Cl^-	642	822	396	384	217	0.05	0.35	0.37	0.35	0.05
H^+	286	343	215	275	212	0.40	0.61	0.26	0.33	0.24
K^+	17	49	5	59	23	0.69	0.53	0.95	0.84	0.47
Mg^{2+}	198	182	115	163	141	0.28	0.56	0.43	0.72	0.11
Na^+	433	604	312	300	222	0.12	0.05	0.54	0.48	0.10
NH_4^+	144	153	22	68	49	1.16	1.20	1.08	1.89	0.05
NO_3^-	817	873	1273	1585	1114	0.15	0.75	0.55	0.82	0.23
$H_2PO_4^-$	3.1	3.0	1.9	7.4	20	0.75	0.88	0.98	1.43	0.88
SO_4^{2-}	1009	944	455	442	257	0.22	0.26	0.48	0.34	0.03
Al/Ca	6.0	7.0	11.0	13.5	4.0	0.56	0.28	0.41	0.62	0.86
K/NH_4^+	2.0	0.4	0.6	5.6	2.5	1.06	-	1.04	1.25	0.16
Mg/NH_4^+	19.6	14.5	26.3	11.0	3.2	0.80	-	0.80	1.80	0.91
n	3	3	10	10	4					

The mean Ca and Mg concentrations did not differ from the control. A strong dilution of K concentration in winter (Fig. 1) depressed the three-year mean, despite relatively high concentrations in summer as a result of the nutrient applications. The P concentrations were highly variable between suction cups, but were high on average (Fig. 1).

The Al/Ca ratios tended to increase in irrigated and fertigated plot and to decrease under the roof, although the three-year mean Al and Ca concentrations were not significantly different between plots. The mean K/NH_4 ratios increased with a factor 5 to 10 at 20 cm in the fertigated soils. Mg/NH_4 ratios were increased in all manipulated soils by a decrease in NH_4 concentration. The average pH (Table 1) seemed higher in the order control < fertigation <

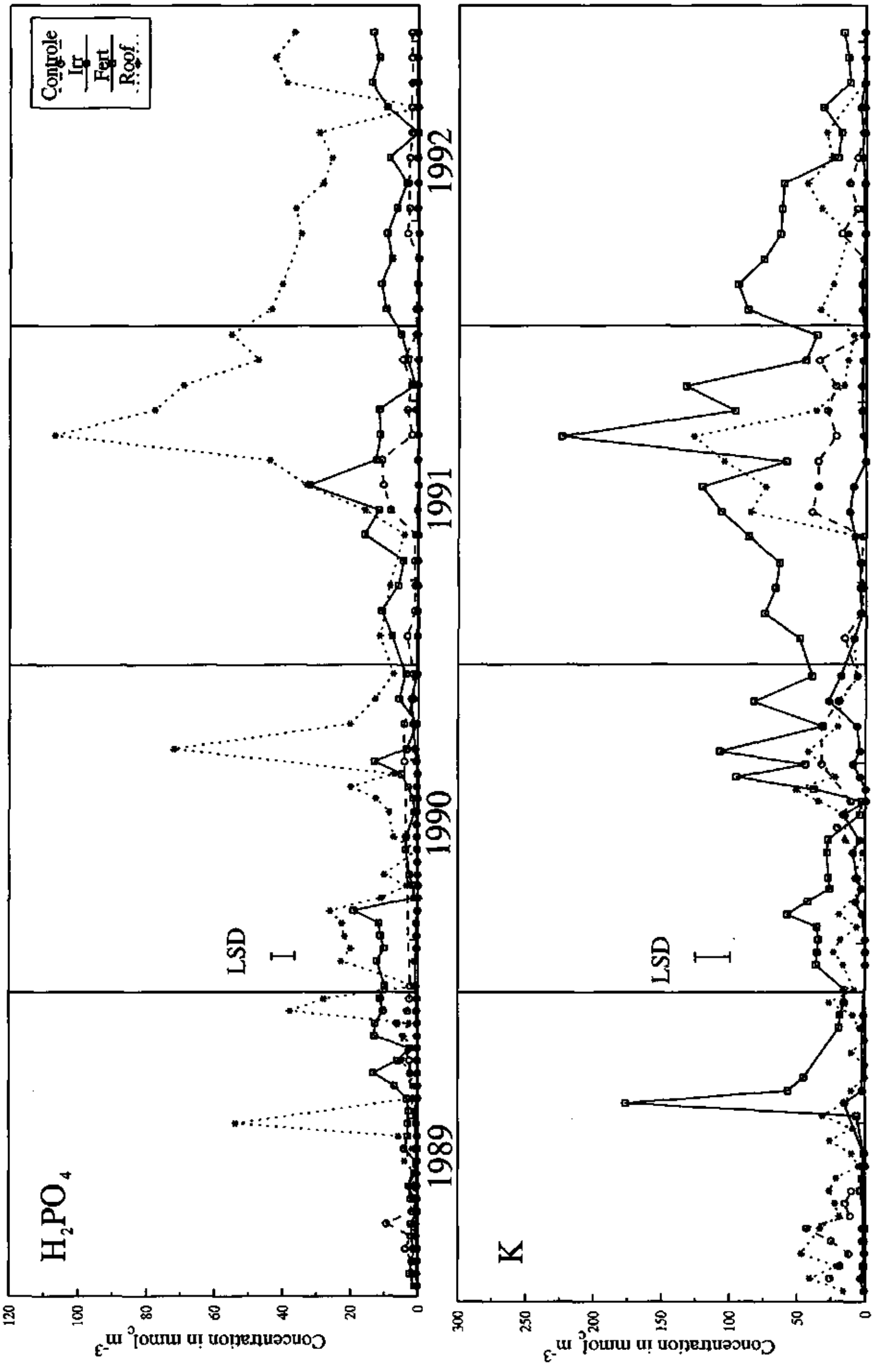

Fig. 1. H_2PO_4 and K concentrations in the soil solution at 20 cm depth in all treatments , that were started in June 1989

irrigation < roof plot.

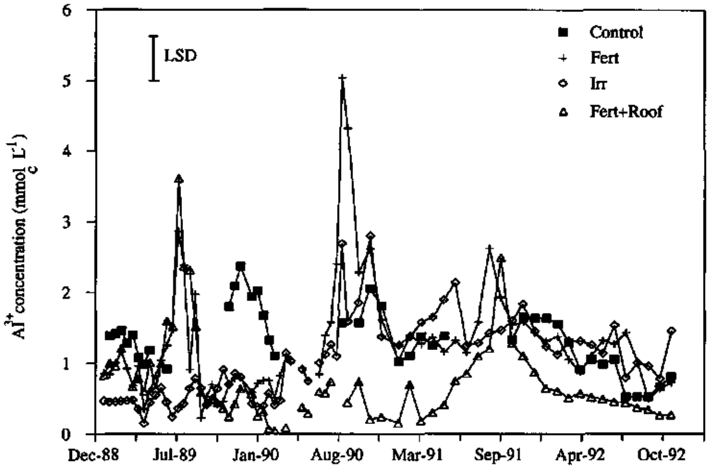

Figure 2. NO_3/Cl ratios in the soil solution at 90 cm depth in three plots.

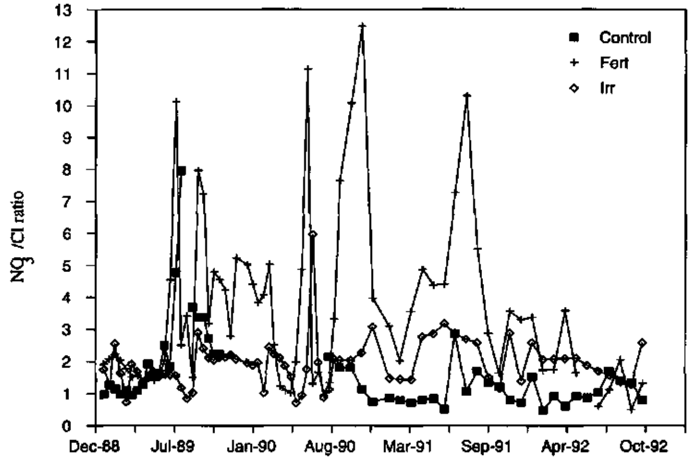

Figure 3. Aluminium concentrations (mmol$_c$ L^{-1}) in the soil solution at 20 cm depth in all treatments.

Needle chemical composition

Chemical composition of current year needles of Douglas fir did not show any severe nutrient deficiency in the ambient situation (Table 2). Potassium, P and Ca supply were near-deficient according to Dutch standards (Anon., 1990), whereas N concentrations ranged from optimal to supra-optimal. The needle

Table 2. Element concentrations (% of dry weight) and element ratios of P/N and K/N in current year needles before (1988) and during the treatment. Significant differences between plots within a column are indicated by a different letter behind the mean (only tested for the years 1991 and 1992, when samples were not pooled). In the right column Dutch criteria for nutrient supply: L=low; N=normal; H=high (Anon., 1990). n.m., not measured.

Treatment	1988	1989	1990	1991	1992	
	N					
Control	1.75	1.86	1.99	1.74bc	1.90a	L:<1.4
Irrigation	1.87	1.70	1.85	1.59c	1.62b	N:1.4-1.8
Fertigation	1.92	2.04	1.85	1.79ab	1.91a	H:>1.8
Fert+Roof	n.m.	1.95	1.87	1.57bc	1.70b	
	P					
Control	0.13	0.13	0.13	0.12b	0.14b	L:<0.14
Irrigation	0.15	0.13	0.14	0.12b	0.15b	N:0.14-0.22
Fertigation	0.15	0.17	0.17	0.17a	0.21a	H:>0.22
Fert+Roof	n.m.	0.15	0.16	0.14b	0.19a	
	K					
Control	0.55	0.66	0.64	0.64c	0.69c	L:<0.6
Irrigation	0.65	0.57	0.60	0.50d	0.59d	N:0.6-0.8
Fertigation	0.75	0.96	0.85	0.89a	0.98a	H:>0.8
Fert+Roof	n.m.	0.65	0.75	0.69b	0.82b	
	Ca					
Control	0.17	0.13	0.22	0.16	0.14b	L:(<0.20)
Irrigation	0.23	0.22	0.26	0.17	0.18ab	N:-
Fertigation	0.19	0.20	0.19	0.15	0.19a	H:>0.20
Fert+Roof	n.m.	0.16	0.21	0.15	0.15ab	
	Mg					
Control	0.10	0.11	0.16	0.13	0.13	L:<0.045
Irrigation	0.12	0.13	0.14	0.12	0.13	N:0.07-0.10
Fertigation	0.15	0.15	0.16	0.12	0.14	H:>0.10
Fert+Roof	n.m.	0.14	0.15	0.12	0.11	
	P/N*100 (%)					
Control	7.4	7.0	6.5	6.9b	7.4b	L:<5
Irrigation	8.0	7.6	7.6	7.5b	9.3ab	N:5-10
Fertigation	7.8	8.3	9.2	9.5a	11.0a	H:10-14
Fert+Roof		7.7	8.6	8.9a	11.2a	
	K/N*100 (%)					
Control	31.4	35.5	32.2	36.8b	36.3b	L<25
Irrigation	34.8	33.5	32.4	31.4b	36.4b	N:25-50
Fertigation	39.1	47.1	45.9	49.7a	51.3a	H:50-100
Fert+Roof		33.3	40.1	43.9ab	48.2a	

concentrations of Ca in the irrigated trees were never deficient and were continuously the highest of all trees during the examined period. The higher Ca contents coincided with higher Ca soil solution concentrations (Table 1) in the period 1990-1992. In the fertigated plot needle N concentration started rather high and even increased in the first treatment year. During the following years however N concentrations were comparable to control values.

Needle concentrations of K and P were higher in the fertigated plot relative to previous years' values and higher than in needles of the control from the first treatment season onwards (Table 2). The ratio of K/N also increased in the first treatment year and reached an optimal value (0.5, see Ingestad, 1979) from 1991 onwards, while the same happened to the P/N ratio, lagging one year. The K and P needle concentrations in the roofed plot increased two years later than in those of the fertigated plot. Needle N concentrations decreased during the treatment years in the irrigated and roofed plot and were significantly lower in 1991 and 1992. Mg supply was always sufficient and no treatment response was found.

Tree growth response

Basal area growth over the four-year experimental period was equal in the irrigated and the fertigated plot and higher than in the control (Table 3). Growth seemed to have increased more in irrigated than in fertigated trees relative to growth before treatment (1988). The highest growth figures were observed in the roofed plot. There was a considerable annual variation in growth response, with a remarkable growth dips of the fertigated trees in 1990 and 1991. Height growth showed the same pattern, with high values in 1989 and low growth in 1991 for all trees. Strong needle shedding was observed in 1989 in the control plot (Table 4). Needle cast was higher in both fertilized plots in 1992. In the irrigation plot needle fall was lower than in the other plots. In summer 1992 the leaf area index (LAI) was ca. 6.48 with no differences between plots. The bole volume increment was higher in the order irrigation, fertigation, to fertigation+-roof plot (Table 5).

Nutrient allocation

Reallocation from dying needles in the control was 35 (K) to 45 % (N and P), but was negligible for Ca and Mg. In the fertigated trees reallocation of K and P was less strong than in control trees, as can be seen from higher N, P and K fluxes at similar rates of litter fall (see Table 5). More Ca was returned with litter in the roofed plot. Total estimated nutrient uptake in aboveground biomass and coarse roots, was highest in the two fertilized plots (Table 5). In the roofed plot this was caused by higher growth rates, while in the fertigated trees the increased tissue concentrations had a bigger impact on the uptake estimate. Calculated total uptake also included the replenishment of canopy leaching losses, amounting annually to 13.7 kg K and 0.7 kg Mg ha^{-1}, which were calculated from total deposition and NH_4 absorption in canopy (see Chapter 4 of this thesis for details).

Table 3. Basal area (BA in m^2 ha^{-1}) before and after the experimental period, annual and mean BA growth (m^2 ha^{-1} y^{-1}) and height (H) growth (m y^{-1}, average of '89-'91) during the treatments. Significant differences (p<0.05) between treatments in each year are indicated by a different letter behind the mean.

	Control	Irrigation	Fertigation	Fert+Roof
BA 1987	30.07	31.60	27.82	32.18
BA 1992	38.62	43.80	39.88	47.19
BA growth				
1988	1.87b	1.82b	1.97b	2.41a
1989	1.66d	2.48c	3.37b	4.46a
1990	1.87b	2.31a	1.74b	2.80a
1991	1.20bc	2.28a	1.43b	1.83b
1992	2.12c	2.69bc	3.10b	4.35a
mean	1.71c	2.44b	2.41b	3.37a
% of 1988	91	134	122	140
Height '91	19.7	18.4	19.0	19.9
H growth	0.38b	0.81a	0.61a	0.68a

Table 4. Annual needle fall (g m^{-2} y^{-1}) in the treatments. Significant differences (p<0.05) between columns are denoted by a different letter behind the mean. n.m., not measured.

year	Control	Irrigation	Fertigation	Fert+Roof
1989	344	228	229	n.m.
1990	243b	266b	264b	295a
1991	363a	296b	325ab	353ab
1992	165b	157b	248a	230a
mean '90-'92	257ab	240b	279ab	293a

Table 5. Mean annual volume growth (m^3 ha^{-1} y^{-1}) and litter fall (Mg ha^{-1} y^{-1}); estimated annual nutrient uptake (total minus fine roots) from soil and element fluxes with litter fall (kg ha^{-1} y^{-1}).

Treatment	Biomass	N	P	K	Ca	Mg
	Growth		Uptake			
	m^3 ha^{-1} y^{-1}		kg ha^{-1} y^{-1}			
Control	21.6 ± 6.1	59.4	4.7	30.3	21.0	7.9
Irrigation	25.8 ± 1.2	60.3	5.4	31.5	20.5	6.9
Fertigation	27.2 ± 4.0	78.1	6.8	41.3	23.1	7.5
Fert+Roof	38.8 ± 2.1	83.1	6.6	40.8	27.3	8.5
	Litter fall		Element flux			
	Mg ha^{-1} y^{-1}		kg ha^{-1} y^{-1}			
Control	3.24 ± 0.28	37.3	2.5	5.9	8.6	4.7
Irrigation	2.75 ± 0.43	32.1	2.4	4.5	9.2	2.8
Fertigation	3.11 ± 0.32	42.4	2.9	7.5	9.9	3.5
Fert+Roof	3.29 ± 0.11	38.9	2.1	5.8	11.2	3.6

Hydrochemical budgets

In 1989 and 1991 precipitation was appreciably below the 30 year average (=853 mm). In the corresponding growing seasons exceptional drought occurred and transpiration was reduced strongly for a number of weeks. The downward fluxes were rather low in 1989 and 1991. In 1990 evaporative demand was low due to a rather cold growing season. In 1992 long periods with high temperatures and solar radiation levels resulted in relatively high transpiration rates (Chapter 8). For autumn that year high downward fluxes were calculated due to high precipitation rates. The calculated four-year-mean seepage of water at 90 cm depth shows similar values for plots I and IF (Table 6). In the roofed plot effluxes were comparable to control values due to the exclusion of big showers in summer by the roof.

The calculated chemical fluxes per sampling depth were corrected on an annual basis with the Cl balance, assuming equal input and output fluxes of Cl in every soil stratum. Elemental fluxes at 90 cm depth had to be changed by -30% to +100% in irrigated and fertigated plot, respectively, to obtain a balanced Cl budget. This method generated rather constant fluxes for Na as well as for SO_4, th't probably resemble Cl in its rather inert behaviour in soil. The annual variation in fluxes was rather large, *e.g.* 78% and 64% for NO_3 and Al fluxes respectively, at 90 cm depth in the fertigation plot. The resulting four-year mean

Table 6. Input/output budget for the applied nutrients in all plots (kg ha^{-1} y^{-1}) in the years 1989-1992. Water input equals throughfall+irrigation; deposition is bulk wet+dry. Standard deviations in balance term were based on variation in output fluxes.

Treatment	H_2O mm	N	P	K	Ca	Mg	Al
(compounds)			**Input**				
Control (deposition)	476	48.8#	0.3	1.1	4.4	2.7	0.0
Irrigation (deposition)	670	48.8#	0.3	1.1	4.4	2.7	0.0
Fertigation (fert.+depo.)	664	83.0#	36.3	61.1	9.2	8.7	0.0
Fert+Roof (fertilizer)	553	42.2#	36.0	60.0	4.8	6.0	0.0
			Output				
Control	130	17.2	0.0	0.8	5.8	2.3	17.8
Irrigation	218	31.4	0.0	0.4	10.1	3.3	33.0
Fertigation	210	54.8	0.0	2.2	5.8	5.9	38.4
Fert+Roof	145	13.0	0.1	0.9	1.6	2.0	17.8
			Input - output				
Control		31.6	0.3	0.35	-1.3	0.4	
Irrigation		17.4	0.3	0.68	-5.6	-0.6	
Fertigation		28.2	36.3	58.9	3.5	2.8	
Fert+Roof		29.2	35.9	59.1	3.2	4.1	
			Wood accumulation				
Control		14.5	0.7	5.4	5.5	0.8	
Irrigation		16.9	0.8	6.3	6.4	1.0	
Fertigation		17.8	0.9	6.6	6.8	1.0	
Fert+Roof		24.7	1.2	9.2	9.4	1.4	

Balance	N	P	K	Ca	Mg
Control	17.1±8.5	-0.5±0.2	-5.1±1.9	-6.8±2.1	-0.9±0.5
Irrigation	0.5±8.9	-0.6±0.1	-5.6±0.4	-12.0±1.8	-1.6±0.7
Fertigation	10.4±4.8	35.4±0.2	52.3±1.6	- 3.3±2.2	1.8±0.6
Fert+Roof	4.5±6.7	34.7±0.1	50.0±0.5	- 6.2±1.0	2.7±0.3

#: a direct canopy uptake of 8 kg N was assumed.

output fluxes are presented in a balance sheet (Table 6). High amounts of N were estimated to leave the rooting zone. The NH_4NO_3 applied with fertigation was totally lost again by leaching. Some K and Mg, which may originate from fertigation, were leached as well.

The balance was used to calculate the retention of nutrient inputs, if we assume: retention = (input) - (output) - (wood accumulation) (2). It was also assumed that litterfall and mineralization are in balance. The retention of nutrients, apart from the fraction stored in wood, can be located in the soil as well as in the aggrading canopy, but this was not quantified further. The coefficient of variation is calculated from standard errors in the output estimate. In the irrigation plot at some soil spots a negative retention was calculated and the mean value suggests a risk of net loss of N from the soil. About 30 kg N ha^{-1} y^{-1} seemed to be retained in the other plots, and half of this N was stored in wood. A considerable part of the applied P and K was retained, since these elements were not traced back in net uptake or leaching. These nutrients could have been partially stored in the crown, since the uptake estimate (Table 5) shows an increase of about 3 kg P and 15 kg K ha^{-1} y^{-1} in the fertigated trees. The negative input/output balance for the base cations in control and irrigation plot indicates that part of the cation supply was derived from weathering and net mineralization. However, a positive balance was estimated for Mg in both fertilized plots.

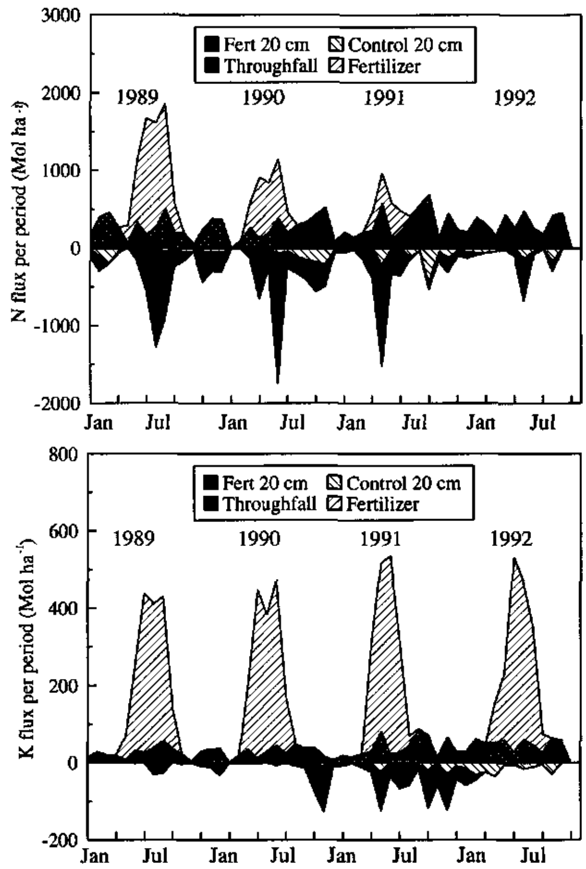

Figure 4. Input of N and K with throughfall and fertilization and output at 20 cm depth in control and fertigation (IF) treatment in kg ha^{-1} per 28 days.

The temporal pattern of nitrate leaching at 20 cm depth, calculated without Cl-correction, showed a clear correspondance with application rate (Fig. 4). The seepage of NO_3 at 90 cm can be demonstrated by the figures of the NO_3/Cl ratio

(Fig. 3), that points at a much higher NO_3 leaching in the fertigation plot than in the control. Most of the applied K seemed to be depleted in the first 20 cm of soil, according to the computed leaching at that depth (Fig. 4).

Net proton production over the experimental period was calculated from the input-output estimates of H, NH_4, NO_3 and SO_4 (see also Van Breemen *et al.*, 1983). In the fertigated plot the modest increase in NH_4 input and the high NO_3 leaching losses resulted in the highest proton production (4.3 kmol H^+ ha^{-1} y^{-1}) of all plots. NO_3 leaching was increased in the irrigation plot and no SO_4 was retained, giving a proton production of 3.4 kmol H^+ ha^{-1} y^{-1}, against 1.8 kmol H^+ in the control plot due to lower outputs of NO_3 and SO_4. Under the roof the proton production decreased relative to the control plot to 1.2 kmol by an increased retention of NO_3, added with Ca and Mg applications and released from mineralization. Yet the four-year mean SO_4 leaching in this plot was similar to control values (1.2 $kmol_c$ ha^{-1} y^{-1}), as was the efflux of Al (17.8 kg ha^{-1} y^{-1}, see Table 6). Most protons were buffered by Al dissolution, although a significant loss of Ca accompanied the NO_3 leaching from the irrigated soil.

Discussion

At the studied site growth of Douglas fir was water-limited in the examined period. Irrigation increased basal area growth by 34% relative to the year before treatment and 40% relative to the control. Water application depressed needle fall, especially in dry years (see also Chapter 3). The same water limitations were reported by Olsthoorn and Tiktak (1991), who observed a strongly negative impact of drought on growth of stems and fine roots in the same stand in 1989. The same authors suggested that probably a higher shoot/root ratio is nowadays present relative to the period before high atmospheric N loads, and this may have increased the water demand and water uptake per unit root length. Consequently, this may show up a stronger response on irrigation. Although needle biomass (see Evers *et al.*, 1991) is moderate, considering stand age (Keyes and Grier, 1981) root biomass indeed seems low (Chapter 3).

Nutrient applications, mainly K and P, did not further enhance diameter growth in addition to irrigation, yet more K and P were taken up in needles. At the site, needle status of P, K and Ca varied annually between deficient and sufficient, but the ratios of K and P to N were wide due to high N concentrations (Anon., 1990; Hüttl, 1990). Nutrient applications improved the nutritional balance of the trees with respect to K/N and P/N ratios. According to K/N and K concentrations the trees may have increased their resistance to drought and frost (Larsen, 1983). This can, in the long run, result in a higher growth, if the stresses would repeatedly occur. The lack of a short-term growth response may point at the rather modest character of the nutrient limitations in the stand. In other Dutch Douglas fir stands on sandy soil positive growth responses to P applications were found, but there P/N ratios were down to 0.05 (Van den Burg, 1991). On the long term the applied nutrients, now mostly retained in the soil, may become available for tree uptake and cycling, as was found eg. for K (Shepard and Mitchell, 1990).

Nitrogen that was applied in addition to the ambient N loads, was leached within half a year. Extra NO_3 leaching was also observed in the irrigation plot, probably by an enhancement of mineralization at moister soil conditions. A decrease in N loads of approximately 7 kg N ha^{-1} y^{-1} in the roofed plot, seemed to result in a reduction in nitrate loss proportional to the input reduction. The response to these three manipulations indicates that the ecosystem was N saturated (Schulze *et al.*, 1990; Van Breemen and Van Dijk, 1988). A further decrease of N input, now almost 50 kg N ha^{-1} y^{-1} including gaseous uptake, to approximately 30 kg N ha^{-1} y^{-1}, *i.e.* the calculated net retention, would probably stop N loss from this stand, assuming denitrification was negligible in this well-drained soil. Under the roof the experimental lowering of NH_4 input and NH_4/NO_3 ratio to the soil decreased acid loads and proton production, but H and Al soil solution concentrations only slightly decreased in the first 40 cm soil and the mean Al and SO_4 output were not decreased relative to the control as well. This might be attributed to the observed stronger tree growth and concomitantly increased uptake of applied base cations, relative to their counter ion (mostly NO_3). Also mineralization and subsequent NO_3 production, and thus soil acidification, might have increased due to the moister conditions, as was observed at irrigation solely. Also the applied base cations might have exchanged some H and Al, increasing base saturation of the soil but temporarily increasing soil solution acidity, as was found at other nutrient applications in forest (Chapter 4) and pot trial (Chapter 6).

The decrease in NH_4 input had decreased needle N concentrations, yet N uptake still seemed high due to the high demand for aboveground growth. Higher gaseous uptake of NH_x may have been involved, since a higher stomatal conductance for water and, consequently, for gases (Mohren *et al.*, 1992) can be expected at optimal water supply. Yet LAI and thus exposure surface to gases was not increased, which was found to be proportional to gas uptake (Whitehead and Lockyer, 1987). The unchanged needle concentrations of Ca and Mg in the roofed plot make it questionable, whether the growth enhancement is an effect of a decrease in competition for uptake between NH_4 and base cations. However, the growth rates give strong, yet indirect evidence for the improved soil conditions. In the roof plot the calculated growth rates actually resemble those of potential primary production, *ie.* 25.1 Mg ha^{-1} y^{-1} or 35 m^3 ha^{-1} y^{-1} in 1989 according to model calculations on carbon assimilation (Mohren *et al.*, 1992).

The figures on drainage fluxes of elements should be viewed with caution, since the estimate is derived from the mean monthly or fortnightly water flux, that does not deal with high local infiltration rates and preferential pathways. The computed mean leaching may hide a considerable spatial variation (Dagan and Bresler, 1983). Especially for the applied K, the soil retention was extraordinary high and some locally high leaching rates must have occurred without notice.

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CHAPTER 6

Growth and nutrient uptake of Douglas fir seedlings at different rates of ammonium supply, with or without additional nitrate and other nutrients

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Co-author: W.G. Keltjens

Growth and nutrient uptake of Douglas fir seedlings at different rates of ammonium supply, with or without additional nitrate and other nutrients

Abstract: Two pot experiments were conducted to study the effects of soil acidification and excess ammonium on root and shoot development of juvenile Douglas fir on an acid sandy forest soil. Experiment I included a control treatment (without fertilizer application) and different supply rates of NH_4. Application of other nutrients to the NH_4-fertilized pots was constant, while at one supply level the added N included 50% nitrate in order to study the effect of the N form. High supply rates of ammonium suppressed root length growth, but did not affect shoot growth during one season of application. Root and stem growth was stronger with a mixture of ammonium and nitrate than with pure ammonium as N source. In the second experiment the effect of balanced fertilization, additional to nitrogen, was studied at low and high NH_4-N supply during a two-year period. In the second year bud break was retarded and shoot growth depressed at high levels of ammonium supply. In August of the second treatment year nearly all trees died that had received a total NH4-N dose of 230 kg ha^{-1}. Addition of base cations and P to the ammonium application raised P and K needle concentrations, but could not prevent adverse effects of NH_4, and even increased acidification of the soil. In both pot experiments the presence of a litter layer tended to increase tree growth, and alleviated adverse effects of ammonium in soil and needles. A corresponding fertilizer application in a mature Douglas fir stand on the same soil improved the nutrition of P and K as well.

Keywords: balanced fertilization, litter layer, needle contents, nitrogen form, *Pseudotsuga menziesii*, root growth, soil acidification, soil solution composition

Introduction

The nutritional balance in Dutch forest ecosystems has been seriously altered by high rates of ammonium deposition, resulting mainly from intensive husbandry. However, the questions how excess NH_4 affects tree vitality and to what extent excess ammonium is responsible for tree damage are difficult to answer. Nitrification of ammonium in the soil leads to increased soil acidification (Van Breemen *et al.*, 1982), dissolvement of Al and Mn and leaching of base cations. High concentrations of H and Al in soil solution hamper root length growth and cause a thickening of roots expressed by a decreased specific root length

(Marschner, 1991; Olsthoorn *et al.*, 1991). In addition to soil acidification, ammonium may cause other damaging effects on plants. This may either be due to an excess of available nitrogen relative to the other nutrients ("imbalanced nutrition", Aronsson, 1985; Ingestad, 1979), or to rhizosphere acidification and indirect root damage (Marschner, 1991). Imbalanced nutrition should be equal with excess ammonium and nitrate N, but rhizosphere acidification should be restricted to NH_4 uptake (Gijsman, 1990).

In order to specify the effects of an increasing load of ammonium on soil characteristics and on growth and nutrient uptake of Douglas fir, two pot experiments have been conducted. In these experiments known amounts of NH_4 have been added to the pots and its effects on soil and plant were recorded. Relevant factors that have been studied were:

- the addition rate of ammonium;
- the partial replacement of ammonium by nitrate;
- the possible amelioration of the nutritional balance by additional K, P, Mg and Ca supply;
- the presence of a litter layer, which could consume protons during decomposition. Its organic matter could buffer NH_4 by a large CEC and bind Al by chelation, thus decreasing their possible toxicity.

In experiment I the factors 1, 2 and 4 will be studied, and in experiment II factors 1, 3 and 4. The effects of the nutrient applications reported here, will also be compared with those of a forest experiment with Douglas fir on the same soil. Also there nutrients are added in addition to the ambient N deposition in order to improve the nutritional balance of the trees.

Materials and methods

Soil material from 0-20 cm depth and a part of the litter layer were collected from an acid forest soil (Plaggic Dystrochrept, USDA 1976) located near Kootwijk, The Netherlands. The soil, a loamy fine sand, was air-dried and passed through a 5-mm sieve. The chemical and physical properties of the soil are: pH (H_2O) 3.8 ; pH (1M KCl) 3.1 ; organic matter (C) 3.1% ; extractable P (H_2O) 256 mg P kg^{-1} soil; extractable Al (1M KCl) 286 mg kg^{-1} soil; CEC (0.01 M $BaCl_2$) 2.8 cmol(+) kg^{-1} soil, exchangeable cations (0.01 M $BaCl_2$): 0.10 Na, 0.20 Ca, 0.03 Mg, 0.06 K cmol(+) kg^{-1} soil. Soil texture: 25% 210-2000 μm, 61.5% 50-210 μm, 13.5% 2-50 μm and <0.5% <2μm.

In December 1988 one-year-old nursery grown Douglas fir seedlings (*Pseudotsuga menziesii* (Mirb.) Franco) were planted in 7 litre plastic pots, each containing 9 kg soil. Two experiments were conducted.

In experiment I four ammonium treatments were applied: 0, 50, 100 and 300 kg NH_4-N ha^{-1}; at 50 kg ammonium an additional dose of 50 kg NO_3-N ha^{-1} was applied. The treatments are further referred to as N0, N50/50, N100 and N300 (see Table 1). In N100 and N300 10 mL of a 1000 times diluted Nitrapyrine solution (nitrification inhibitor) was added to each litre of fertilizer solution. Pots of the N0 treatment were not fertilized at all. With the other treatments nitrogen applications were (kg N ha^{-1}): 100 and 300 as $(NH_4)_2SO_4$ for N100 and N300 respectively, and 100 as NH_4NO_3 for N50/50. The supply of all other nutrients was the same for all three treatments, (kg ha^{-1}): 50 K as K_2SO_4 and KH_2PO_4 ; 30 P as KH_2PO_4 ; 4 Ca as $CaCl_2$; 6 Mg as $MgCl_2$ and micronutrients Mn 0.43, Fe 0.75 as FeEDTA, B 0.22, Zn 0.03, Cu 0.03 and Mo 0.007 (optimal relative to 100 kg N ha^{-1}; Ingestad, 1979). Nutrient additions (nutrient solution) were divided in 20 weekly applications of each 50 ml per pot supplied during the period 26 April to 7 September 1989. In each fertilizer treatment eight pots were used, each containing two seedlings. On top of four pots of each N treatment a double litter layer was created by adding O_h- and O_l-material of the forest soil (90 and 50 g dry-weight per pot, respectively), further referred to +L. During the experimental period the pots were kept in an open greenhouse. The moisture content of the soil in the pots was kept at around 9% (w/w), equalling -100 cm soil water pressure, by weighing and adding demineralized water accordingly. Soil solution was collected by suction cups (Soil Moisture Equipment) eight times during the growth period and analysed for pH, Ec and concentrations of NH_4, NO_3, H_2PO_4, K, Ca, Mg, Mn, Al and Fe according to Begheyn (1980).

Table 1. Experimental design. Addition of N in kg N ha^{-1}. Every treatment has 4 pots with and 4 without a litter layer. F: additional application of K, P, Ca, Mg and micronutrients in optimal proportion to N application as indicated under F (kg N ha^{-1})

Experiment		Code	NH_4-N	NO_3-N	F
No.	duration				
I	26/4/89- 7/9/89	Control	0	0	0
		N50/50	50	50	100
		N100	100	0	100
		N300	300	0	100
II	22/3/90-16/8/91	N30-	30	0	0
		N120-	120	0	0
		N30+	30	0	30
		N120+	120	0	120

In October 1989 the trees were harvested and divided into roots, stem+branches and needles. The soil was washed from the roots with tap water and subsequently washed two times with demineralized water. Total root length was determined (Tennant, 1975) on the roots of all the treatments without litter layer (-L). All sampled plant parts were dried at 70°C for 48 hours, weighed and ground to pass a 0.5-mm sieve and then digested in a mixture of sulphuric and salicylic acid, H_2O_2 and selenium. In the digests total N, P, K were determined colorimetrically, Ca by atomic emission spectrometry and Mg by atomic absorption spectrometry.

Experiment II was started at the same time as experiment I. During the first year no nutrients were added and soil moisture was kept constant at an optimal level. The second year four treatments were initiated that were replicated four times. On each pot only one Douglas fir tree was grown. Two levels of ammonium were supplied, in total 30 and 120 kg N ha^{-1} y^{-1}. Each N level was split into two treatments (see also Table 1): without (N30- and N120-) and with additional application (N30+ and N120+) of the other nutrients in optimal proportions to N (Ingestad, 1979). These proportions were equal to those of the N50/50 and N100 treatment of experiment I. Nutrients and N-serve were added by dissolution in the irrigation water with NH_4-concentrations of 0.8-2.0 and 4-10 mmol/L for the low and the high ammonium addition rate treatment, respectively. The soil was kept at an optimal soil moisture content of 22% (w/w), equal to -40 cm soil water pressure, an improvement of the soil water status relative to experiment I, where sometimes drought stress occurred. Soil solution was collected before and at the end of the experiment and analysed in the same way as in experiment I. Treatments were stopped on 16 August 1991 when growth seriously declined with the high N treatment. In September 1991 the trees were harvested and examined according to the procedure of experiment I.

Data of both experiments were evaluated by analysis of variance (STATGRAPHICS), followed by a Student *t*-test or a Bonferroni multiple range test when interactions were present.

Results and discussion

Level of ammonium application

Soil solution composition. Regular addition of ammonium and the nutrients P, K, Ca, Mg and micronutrients during experiment I was clearly reflected by a gradual increase of their concentrations in the soil solution (Fig. 1). With treatments N0, N100 and N300 nitrate concentrations diminished gradually with time (Fig. 2). Concentrations of K, Ca and Mg showed higher values with increasing NH_4 addition rato (Fig. 1). At the end of the treatment period much more Ca was present in soil solution than was added. Base cations and Al were exchanged from the soil exchange complex by added NH_4 and by H originating from root excretion. Soil solution P concentration was very low (< 5 mmol(-)

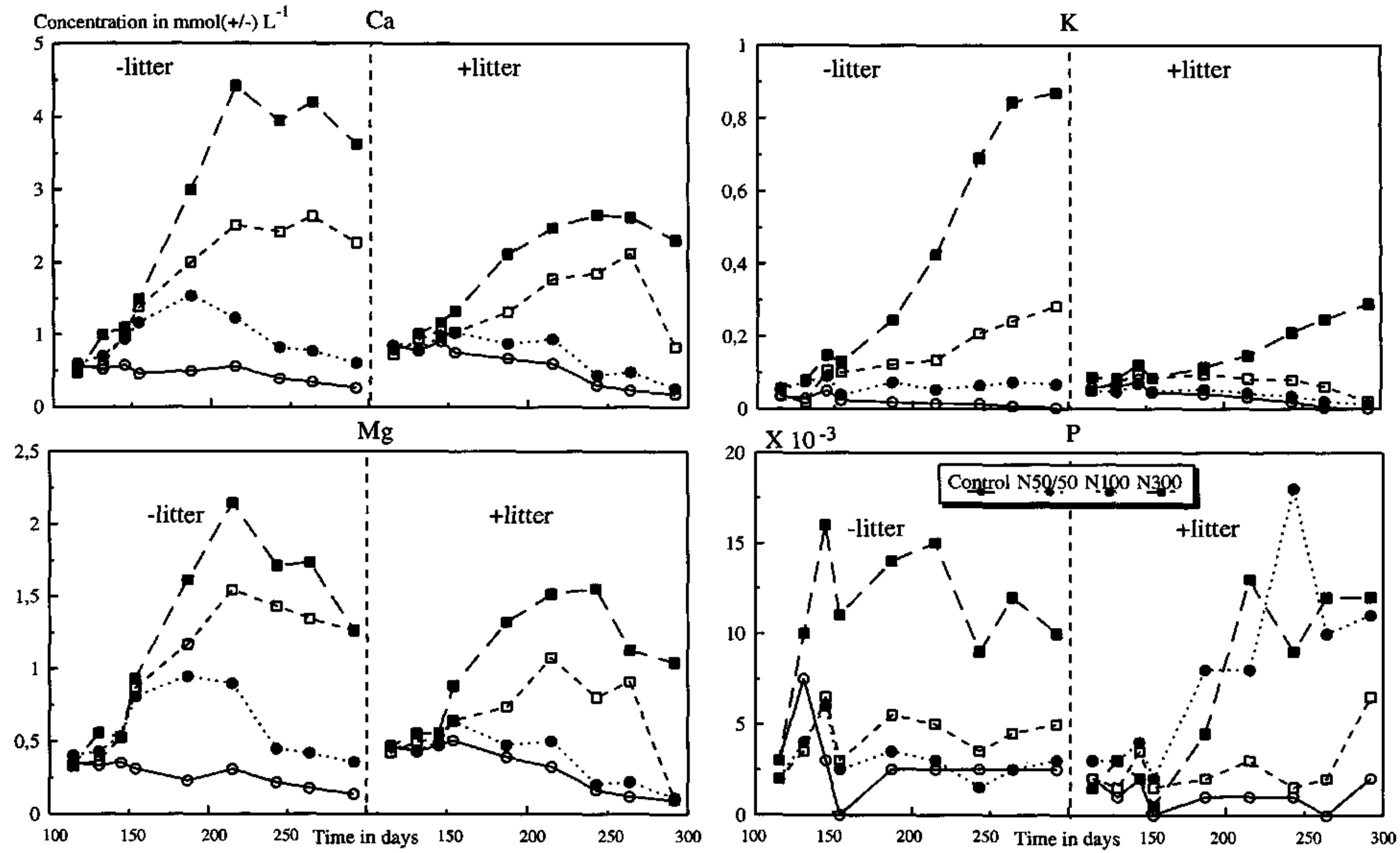

Fig.1. Concentrations of Ca, Mg, K and H_2PO_4 in the soil solution at four treatments with and without a litter layer (Exp.I) that started on day 116 (April 26 1989).

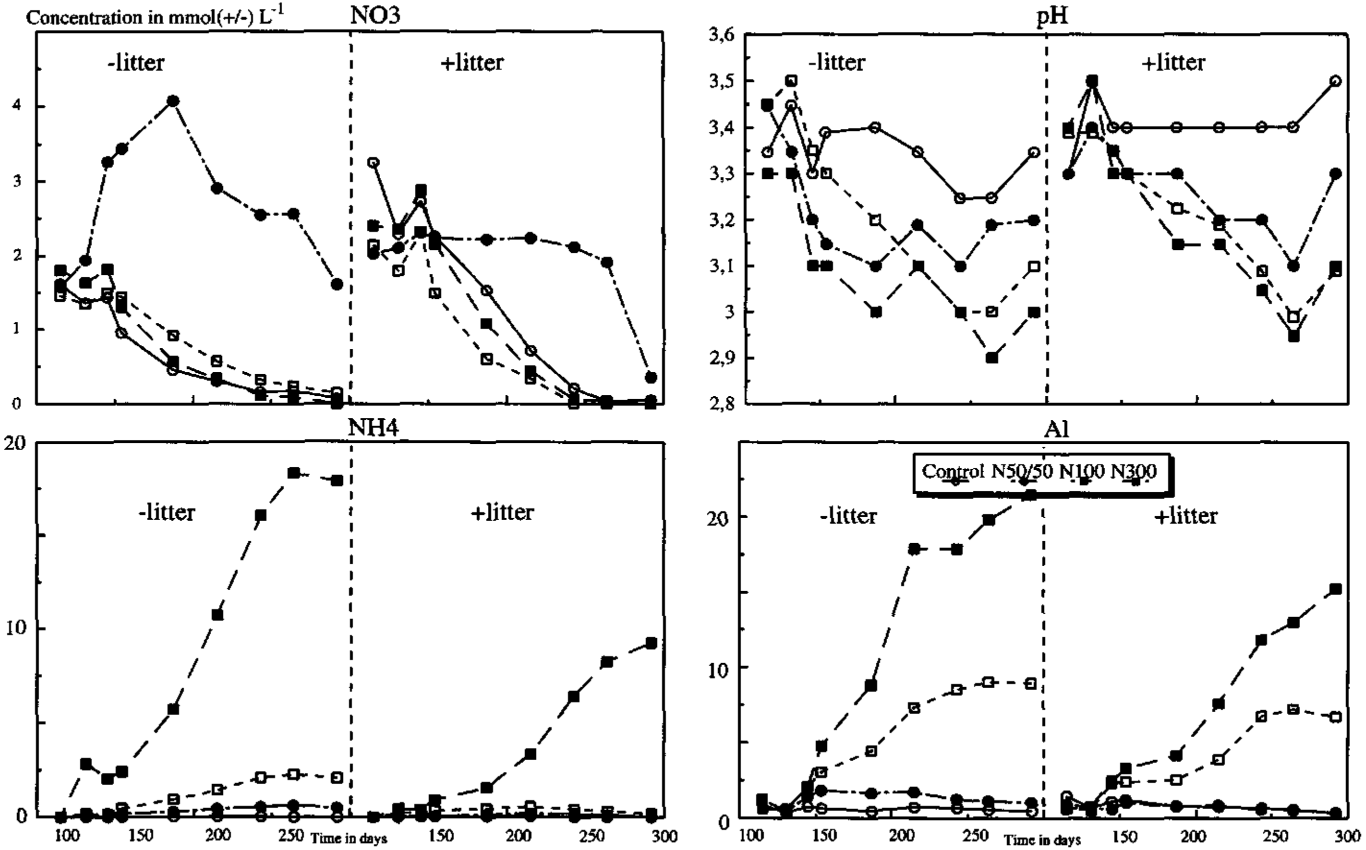

Fig. 2. Time course of pH and concentrations of NH_4, NO_3 and Al in the soil solution of the pots. See Fig. 1 for details.

m^{-3}), but increased in treatment N300 (±10 mmol(-) m^{-3}). pH in the soil solution decreased rapidly with time in the N300 treatments, followed by N100. The increase in aluminium concentrations followed the pH decrease, and reached very high values (8900 and 21500 mmol(+) m^{-3}, for N100 and N300 respectively). As a consequence, during the major part of the growing season molar Ca/Al-ratios in the soil solution were low (ending at 0.2).

High ammonium additions in experiment II resulted in a considerable pH decrease of the soil solution as well. Because nitrification was inhibited by N-serve, increased soil acidity in both experiments will be the direct result of ammonium uptake and the resulting proton excretion by tree roots. In experiment I the difference in total ammonium uptake between N100 and N300 (-L) was 11 mmol(+) per pot, while a total difference in cation and anion uptake of 13 mmol(+) relative to N100 was estimated, resulting in an extra proton excretion of 13 mmol per pot. The difference between the two treatments in release of Al from exchange sites and weathering of soil amounted about 19 mmol(+) per pot, present in the soil solution. Also in experiment II the release of Al can to a large part (± 70%) be attributed to acidification due to the excess cation uptake.

Nutrition. In experiment I the nitrogen concentration in the needles reached the highest values in N300 (Table 2). With increasing ammonium application the needle concentrations of P, K, Mg and Ca significantly decreased, despite increasing soil solution concentrations. Especially with K, even at very high concentrations of K in soil solution with N300, K uptake was hampered and needle K concentrations were rather low (Table 2). Symptoms of phosphorus deficiency occurred in the trees of N300 and in some of N100. In experiment II both N and K concentration in current year needles were increased at the high N supply level, whereas Ca and Mg concentrations were lowered. This was also found in the first year needles (data not shown).

Tree growth. In experiment I weight of most plant parts tended to be slightly higher when the NH_4 level was increased from N100 to N300 (Table 3), but this was never significant. Biomass was generally higher in the fertilized trees than in the control. Specific root length significantly decreased with increasing ammonium level.

In experiment II growth was initially stimulated by a higher ammonium application: shoot length growth in 1990 tended to be slightly higher at the high ammonium addition rate (Table 4). In 1991 however, with the N120 treatment a retarded bud break and a significant decline in shoot growth was observed relative to 1990 and relative to the N30 treatments ($p<0.001$). The total effect of a two-year application of a high NH_4 dose was more pronounced than in ex-

Table 2. Element concentrations (% of dry weight) in current year needles at the end of experiments I (1989), II (1991) and in a forest trial after one season of liquid fertilization. In the forest nitrogen and optimal proportions of fertilizer (see text) were applied in 1989 with a total of 120 kg N ha^{-1}. p-values of Multifactor ANOVA of <5% and <1% are marked with "*" and "**".

Treatment	N	P	K	Ca	Mg
	Experiment I				
-litter layer					
Control	1.33±0.23	0.23±0.07	0.59±0.11	0.45±0.17	0.24±0.06
N50/50+	3.25±0.95	0.16±0.06	0.70±0.20	0.50±0.28	0.14±0.03
N100+	4.02±0.69	0.08±0.03	0.60±0.13	0.26±0.08	0.09±0.03
N300+	4.35±0.69	0.06±0.02	0.59±0.14	0.22±0.08	0.11±0.02
+litter layer					
Control	2.49±0.78	0.19±0.07	0.68±0.14	0.39±0.15	0.19±0.06
N50/50+	2.43±0.35	0.19±0.02	0.85±0.18	0.36±0.08	0.15±0.04
N100+	3.71±0.34	0.17±0.03	0.81±0.14	0.33±0.10	0.15±0.03
N300+	4.90±0.35	0.10±0.02	0.46±0.11	0.19±0.04	0.09±0.02
	Experiment II				
-litter layer					
N30-	0.86±0.02	0.11±0.02	0.28±0.02	0.18±0.04	0.08±0.01
N120-	1.69±0.17	0.08±0.02	0.40±0.04	0.12±0.03	0.08±0.02
N30+	0.81±0.09	0.16±0.01	0.59±0.02	0.29±0.04	0.12±0.01
N120+	1.56±0.20	0.13±0.03	0.80±0.19	0.08±0.01	0.07±0.01
+litter layer					
N30-	1.12±0.14	0.11±0.03	0.30±0.04	0.12±0.02	0.07±0.01
N120-	1.95±0.26	0.08±0.02	0.34±0.03	0.07±0.01	0.06±0.01
N30+	0.87±0.09	0.11±0.02	0.50±0.09	0.16±0.03	0.09±0.01
N120+	1.70±0.14	0.17±0.03	0.69±0.05	0.08±0.01	0.08±0.02
	Forest				
Control	1.86	0.13	0.66	0.17	0.11
Fertilization	2.04	0.17	0.96	0.20	0.15

ANOVA Results			Variable		
Source of variation	N	P	K	Ca	Mg
	Experiment I				
NH_4 level	**	**	**	**	*
Litter	-	**	-	-	-
Interaction	*	*	**	-	**
N form	**	**	-	*	-
Litter	*	**	**	-	*
Interaction	-	-	-	-	*
	Experiment II				
Balanced supply	*	**	**	*	**
NH_4 level	**	-	**	**	**
Litter	**	-	-	**	-
Interactions					
Balance x N-level	*	-	-	**	*
Balance x litter	-	-	-	-	-
Litter x N-level	-	-	-	*	-

Table 3. Biomass yield and specific root length (SRL; m g^{-1} dry root) of 2 (Exp.I) and 4 (Exp.II) years old Douglas fir. *P* values of Multifactor ANOVA of $p<5\%$ and $<1\%$ are marked with "*" and "**". n.a. is not available.

Treatment	Biomass (g dry weight per plant)					
	Total	Needles		Roots	Stem	SRL
		current year	first year			
		Experiment I				
-litter layer						
Control	8.78±1.67	2.16±0.49		4.55±0.71	2.08±0.55	13.71±1.63
N50/50+	15.96±5.19	3.86±0.84		7.59±2.64	4.51±1.97	13.32±3.61
N100+	10.64±4.23	3.35±1.57		5.19±2.30	3.40±1.64	11.22±1.42
N300+	13.70±6.42	4.30±2.04		5.10±2.52	4.30±2.02	8.00±1.37
+litter layer						
Control	8.36±2.26	1.96±0.53		4.43±1.33	1.98±0.54	-
N50/50+	19.85±5.94	4.59±1.37		8.55±3.35	6.71±1.93	-
N100+	13.73±3.75	3.23±1.11		6.91±1.58	3.59±1.22	-
N300+	15.43±6.49	4.29±2.22		7.00±2.69	4.14±1.72	-
		Experiment II				
-litter layer						
N30-	87.24± 6.96	20.04±3.75	9.68±2.32	36.34±4.07	21.18±3.62	7.65±1.03
N120-	57.43±13.35	11.43±4.76	12.84±7.67	17.14±3.90	16.02±2.43	5.09± n.a.
N30+	102.80±14.63	25.07±2.60	7.11±2.34	36.14±4.73	34.49±8.16	7.26±1.76
N120+	116.63±17.10	29.86±4.88	17.79±3.81	23.13±2.05	45.83±7.84	5.80±0.73
+litter layer						
N30-	92.21±15.65	14.20±6.41	13.80±3.51	34.25±10.10	29.96±3.66	4.30±0.08
N120-	81.54±12.72	14.57±7.04	12.45±1.78	23.65±6.58	30.86±3.85	6.43±1.18
N30+	122.61±19.46	31.99±2.44	9.14±3.68	40.77±8.45	40.72±8.58	5.19±0.49
N120+	142.05± 1.08	45.26±6.98	14.78±5.60	35.54±2.02	46.49±1.36	4.27±0.15

ANOVA Results Variable

Source of variation	total weight (dry weight)	current needles (dry weight)	shoot length (cm)	roots (dry weight)	stem (dry weight)	SRL
		Experiment I				
NH_4 level	-	-	n.a.	-	-	**
Litter	-	-	n.a.	-	-	n.a.
Interaction	-	-	n.a.	-	-	
N form	*	-	n.a.	-	**	*
Litter	-	-	n.a.	-	-	n.a.
Interaction	-	-	n.a.	-	-	
		Experiment II				
Balanced supply	**	**	**	*	**	-
NH_4 level	-	-	**	**	-	-
Litter	**	*	-	*	**	*
Interactions						
Balance x N-level	**	*	-	-	*	-
Balance x litter	-	*	-	-	-	-
Litter x N-level	-	*	-	-	-	-

periment I: shoot length and root biomass was significantly decreased. Needle and total biomass was not affected or slightly decreased at the high NH_4 level (Table 3).

Time course of soil acidification and root dieback. In experiment I the soil was being acidified from day 40 after the start of high addition rates of dissolved ammoniumsulphate. Base cations, Al and protons were exchanged by NH_4 from the soil CEC into solution and the soil was not able to buffer generated acidity. The unconstrained uptake of NH_4 and its attendant proton excretion continued, but uptake of base cations and P was completely stopped, except for K. This unlimited uptake of NH_4 was also found by others (Hällgren & Näsholm, 1988; Tamm, 1991). Due to ion antagonism NH_4 must have hampered uptake of other cations. The poor Ca nutrition in the N300 needles might also be due to malfunctioning and death of root tips caused by excess Al.

In the first treatment year of the second experiment, the same processes took place at high supply rates of NH_4 as for experiment I. Tree growth was stimulated by NH_4 and other added nutrients. In the second treatment year however, in N120 poor shoot growth and considerable decrease of water uptake pointed at detiorated root functioning due to soil-chemical stress. At the end of the experiment the concentrations of free Al were similar (N30) to far above (N120) the level that would kill hydroponically grown Douglas fir seedlings (Keltjens & van Loenen, 1989). After an artificial drought period induced during the last phase of the second experiment, 90% of the N120+ trees and 15% of the N120- trees were died, whereas the N30 trees survived.

Table 4. Annual shoot growth (cm). +L means a litter layer is present. In experiment II treatments were started in 1990.

Experiment I		1989	Experiment II	1989	1990	1991
-L	Control	7.6	N30-	9.0	14.0	18.9
	N50/50	16.4	N120-	10.3	19.3	8.3
	N100	12.0	N30+	11.5	24.3	26.0
	N300	14.6	N120+	10.0	37.3	10.6
+L	Control	9.1	N30-	13.3	18.3	16.8
	N50/50	25.6	N120-	10.8	23.8	7.4
	N100	12.8	N30+	12.3	25.5	22.1
	N300	12.3	N120+	14.5	39.0	10.4

Partial replacement of ammonium by nitrate

Soil solution composition. In the soil solution of N50/50 nitrification occurred (no N-serve was added), reflected by a decreased pH and a rise in NO_3

concentration. Nitrate concentrations in soil solution increased to 4 mmol L^{-1} around day 200 and decreased afterwards (Fig. 2) as a result of plant uptake during a second growth flush. This pattern was also observed for Ca, Mg and H. Lower concentrations of Ca and Mg in soil solution were observed in N50/50 than in the pure ammonium treatments, although base cation supply was the same for N50/50, N100 and N300. This difference mainly resulted from exchange of base cations from soil-CEC by ammonium fertilizer, and is most obvious in N300. At N50/50 the Ca/Al molar ratio in soil solution had an optimal ratio of 1.0 compared with 0.3 and 0.2 at the N100 and N300 treatments. This is, apart from the higher pH values, an indication for the lower rate of soil acidification when N is partially supplied as nitrate.

Nutrition. The N concentration in the needles was lower in N50/50 than in the pure ammonium treatments N100 and N300 (Table 2). Needle concentrations of P and Ca were higher when NH_4 was partially replaced by NO_3 ($p<0.05$, treatments -L). For Mg concentrations the same tendency was observed. This has to be attributed partly to differences in pH, partly to the antagonistic effect of NH_4 on uptake of these nutrients.

Tree growth. Equal addition rates of nitrate and ammonium (N50/50) were more favourable for shoot growth and total biomass (p=0.0108), stem biomass (p=0.0046) and root length (p=0.0163) than addition of ammonium solely (Table 3). Specific root length was equal for control and N50/50, but was reduced relative to N50/50 by pure ammonium addition (p=0.0019).

Table 5. Concentration of some solutes (mmol(+/-) m^{-3}), pH and ratio of [K+Mg+Ca] to NH_4 (BC/NH_4 in molar equivalents) in the soil solution before and after experiment II.

		Treatment	pH	Al	NH_4	NO_3	BC/NH_4
Start	-L		3.55	284	1	142	319.0
	+L		3.43	420	1	254	441.0
End	-L	N30-	3.1	2479	54	37	16.9
		N120-	3.0	12191	16746	196	0.2
		N30+	3.1	-	51	33	101[a]
		N120+	2.9	22641	12349	319	0.9
	+L	N30-	3.1	2304	202	16	3.0
		N120-	3.0	7644	7209	544	0.2
		N30+	3.0	6096	10	24	256.7
		N120+	2.9	39618	9901	457	1.1

[a] means estimated from ionic charge balance. Missing values are indicated by '-'.

Balanced nutrient supply

Soil solution composition. In the balanced nutrient supply treatments of experiment II higher concentrations of base cations, Al and H were observed in the soil solution than without additional nutritions. The increase in Al tends to correspond to the increase of NH_4 taken up by the tree, increasing from 2.3 mmol(+) L^{-1} with N30-(+L) to 40 mmol(+) Al L^{-1} in N120+(+L) (Table 5).

Although additional nutrients were expected to balance the increased NH_4 supply, the base-cation/ammonium ratio in soil solution was far lower at the N120(+) than at the N30(+).

Nutrition. In current year needles concentrations of all elements were affected by balanced nutrition (Table 2). At the N30 level, nitrogen concentrations were slightly decreased, whereas concentrations of all other elements increased with balanced nutrition. At both N30 and N120 concentrations of K and P and their ratios to N increased by balanced nutrition, with K/N ratios higher than the optimal value of 50 (Fig.3).

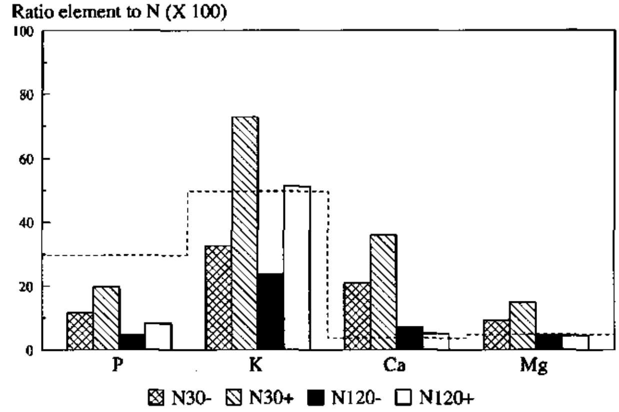

Figure 3. Element/Nitrogen weight ratio (*100) in current-year needles in Experiment II. The broken line indicates the optimal ratio of the specific element relative to N (Ingestad, 1979).

For certain variables an interaction of balanced nutrition with N level was observed (Table 2). With N30 needle concentrations of Ca and Mg increased when combined with balanced nutrition. While at N120 additional nutrient supply did not affect concentrations of Ca and Mg. Due to ammonium stress the concentration of these elements were at a deficiency level with N120. P/N ratios increased by balanced nutrition at both N levels, but were lower at the high application rate of N (Fig. 3).

A comparison of the chemical composition of needles of the juvenile trees in the pot experiments and those of 40-year old trees in a forest experiment (Table 2) gives rise to the following remarks:

- Needle element concentrations of treatments Control+L and N50/50+L (Exp.

I) resemble most to the values found in the forest trees. In the forest trial and in experiment II application with P and K were the same, but only with the small trees in the pot experiment Ca and Mg levels were very deficient. The forest trees were probably favoured by NO_3, the dominant N form in this forest soil (Beier & Rasmussen, 1993), and the possibility to retranslocate nutrients from older tissue;

- Nitrogen concentrations in most needles of experiment I are supra-optimal due to fertilization, yet optimal in the forest trees (van den Burg, 1988). The trees in pots have taken up N excessively. In experiment II however, needle concentrations of N and other elements except K, decreased from the first to the second treatment year to values that were distinctly lower than found in forest trees. This might be an indication of inhibited root activity, since N was abundantly available.

Tree growth. Biomass production of most plant parts in experiment II was significantly changed when a balanced nutrient supply completed the ammonium application (Table 3). Statistical tests on differences of means showed that all values were higher at balanced nutrition ($p<0.001$), except root biomass ($p=0.103$) and SRL. Biomass production as a total for 1990 and 1991, was highest in treatment N120+ and lowest in the N120- treatment (Table 3). Shoot length growth of N30 was also higher with balanced nutrition in both the treatment years 1990 and 1991 (Table 4). However, at high N application shoot growth was severely reduced from 1990 to 1991 even with a balanced nutrition.

The effect of a litter layer

Soil solution composition. In experiment I soil solution concentrations of nitrate, Ca and Mg were slightly higher in the pots with litter when no nutrients were added (N0). With litter the pH was also somewhat higher. In combination with fertilizer application the concentrations of NH_4, NO_3 and K in the +L treatments were only half of those in -L (Figs.1 and 2). Aluminium in soil solution of treatment N300 increased to 15 mmol(+) L^{-1} in +L, and to 20 mmol(+) in -L. In the +L treatments the lower NH_4 concentrations resulted in a less steep rise in Ca and Mg in soil solution than without litter. At the end of experiment II soil solution concentrations of base cations and NH_4 were slightly lower with litter.

Nutrition. Needle concentrations of P and K increased with litter in exp.I, while N concentrations differed depending on the treatment combination (Table 2). In exp.II three years after planting, concentrations of N in needles were increased and Ca concentrations decreased with litter. The litter of Douglas fir can still release considerable amounts of nitrogen three years after needle shedding (Tietema, 1992).

Tree growth. The presence of a litter layer enhanced tree growth in experiment II, while in the shorter experiment I the same tendency was observed (Table 3). In experiment II stem and total weight were significantly higher with litter and the increase in current year needle biomass was higher with litter when combined with balanced nutrition. On the contrary specific root length was lower with litter (exp.II). Root elongation was probably inhibited by the soil solution concentrations of Al, that were sometimes higher with litter (Table 5). These higher concentrations are probably the result of an increased total proton excretion per tree due to higher growth.

Conclusions

The four factors that were studied, have the following effects on growth of Douglas fir:

1. In a pot experiment the low application rate of 30 kg N ha^{-1} creates a N deficiency, whereas N doses of 100 kg N ha^{-1}, applied in experiment I, are never growth-limiting. Higher addition rate of ammonium can increase N uptake and biomass production only slightly and decreases the specific root length (Exp.I).
2. At a supply level of 100 kg N ha^{-1} yr^{-1} the N uptake is equal when supplied as pure ammonium or as a NH_4NO_3. When nitrate is present, antagonistic effects of ammonium are less severe and more P, K and Mg is taken up. Rhizosphere acidification is less when N is partly taken up as nitrate (see also Gijsman, 1990; Rygiewicz *et al.*, 1984) and negative effects on root length growth and biomass increment will be less than with a pure NH_4 nitrogen source.
3. Balanced nutrition at a low NH_4 level results in an improved internal nutrient status for all macronutrients and a higher shoot growth. At NH_4-N levels of 120 kg ha^{-1} yr^{-1} additional fertilizer supply increases needle K and P concentrations, while concentrations of Mg and Ca remain equal severely decrease, respectively. Potassium supply can be balanced for all application rates of N, but with nitrogen fertilization without additional K a severe K deficiency will occur with the soil used. At the low NH_4 supply rate combined with additional nutrients, the root system can function well and the trees also maintain a better nutrient balance than trees without additional fertilizer. The effects of fertilization on vitality and drought tolerance will be reported in another paper (de Visser, 1994).
4. The presence of litter increases growth and most element concentrations in

needles during the first year after planting, thereafter only growth and needle N concentration is increased. This phenomenon can result in a dilution of the concentrations of other macronutrients in the needles, despite nutrient additions. However, in the presence of litter total nutrient uptake per tree was increased.

The most severe attack on tree vitality can be subscribed to the forced, high and pure NH_4 uptake, which results in very acid soil conditions and subsequent hampering of root growth and root extension. If a neutral ionic uptake balance (no net H efflux) is aimed at, several authors (Arnold, 1992; Gijsman, 1990) state that nitrate has to contribute for 61 to 65% of the total N uptake. Douglas fir as well as most other tree species show a preference for ammonium uptake (Keltjens & van Loenen, 1989; Gijsman, 1990), but whether ammonium nutrition also results in higher growth relative to nitrate depends on some other soil conditions, like buffer capacity, moisture content, pH, N-level etc. This research demonstrates that ammonium supply can be growth-stimulating at the start, but will result after some time in root-menacing soil acidification when plants are grown in a closed soil system with a low buffer capacity. Determination of the optimal doses of nitrogen and adequate ratio of nitrate versus ammonium in a soil system should therefore be accompanied by an estimate of the net effect on soil acidification.

Under field conditions the addition of base cations in the form of soluble fertilizers may cause extra acidification when applied to soils with a high portion of exchangeable acidity. In several experiments a pH decrease was observed after addition of K and/or Mg sulphates (Beier *et al.*, 1993; Matzner, 1985; Tamm, 1991). This study shows that K nutrition can be improved under conditions of excess NH_4 by K applications, but the use of slow release K fertilizers is recommended in stead of soluble fertilizers to avoid extra acidification. Since the major N form in atmospheric deposition in the Netherlands is NH_4-N (Van Breemen *et al.*, 1982) this potentially leads to higher soil acidification due to root uptake and nitrification. Although application of fertilizer or lime can ameliorate the forest soil on the short term, finally the best measure for the ecosystem as a whole is to decrease the atmospheric deposition of nitrogen (Van Dijk, 1993).

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Chapter 7

Transpiration and drought resistance of juvenile Douglas fir exposed to excess ammonium

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Co-authors: W.G. Keltjens and G.R. Findenegg

Transpiration and drought resistance of juvenile Douglas fir exposed to excess ammonium

Abstract: In a pot trial growth and transpiration of three-year old Douglas fir seedlings on acid sandy soil was examined at a deficient (30 kg N ha^{-1} y^{-1}) and an excessive level (120 kg N ha^{-1} y^{-1}) of NH_4 application. Dissolved ammonium sulphate was applied to the pots weekly for two growing seasons. In half of the pots a complete set of other nutrients was applied in optimal proportions to the applied nitrogen. Water supply was optimal and transpiration was recorded. At the end of the second treatment season irrigation was stopped for two weeks during dry and sunny weather. Both high application of NH_4 and additional nutrients increased shoot growth and evaporative demand in the first treatment year. The root system was smaller at higher N level and this reduced water uptake accordingly. In the second year the combination of high NH_4^+ and additional nutrients detiorated root functioning due to soil acidification and this seriously decreased water uptake capacity and shoot water potentials, finally resulting in tree death. Without addition of other nutrients the high NH_4^+ application resulted in a lower degree of soil acidification, but roots were still injured and could not recover after water stress. At the low NH_4 supply level soil acidification was lower, and root functioning was not affected, and the trees recovered quickly from the imposed drought. Higher needle K and P status depressed transpiration rates at the low NH_4 application rate.

Keywords: K, P, *Pseudotsuga menziesii*, root/shoot ratio, soil acidification, water potential

Introduction

In Northwestern Europe forests receive high loads of nitrogen. The predominant form of N in deposition is NH_4, as it originates from ammonia volatilization due to intensive animal husbandry. Excess supply of N in soil can interfere with the water economy of the tree in various ways. Increased supply of N (both NO_3 and NH_4) will result in a lower root/shoot (R/S) ratio and will thus increase the water uptake per unit root length (Van der Eerden and Pérez-Soba, 1992) and drought sensitivity. Ammonium excess may additionally hamper root growth by NH_4-induced soil acidification due to excess cation uptake by the plants and nitrification. Acidification and Al toxicity is often more pronounced in deeper soil layers. The resulting superficial rooting system may additionally increase drought sensitivity (Marschner, 1991). Furthermore, roots might suffer from salt stress during summer drought, since occasionally very high solute concentrations were recorded in well-drained forest soils affected by high NH_4 loads (*cf.* Chapter 4 of this thesis; Van Dobben *et al.*, 1992).

There are several indications that the negative effect of NH_4 on water economy of plants may be alleviated by addition of other nutrients, with special attention to K. Low K concentrations and low K/N ratios in needle tissue were related to a NH_4-enhanced K leaching from the tree canopy (Flückiger *et al.*, 1988; Roelofs *et al.*, 1985) and/or loss of base cations from the soil due to soil acidification (Zöttl and Hüttl, 1985), but also by direct competition of NH_4 ions with K for uptake (Chapter 6). In agricultural crops this shortage of K can impair stomatal control and, consequently, decrease water use effickenc{ (Nelson, 1980). Christerson (1973) observed a beneficial effect of improved K supply on water use efficiency in Scots pine. Larsen (1983) found an improved drought tolerance and a decreased transpiration rate in Douglas fir seedlings at a higher K, and to a lesser extent P, supply.

In this study the first goal of the present study was to evaluate the water uptake capacity of Douglas fir at different R/S ratios induced by different supply rates of N. The N levels are chosen at near-deficient and excess N supply. The second goal was to quantify water uptake capacity of roots at low and high rates of soil acidification, induced by low and high supply levels of NH_4. In a pot experiment Douglas fir roots were exposed during two growing seasons to an artificially increased soil acidity. The third goal was to determine the effects on transpiration of the addition of other nutrients in optimal proportions to the applied N levels, with special attention to K and P. We hypothesize that ratios of nutrients to N that are optimal for growth (Ingestad, 1979) might also optimize transpiration control.

Transpiration will be related to biomass characteristics during unconstrained water uptake and during strong drought. The ability of the tree to recover from a period of drought at various levels of NH_4 supply will be examined.

Material and methods

Pots (7 L) were homogeneously filled with 9 kg of soil material of the A_p horizon of a fine sandy acid forest soil. The chemical and physical properties of the loamy fine sand were: pH (H_2O) 3.8 ; pH (1M KCl) 3.1 ; organic matter (C) 3.1% ; extractable P (H_2O) 256 mg P kg^{-1} soil; extractable Al (1M KCl) 286 mg kg^{-1} soil; CEC (0.01 M $BaCl_2$) 2.8 cmol(+) kg^{-1} soil, exchangeable cations (0.01 M $BaCl_2$): 0.10 Na, 0.20 Ca, 0.03 Mg, 0.06 K cmol(+) kg^{-1} soil. Soil texture: 25% 210-2000 μm, 61.5% 50-210 μm, 13.5% 2-50 μm and <0.5% <2μm. Each pot contained one Douglas-fir tree (*Pseudotsuga menziesii* (Mirb.) Franco), planted as a one-year-old seedling in December 1988. In the first year, 1989, only demineralized water was added to account for transpiration losses. In 1990 two levels of ammonium were supplied, in total 30 and 120 kg N ha^{-1} y^{-1} based on soil surface area in the pots (450 cm^2). At each N level additional nutrients were added (N+) or not (N-). These nutrients were applied in optimal mass proportions to N addition, according to Ingestad (1979), with percentages (%) of N mass for K 53, P 31, Ca 4, Mg 6, Fe 0.75, Mn 0.43, B 0.22, Zn 0.03, Cu 0.03 and Mo 0.007. Nutrients were dissolved in the irrigation water with NH_4-concentrations that ranged from 0.8-2.0 and 4-10 mmol/L in the low and the high ammonium addition rate treatment respectively. N serve (a nitrification inhibitor) was added to the fertilizer solution (see Chapter 6). During the experiment the soil was kept at an optimal soil moisture content of 22%, that equalled -4 kPa soil water pressure. A control treatment without trees was included. The whole experiment was repeated with a litter layer of 5 cm on top of the mineral soil, and consisted of 90 g O_h- and 50 g O_l-horizon air-dried material with a bulk C/N ratio of 28. Thus, the total pot number was 2 x 5 (N30-, N120-, N30+, N120+, Control) = 10 treatments with four replicates = 40. In 1991 the treatments were continued and were followed by an artificial drought period from 5 to 19 July, when the total addition of ammonium in 1991 had accumulated to 21 at the low N level and 110 kg N ha^{-1} at the high N level. During this drought period the warm and sunny weather created a high evaporative demand.

Weight loss of each pot was recorded and compensated by the addition of water weekly. Transpiration of trees was calculated from loss of pot weight, accounting for tree mass growth and soil evaporation (weight loss of control pots). Soil solution was sampled in half of the pots by suction cups before the start of fertilization (March 22 1990) and drought (June 25 1991) and analysed on pH, Ec and concentrations of K, Na, Ca, Mg, Al, NH_4, NO_3, Cl, SO_4 and H_2PO_4, see Chapter 4 for methods, for further details see Velthorst (1993). During the first treatment season the pH, NH_4 and H_2PO_4 in soil solution were also determined on April 19, May 29 and August 13.

Growth of the top shoots was recorded monthly. In August 1991 trees were harvested and divided into fine (ϕ < 2 mm) and coarse roots, stems+branches and needles. All plant parts were dried at 70 °C for 48 hours and weighed.
During the drought treatment every four days water potentials were measured with the aid of a Scholander pressure bomb on two second-order shoots of 5 cm length of two trees of each treatment between 12 and 16h. Also soil pressure heads were registered in half of the pots. Root and stomatal resistance were calculated with the data of July 14 according to Ohm's law, from differences in water pressure in soil, plant and air, divided by the maximum hourly transpiration per surface area of root and needle, assuming that xylem and aerodynamic resistance were negligible. After the drought period irrigation with demineralized water was continued. The experiment was stopped on 16 August

when growth at the high N treatments had seriously declined.

On all data analysis of variance (STATGRAPHICS) was carried out, followed by a multiple comparison test based on least significant difference.

Results

The presence of litter enlarged the positive effect of additional nutrition on growth (Table 1) and transpiration in 1990 significantly. Despite this interaction effect in the ANOVA, there were no main effects of the litter layer on transpiration. Therefore, for the further statistical evaluation, pots with and without litter layer were considered to represent the same treatments (n=8).

Table 1. Shoot growth (in cm) in both treatment years and needle and root biomass (g dry weight per tree) at the end of the experiment (August 1991), with and without a litter layer on the soil. Data derived from Chapter 6. Different letters behind the mean indicate a significant difference within one column ($p<0.05$).

	Treatment	Shoot growth		Needles	Roots	Roots/Needles
		1990	1991			
-litter	N30-	14.0b	18.9ab	29.8b	26.0a	0.86ab
	N120-	19.3b	8.8c	24.3b	10.3b	0.51ab
	N30+	24.3b	26.0a	32.2ab	25.8a	0.82a
	N120+	37.3a	10.6bc	47.6a	12.5b	0.27b
+litter	N30-	21.3b	12.6b	28.0c	23.7a	0.84a
	N120-	23.8b	7.4c	27.0c	14.2b	0.54b
	N30+	25.5b	22.1a	41.1b	26.5a	0.67b
	N120+	39.0a	10.4bc	60.0a	19.3ab	0.32c
Mean	N30-	17.6b	15.8b	28.9c	24.9a	0.85a
	N120-	21.5b	8.1c	25.7c	12.3b	0.52b
	N30+	24.9b	24.1a	36.6b	26.2a	0.74a
	N120+	38.1a	10.5c	53.8a	15.9b	0.30c

Transpiration per tree

In 1990 after shoot extension the N120+ trees transpired more water than the other trees (Figure 1a). From day 197 onwards, transpiration of both N120- and

N120+ trees drastically decreased relative to the N30 treatments and were lower than the latter in August. This points to a negative effect of high ammonium supply on growth or functioning of roots since aboveground biomass did not decrease. Before this decrease, differences in transpiration were explained by the variation in shoot length of that year (R^2=33.3 with $p<0.001$; days 187-197), not however at the end of the season (R^2=3.2 with $p=0.33$; days 212-233). As a result of this change in transpiration pattern, total transpiration in 1990 (Table 2) in the N120 trees was corresponding those of the N30 trees, despite their difference in size (Table 1). At the start of the 1991 growing season the downward trend of tree transpiration in N120 proceeded (Fig 1b) and transpiration became three times as low as that of N30. In spring 1991 the N120- and N120+ trees had the same average transpiration per tree (Table 2). The transpiration in N120+ gradually decreased relative to N120-, and was about 25 g day^{-1} lower at the moment the drought treatment started. This difference persisted until the end of the experiment.

Table 2. Transpiration (g per tree per day) in both treatment years, as an average of treatments with and without litter layer. Different letters behind the mean indicate a significant difference within one column ($p<0.05$).

Treatment	1990	1991		
		Spring	Drought	Afterwards
N30-	47 b	97 b	126 a	120 a
N120-	55 b	56 c	58 b	43 b
N30+	70 a	113 a	124 a	115 a
N120+	65 a	62 c	34 c	19 c

At the start of the drought treatment transpiration in most trees increased for a few days as a result of extraordinary sunny and warm weather conditions. Consequently, a strong transpiration reduction occurred in all trees (Fig 1b). After a drought of 10 days the lowest soil pressure heads were observed in N30 (Table 4). After rewatering of the pots the N30 trees returned to their old transpiration rates quickly, yet the N120 trees hardly restored from the drought. Both N30 treatments had the same transpiration rate per tree during and after the drought (Table 2).

Transpiration per unit biomass

Given the shoot growth data of the N120+ trees in 1990 (Table 1), their transpiration per unit shoot length, and thus per unit needle mass if we assume length and mass are correlated (no mass data available for 1990), strongly

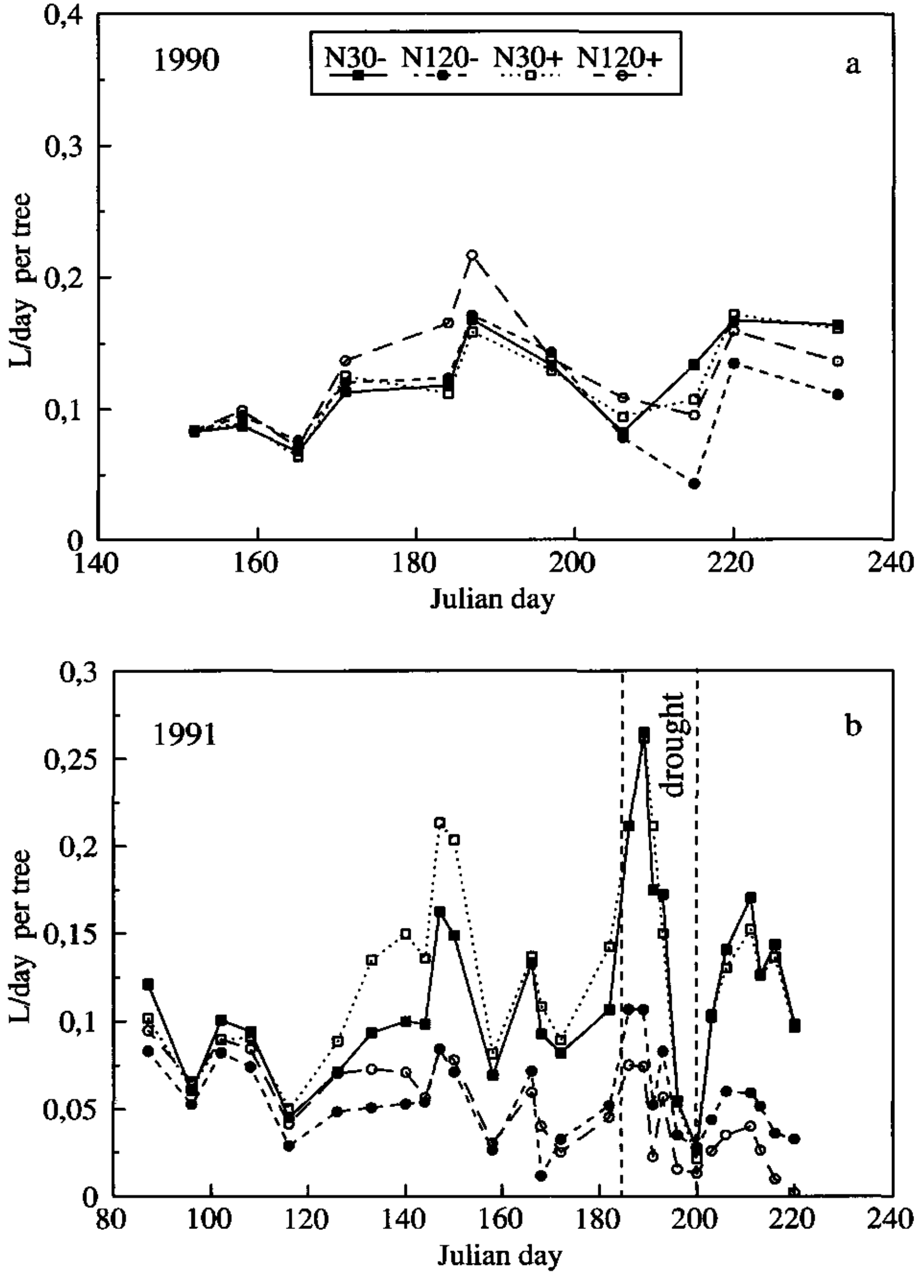

Figure 1. Transpiration per tree per day(L) versus time. a) 1990; b) 1991.

decreased relative to all N30 trees during that growing season. In 1991 this decrease continued (Table 3) and finally ended in tree death in August. In 1991 the N120- trees had a higher transpiration per unit needle mass than the N120+ trees, but lower than that of the N30 trees (Table 3). Transpiration in N120- ceased after the drought period and these trees died two weeks after the N120+ trees. The highest water uptake was observed for trees at the low N level, where the N30- trees generally showed higher transpiration rates per gram needle than at N30+ (Table 3).

Table 3. Average transpiration rates during the last 12 weeks of the experiment in 1991, related to the final weight of needles and roots (g H_2O (g dry weight day)$^{-1}$). Different letters behind the mean indicate a significant difference ($p<0.05$).

Treatment	Before	During	After drought
	Transpiration (g water/ g dry needle)		
N30-	4.34a	4.47a	4.20a
N120-	2.54b	2.42c	1.81
N30+	4.09a	3.46b	3.24b
N120+	0.89c	0.65d	0.34d
	Transpiration (g water/ g dry root)		
N30-	4.53ab	4.68a	4.66ab
N120-	4.99a	4.73a	3.33b
N30+	5.73a	4.85a	4.34a
N120+	3.22b	2.35b	1.21c

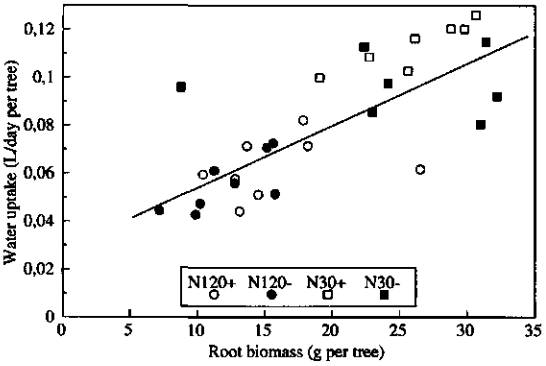

Figure 2. Relation between fine root biomass and tree transpiration in 1991.

Before drought, water uptake per gram of fine root was almost the same for all treatments, suggesting that the water uptake capacity of the trees depended on the amount of their fine roots: the N30- trees had the highest fine root mass and root/shoot ratio (Table 1) and the highest water uptake. The transpiration of the N120+

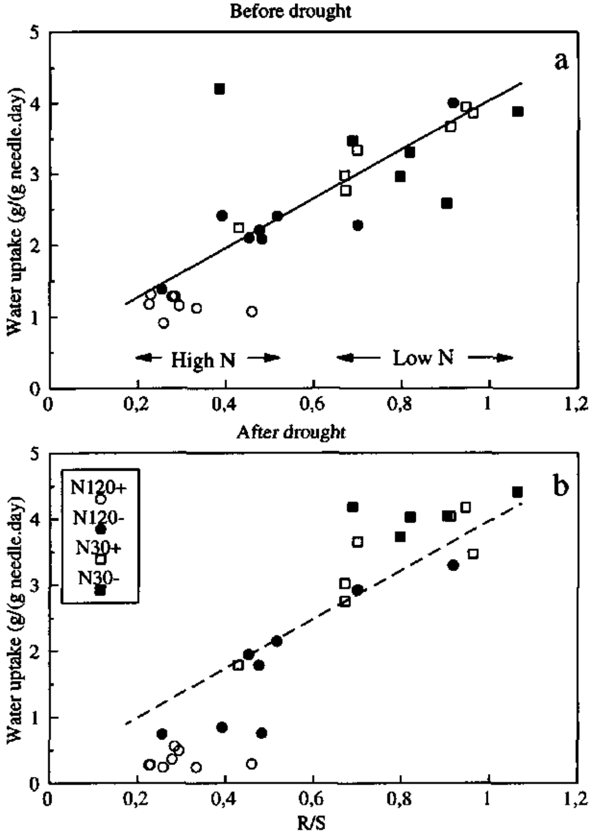

Figure 3. Relation between root/shoot ratio and water uptake per unit needle dry weight. Regression line of Fig. 3a is dashed in Fig. 3b. Arrows in Fig. 3a indicate the range of R/S values for high and low N application rate.

trees, having less fine roots but more needles than N30-, was low. This relation between final fine root mass and tree transpiration was linear (Fig 2) with an intercept close to zero. This figure also clearly illustrates that root biomass per tree is strongly affected by the N level, with low root biomass at high level of NH_4 application (H) and visa versa. A similar relation was found between transpiration per unit needle weight and the root/shoot ratio ($R^2 = 0.91$) (Fig 3a). The relation root mass or root/shoot ratio *vs.* transpiration was altered during the 1991 growing season, since water uptake per gram root decreased at N120 (Table 3). This resulted in a shift of the data points of N120 (or H) to well below the regression line due to a decrease in relative water uptake (Fig 3b).

Water potentials in soil and trees

At the beginning of the drought period soil and shoot water potentials were high, except for the N120+ trees, that already started with very low water potentials (-1.9 MPa) (Table 4). Later shoot water potentials decreased by 0.2 in N30 to 1.0 MPa in N120+, that reached values of less than -3.0 MPa at the end. The soil in the N120 pots remained rather moist throughout the drought period (Table 4), indicating that almost no water was extracted by the roots. In these trees transpiration was fully blocked after ca. 5 days of drought (Fig 1). Specific root resistance and stomatal resistance showed high (N30-) to extremely high values (others)(Table 4), since they were calculated from rather low transpiration rates on July 14 1991 of about 0.02 g m^{-2} s^{-1} at most.

At the start of the drought treatment the soil solution contained high amounts of NH_4, Al and SO_4 and had a low pH (Table 5). Osmotic potentials in soil solution were six times lower in N120 than in N30 and twice as low due to the additional fertilizer applications. A lowest value of 64 mosmol L^{-1} (= -0.152 MPa) was measured at N120+. The N30+ trees had the highest water potentials of all treatments, with little decrease during drought. The soil hydraulic head in the N30 pots decreased considerably due to water consumption, but was still above the wilting point (-1580 kPa) at the end of the drought period. Figure 4 shows the course of the shoot water potentials during the 10th day of drought. The low and high N level treatment differed in daily fluctuation of water potential, with the N30+ trees having the most dynamic transpiration pattern, while the N120+ trees hardly changed during the day. The highest water uptake was observed for N30- (9 g day^{-1} per tree), in agreement with the high mean values of water use in N30-(Table 2). Most of the N120+ trees died one month after restarting the water additions.

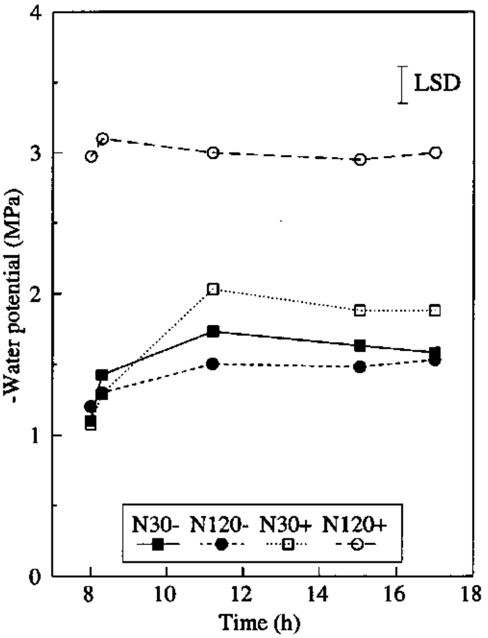

Figure 4. Diurnal course of the shoot water potential during the drought (July 14 1991).

Table 4. Shoot water potentials (-MPa; measured between 12 and 16h) and pressure heads (- kPa) in the soil during the drought period starting at 5 July, and stomatal resistance (R_s in s m^{-1}) and specific root resistance (R_r in bar kg s g^{-1}) on July 14.

Treatment	5 July	8 July	12 July	14 July
		Shoot water potential (-MPa)		R_s
N30-	1.40	1.48 ± 0.21	1.63 ± 0.16	710
N120-	1.15	1.76 ± 0.05	2.09 ± 0.50	1950
N30+	1.15	1.05 ± 0.24	1.49 ± 0.18	1700
N120+	1.90	2.53 ± 0.56	2.99 ± 0.31	12200
		Soil water potential (-kPa)		R_r
N30-	3.8 ± 0.7	8.8 ± 2.9	36.8 ±15.9	21
N120-	2.5 ± 0.3	4.2 ± 0.5	6.2 ± 2.5	106
N30+	3.0 ± 0.1	7.8 ± 1.4	25.3 ± 2.7	94
N120+	2.6 ± 0.4	4.0 ± 0.9	4.9 ± 0.5	684

Table 5. Some characteristics of the soil solution in the pots at the end of the experiment. The calculated osmolarity also included the ions Na, K, Mg, Ca, Cl, NO_3 and H_2PO_4.

Treatment	pH	EC	NH_4	Al	SO_4	Osmolarity
		µS cm^{-1}		$mmol_c$ L^{-1}		mosmol L^{-1}
N30-	3.12	672	0.13	2.40	4.71	5 ± 1
N120-	3.01	2504	13.57	10.68	28.13	35 ± 10
N30+	3.08	951	0.04	3.10	6.54	11 ± 5
N120+	2.89	3915	11.13	31.12	49.82	64 ± 13

Discussion

In this experiment the root/shoot ratio strongly decreased with increasing NH_4 supply. This decrease resulted from both a stimulated shoot growth, as commonly found at a higher N supply, and a simultaneous hampering of root growth due to adverse soil conditions. The relative decrease in root development limited the water uptake and consequently the transpiration rate. The dependence of the transpiration rate on root amount at unlimited water supply is well established (De Willigen and Noordwijk, 1987). This dependence on root mass is even stronger at a rather low water uptake capacity of the roots, as found in all our treatments before drought stress (Table 3). To illustrate this, we calculate that the maximum uptake capacity we observed (5.7 g H_2O g^{-1} root, see Table 3), would result in a forest stand transpiration of maximally 2.4 mm, assuming a fine root biomass of 4.3 Mg ha^{-1} (Olsthoorn and Tiktak, 1991). During drought the same dependency of transpiration on root mass occurred, yet the limitation to withdraw water was aggravated due to the combination of drought and soil-chemical stress. Root resistance must have increased due to adverse soil conditions.

Development of root damage with time

Root growth and functioning decreased at the high NH_4 application rates after about 80 days, as was concluded from a comparison with the water uptake of the low NH_4 treated plants some weeks before and after that moment. Soil conditions became unfavourable due to soil acidification and consequent increase of Al and H solution concentrations. In experiment I in Chapter 6 high NH_4 availability also hampered root growth within one season. Further evidence for an impaired root system is given by the depressed water uptake per unit root mass early in the second growing season, especially in the treatment combination N120+. The root dieback was also illustrated by the calculated root resistances, that were much higher then those reported for Douglas fir (Nnyamah *et al.*, 1978). Soil solution concentrations of Al must have been toxic for Douglas fir at the start of the second treatment year, and were found to increase to values far above the toxic levels found by Keltjens and Van Loenen (1989) in hydroculture (Table 5). A possible salt damage might also have occurred since nutrient additions exceeded uptake capacity of the trees. The combination of osmotic stress and high concentrations of Al and H finally caused root and tree death, despite the restarted water additions. Osmotic pressure and soil acidity were twice as high, if nutrients were given in addition to the high NH_4 application. Actually, only since the drought period high NH_4 supply without nutrients caused a slightly lower water uptake per gram root relative to low NH_4. Root dieback could have been caused by peaks in Al concentration during drought, that were comparable to those in the N120+ pots before drought. It is of great importance to examine these effects on water uptake not only in juvenile, but also in mature forest trees (see Chapter 8). Large trees might built up larger carbohydrate pools during drought than young trees do, and these pools can be used for renewed root growth when the soil is rewetting (Olsthoorn and Tiktak, 1991).

Nutritional balance and transpiration

Application of other nutrients in optimal proportions to the NH_4 supply promoted growth and needle nutritional balance, shown by an increase in K and

P concentration by a factor 2 and 1.5 respectively (Chapter 6). At low application rates of N the additional nutrients seemed to improve transpiration control: shoot water potentials were highest and stayed fairly high even under water stress. Also transpiration rates per unit needle weight were lower with additional nutrients than without, which might be related to needle K concentrations (0.55 and 0.29 % of dry weight respectively, see Chapter 6). This is in agreement with the results of Larsen (1983) and Christerson (1973) but in contrast to several papers reviewed by Hsiao and Läuchli (1986) where higher transpiration rates at an improved K supply has been observed in several plant species.

Drawbacks of fertilizer additions

NH_4-induced root damage was not counteracted by the addition of other nutrients and NH_4 uptake was not depressed by the competitive K ion (Chapter 6; Flaig and Mohr, 1992). Instead, the extra salts can increase osmotic and acid stress (Table 5). Under field conditions application of comparable amounts of base cations, dissolved in irrigation water, also increased soil acidification to a small extent, but salt effects were negligible due to leaching (Chapters 4 and 5 of this thesis). Although forest fertilization might temporarily eliminate nutrient shortages (Hüttl, 1990), nutrient applications including Ca and Mg to increase the (Ca+Mg)/Al ratio, might not be the appropriate way to decrease Al damage to the tree roots. Fertilization might be more helpful if done in combination with proton consuming substances like carbonate or silicate, as was shown by Hildebrand (1986). In combination with rather low root/shoot ratios, the increased susceptibility to drought reflects one of the most important consequences for the vitality of forests by high NH_4 deposition.

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CHAPTER 8

Water economy of Douglas fir trees during artificial drought and optimal water and nutrient supply

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Co-authors: W.G. Keltjens, G.M.J. Mohren, J. Čermák

Water economy of Douglas fir trees during artificial drought and optimal water and nutrient supply

Abstract: The seasonal course of transpiration in Douglas fir was monitored by means of sapflow measurements and at different levels of water availability. Water stress was induced by interception of throughfall water by a roof above the forest floor. Water supply was optimized by irrigation. The water status of Douglas fir was decribed for three days in the course of season in relation to the different soil water availabilities. Osmotic potentials were determined from pressure sap and indirectly from pressure-volume analysis. Transpiration was optimal in the irrigated trees with maxima of 6 mm day^{-1}. Transpiration was maximally reduced for 90% at current weather conditions and for almost 100% by artificial soil drought. Lowest shoot water potentials of -2.2 MPa in the afternoon were observed in all treatments. This value was in accordance with the values on the turgor loss point (*ca.* -2.4 MPa) and the cell sap osmotic pressure (*ca.* -2.3 MPa). Transpiration reduction was maximal at a soil water content of 2.8%, *i.e.* a soil suction of -2 MPa. No evidence was found for osmotic adjustment and carbohydrate accumulation in the needles at water stress. Occasional rain showers in July and beginning of August did hardly promote transpiration rate, unless soil conditions were moist beforehand. Shoot water storage capacity was increased by the combination of irrigation and nutrient applications, and was related to an increased cell size. Simulation results of stand transpiration were in agreement with results from sapflow measurements.

Keywords: irrigation, model, osmotic potential, sapflow, stress, transpiration, water potential

1. Introduction

During the last decades high atmospheric inputs of nitrogen have affected forest ecosystems in the Netherlands. One of the effects of an increased availability of N is the increase in canopy biomass relative to root biomass (cf. Binkley and Reid, 1984). As a consequence the root system may not be able to meet the water requirement of the tree crown during periods of high radiation and drought. Such effects of N enrichement on drought sensitivity can be quite dramatic, as was shown by Linder *et al.* (1987) for *Pinus radiata*.

Forest transpiration depends on external factors such as atmospheric conditions and soil water status and internal, tree-related factors. The transpiration dependence on soil water status is often described as a reduction function (Bosveld *et al.*, 1993; Jarvis, 1976; Mohren, 1987). Irrigation treatments give the possibility to study this dependence on soil moisture synchronously at different water regimes. At optimal water supply the transpiration rate is mainly determined by weather conditions (Jarvis, 1976) and physical properties of the trees. At dry soil conditions the tree chemical properties will determine the transpiration rate to a greater extent than at moist conditions. Osmotic pressure in tissue determines the turgor loss point in needles and root, and the function of K will be more prominent, especially in the stomatal control (Schulze, 1986) and cell wall elongation (Hsiao, 1973). Water stress can enhance the production of osmotically active substances in the cell symplast (Levitt, 1980). In Douglas fir Livingston and Black (1987) found a higher production of soluble compounds than in silver fir and Canadian fir during drought. This process may be related to hydrolysis of cell wall pectins (Zwiazek, 1991), that can result in an increase of solutes and osmotic pressure in the cell symplast, and can decrease cell wall elasticity, thus promoting drought tolerance (Milburn, 1979).

The first aim of this study was to estimate the water requirement of Douglas fir during one season. In earlier investigations Douglas fir showed strong water limitations in the selected stand (Olsthoorn and Tiktak, 1991; Chapter 5). The maximum consumption of water by trees was enabled by irrigation and was also estimated with a deterministic model. Transpiration and water status of Douglas fir were monitored during a period of progressing drought and during irrigation. The second aim was to study the adjustment of Douglas fir to drought. The effects of water availability on the turgor loss point and on the osmotic potentials in tree needle tissue were determined. Starch and carbohydrates contents in needles were followed with time.

2. Material and methods

The forest stand consisted of even-aged Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), planted 40 years ago as two year old seedlings and was situated near the village Kootwijk, the Netherlands. Stand density was 992 trees ha^{-1}. No understorey was present. The fine sandy soil was a Plaggic Dystrochrept (Soil Survey Staff, 1975). Chemical properties were described elsewhere (Chapter 5).

The measurements were carried out in 1992 in the following treatment plots (n=1): **C**, control (plot size 1200 m^2); **IF**, fertigation (plot size 900 m^2) started on May 16 and consisted of irrigation of 4 mm day^{-1} demineralized water, containing dissolved fertilizers dominated by K and P, applied at rates of 60 and 36 kg ha^{-1} y^{-1} respectively (see Chapter 5 for details); the fertigation treatment had been carried out in the three previous years as well; **D**, drought (plot size 100 m^2), induced by a 96% throughfall interception by a roof cover at 1 m above the soil surface, and started on June 25, intercepting a total of 60 mm throughfall water in July and August.

Xylem sapflow was measured in order to determine daily tree transpiration and is further called "transpiration" for reasons of convenience. Sapflow is measured in the sapwood at a height of approximately 1.80m with the heat-balance method. The temperature loss of directly heated tissue was a measure of sapflow (Kucera *et al.*, 1977). Sapflow in three trees of different size class, each having two sensors, was measured simultaneously for one month before treatment start, to estimate variation between trees. On June 25 sapflow registration started in trees that were larger than the mean basal area tree (diameter at breast height, DBH, >21 cm), in two trees in **C** (each having one sensor), in one tree in **D** (two sensors), and in one tree in plot **IF** (two sensors).

On June 29, July 31 and August 27 xylem potentials of shoots were determined on two to six moments during the day. Two shoots of three trees on a plot were taken each time (n=2x3=6). The sampled second-order shoots were located on the 10th whorl from the top, on the sunny side of the crown and consisted largely of one-year- and current-year needles. Shoot weight was measured immediately after cutting and after drying at 70°C for 48 hours in order to determine the water content. Xylem potentials were measured in a Scholander pressure bomb within five minutes after cutting. The monitoring of xylem potentials was done on control and fertigation plot on all three days, whereas the water-stressed trees were only sampled on August 27.

Contents of starch, water-soluble carbohydrates and pyruvate were determined on current-year needles of the same sample branches of control and fertigated trees on June 29, July 31 and November 30, and of water-stressed trees on August 27. Needle samples were dried at 70°C and grounded. Water-soluble carbohydrates (WSC) and starch were determined spectrophotometrically at 630 nm after step-wise extraction of the sample in boiling water, followed by clearing with Carrez reagens and dehydration with sulfuric acid and anthrone at 100 °C. Pyruvate content was determined enzymatically after sample extraction with trichloric acetic acid, followed by pyruvate reduction to lactate. On July 16 pressure-volume curves were constructed by drying in the open air (Neufeld and Teskey, 1986) of shoots of control and fertigation treatment, that were sampled according to the procedure mentioned above (n = 6) and were subsequently periodically measured during drying on water potential and fresh weight, later followed by a determination of oven-dry weight.

Diameter increment was determined before (April 24 - June 25) and after the treatment (June 25 - December 22) in all the plot trees.

Soil moisture content was measured biweekly in the first 50 cm by Time Domain Reflectometry (TDR) in the control plot. In the fertigation and drought plot soil moisture content was determined from soil samples (8 and 31 July, 12 August), and derived from biweekly measurements of soil pressure heads (only fertigation).

Precipitation, throughfall and temperature within the canopy were measured daily. Solar radiation above the canopy was registered every 15 minutes. The FORGRO model (Mohren *et al.*, 1992, version 3.1) was used to calculate potential forest transpiration on basis of the Penman-Montheith equation. For this model, wind speed and early-morning vapour pressure deficit on a daily basis were obtained from a weather station in Wageningen, a town at a distance of 25 km from the forest site. All relevant stand characteristics were incorporated in the model.

3. Results and discussion

3.1. Tree versus stand transpiration

From May to June the sapflow per unit sapwood, or flux density, differed by more than a factor two between the three control trees (Table 1). The sapflow trees were assumed to each represent 1/3 of the trees in the stand. The three catogories were named suppressed, intermediate and dominant. The multiplication of their flux density and fraction of stand sapwood basal area (BA) gives the stand transpiration for each category (Table 1). Hereby sapwood BA is assumed to be proportional to total BA. This is very probable, since De Kort (1991) found a strong linear relation between basal area and sapwood basal area in this stand (r^2=0.955). The estimated contribution to stand transpiration in May of the suppressed trees was ca. 1%, of the intermediate trees 16% and of the dominant trees 83%. A 70% contribution of similarly categorized dominant trees was calculated by Cermák (1989) for oak and was measured by Granier (1987) for Douglas fir. Especially transpiration of the suppressed trees in our stand was relatively low and this can be illustrated by the flux density, that was approximately seven times lower than in the dominant trees. Probably the crowns of the suppressed trees received lower radiation loads due to shading of neighbouring, larger trees in full daylight. Sapflow flux densities were comparable to those from other studies, where maxima of 3.2 $Mg.m^{-2}$ (or m) per day were reported (Granier *et al.*, 1990).

From June 25 onwards the continuous sapflow measurements on two points per treatment plot in intermediate and dominant trees were scaled to stand level, according to the values on their transpiration contributions in Table 1. The total stand sapwood BA of intermediate and dominant trees was 20.6 m^2 ha^{-1}. Transpiration of suppressed trees was assumed negligible (<1%).

Table 1. Sapwood characteristics at 1.80 m height and mean sapflow rates from May 19 to June 16 1992 in three trees of different size. DBH, diameter at 1.3 m height; BA_s, sapwood basal area.

Category	DBH	BA_s	% of stand BA_s	Mean sapflow	Water flux density	% of stand transpiration
	cm	cm^2	-	L day^{-1} $tree^{-1}$	m day^{-1}	-
Suppressed	< 19	78	18	2.5	0.32 ± 0.15	1
Intermediate	19-23	184	35	18.6	1.01 ± 0.45	16
Dominant	> 23	320	47	71.2	2.22 ± 0.91	83

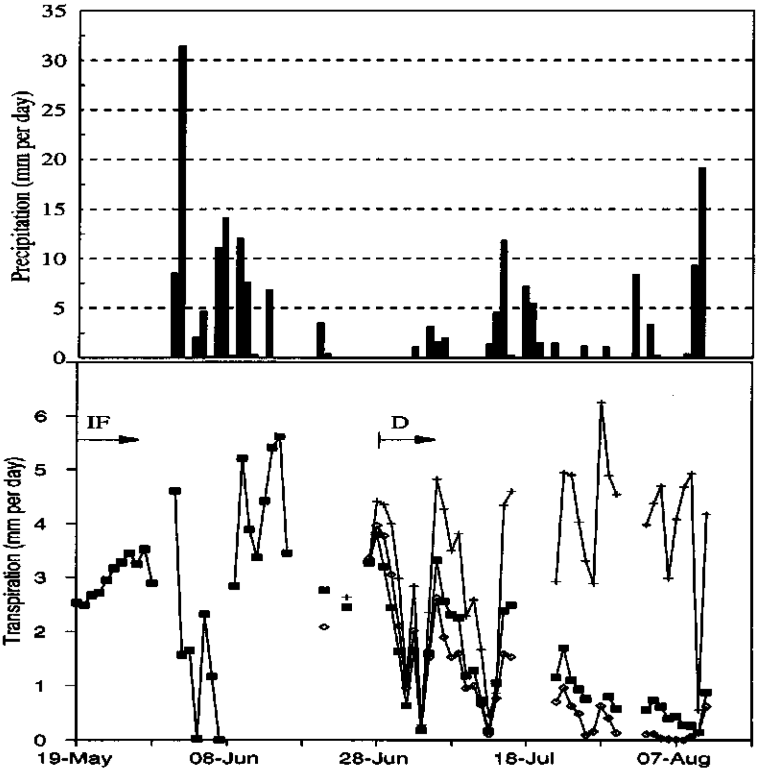


Figure 1. Precipitation and stand transpiration (mm day^{-1}) during the growing season of 1992. Arrows indicate the treatment starts. **C**, control (■); **IF**, fertigation (+); **D**, drought (◇).

3.2. Seasonal pattern of transpiration

In the middle of May stand transpiration (Fig. 1), as calculated from sapflow measurements in three diameter classes, slightly increased on 10 consecutive sunny, days with comparable mean air temperatures (19.5 ± 1.4 °C), solar radiation levels (24.5 ± 1.4 MJ m^{-2}) and early-morning vapour pressure deficits (1.19 ± 0.20 kPa). The transpiration increase of *ca.* 1 mm in total, could have resulted from the increase in leaf area index (LAI). After a number of rain showers at the beginning of June, daily transpiration reached values of almost 6 mm.

Stand transpiration was only slightly different between the treatments at the end of June. In July however, transpiration decreased rapidly and in a linear fashion in control and drought treatment, while the fertigated trees maintained a transpiration of *ca.* 4 mm per day. The control trees did not increase transpiration rate after a few rain showers in July. In the artificial drought plot tree transpiration almost stopped one month after water stress initiation.

3.3. Diurnal pattern of transpiration and water status

3.3.1. Sapflow

On June 29 solar radiation followed a smooth sinusoidal curve (Fig. 2). Daily global radiation was 26.03 MJ m^{-2} day^{-1}, mean air temperature was 25 °C and early-morning vapour pressure deficit (VPD) was 1.29 kPa. The sapflow responded on radiation with a delay of approximately two hours. In the fertigated tree sapflow steadily increased until 15h, with a small retardation after 10h. The flux decreased again two hours after the moment of highest radiation. Daily total transpiration in the fertigated plot was estimated low (3.7 mm) relative to the Penman-Monteith transpiration (7.1 mm), calculated with the model FORGRO. In the control and drought trees sapflow did not further increase from 10h onwards. The differences in sapflow between treatments appeared to be significant during most of the day.

On July 31 radiation totalled 19.38 MJ m^{-2} day^{-1} and average temperature was 23.4 °C, being a little lower than on June 29, but VPD was somewhat higher (1.34 kPa). The equal slopes of radiation and mean sapflow in the fertigated tree indicate that almost no tranpiration reduction occurred. Indeed the transpiration estimate of 3.6 mm resembled that of calculated potential transpiration (4.0 mm). In the control trees sapflow was strongly reduced, and was estimated 0.6 mm day^{-1}. In the water-stressed tree almost no sapflow was detected.

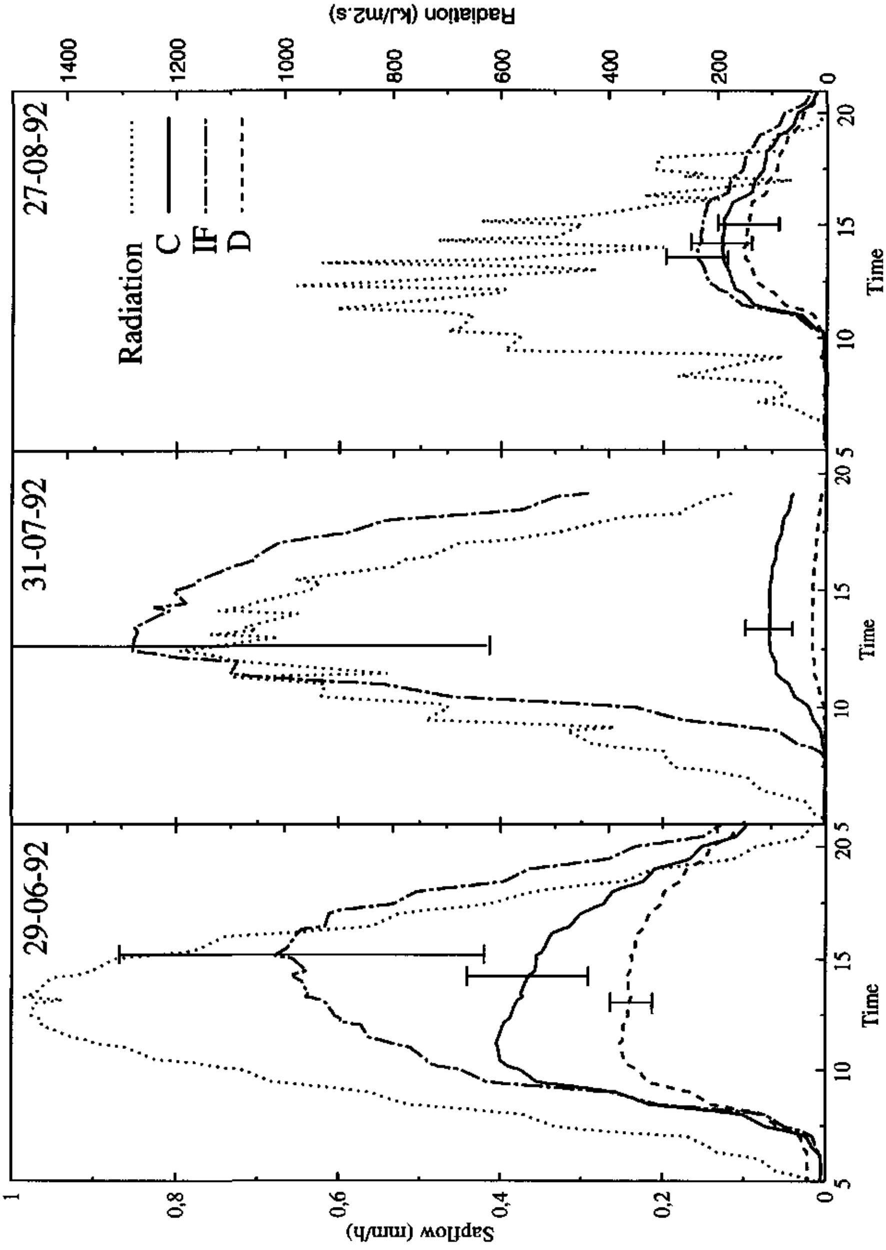


Figure 2. Diurnal course of tree transpiration (mm h^{-1}) according to sapflow in three treatment plots on three days. C, Control; IF, fertigation; D, drought; error bar: difference between replicates.

On August 27 total radiation (11.1 MJ m^{-2} day^{-1}) was less than half of that on June 29, and mean temperature was 3 degrees less. The sapflow pattern and amount was the same for all measured trees. Trees in the drought plot had probably received enough water, passing through the roof gaps around the tree trunks, to recover from the imposed water stress. Total estimated transpiration of 0.8 mm was one fifth of that on June 29. The relative increase of sapflow, with a time-lag of *ca.* two hours relative to radiation, does not indicate a reduction of transpiration at the moderate evaporative demand.

3.3.2. Xylem potentials

On June 29 the xylem potentials in the control trees were 0.4 to 0.6 MPa lower ($p<0.05$) than in the fertigated trees (Fig. 3). The potentials in the control hardly decreased anymore after 10h. The value of -2.1 MPa corresponds to the stop of sapflow increase (Fig. 2) and indicates partial stomatal closure. These values agree with needle water potentials found for total stomatal closure in Douglas of -2.2 (Waring and Running, 1978) to -2.5 MPa (Harrington *et al.*, 1994).

The predawn water potentials (*i.e.* the water potential determined before sunrise) on July 31 were 0.6 MPa higher in fertigated trees than in control trees and indicated a higher soil water availability by fertigation. Before, on July 16 a smaller difference of predawn potentials was observed, with -0.76 MPa in the control and -0.53 MPa in the fertigated trees respectively. This indicates that the effects of water stress increased with time. Xylem potentials on July 31 were higher in early-morning and late-afternoon ($p<0.05$) as a result of fertigation, but in all treatments values were down to -2.1 MPa around noon.

On August 27 the xylem potentials were in general not different between treatments. The low control values relative to fertigation around 11h disappeared within two hours and might be caused by the later sampling time in the control plot, *i.e.* on the moment when trees responded to the drastic increase in radiation (Fig. 2).

3.3.3. Response of sapflow to rain events

Figure 4 shows the diurnal course of transpiration (sapflow) during four consecutive days. The first day represents the last day of a period with low amounts of precipitation. It shows an almost unrestricted water consumption of the fertigated tree and a stressed water supply in control and drought plot.

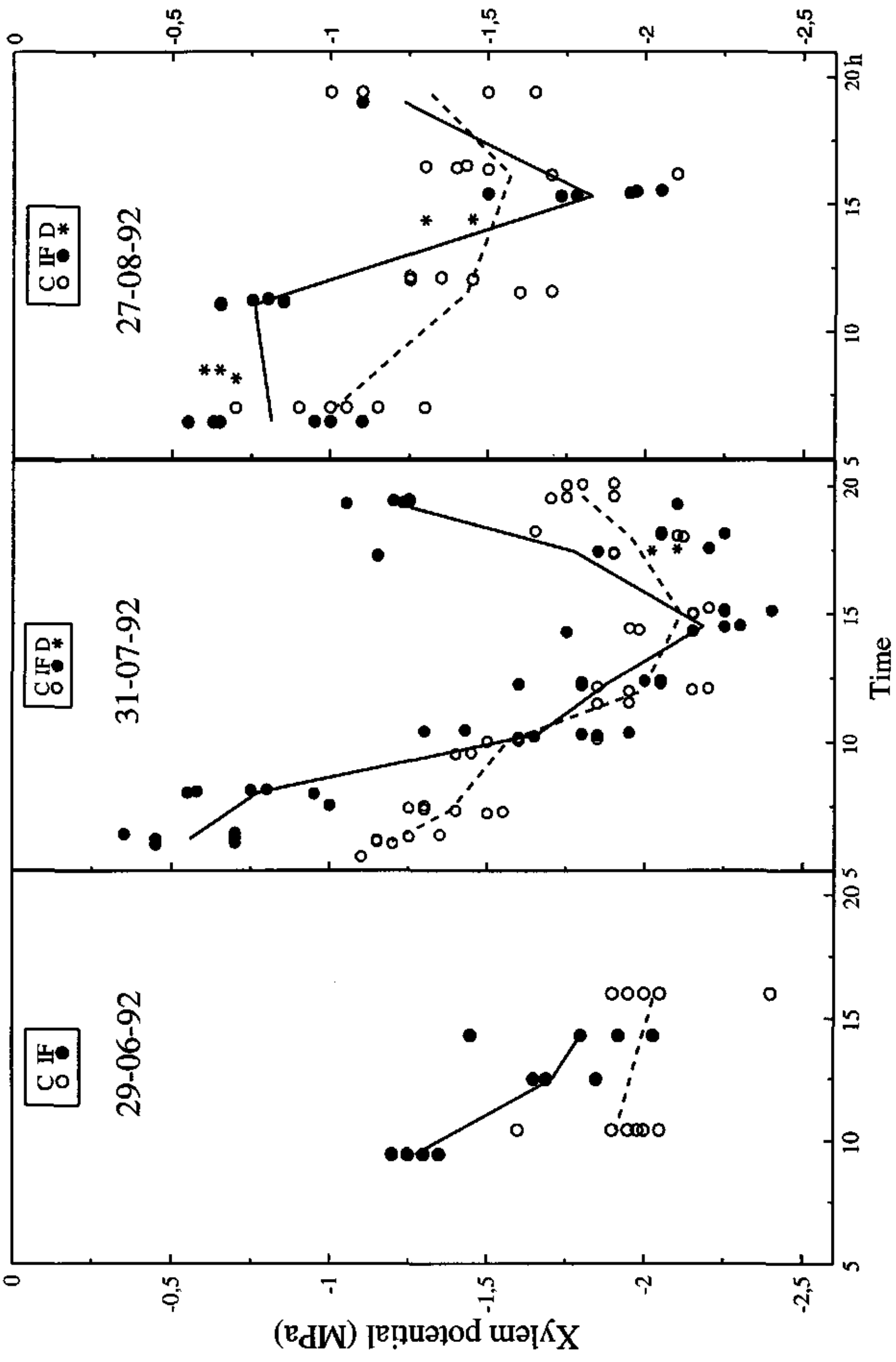


Figure 3. Shoot water potentials (MPa) on three days. A solid (**IF**, fertigation) or dashed line (**C**, control) is drawn between the mean values. **D**, drought treatment.

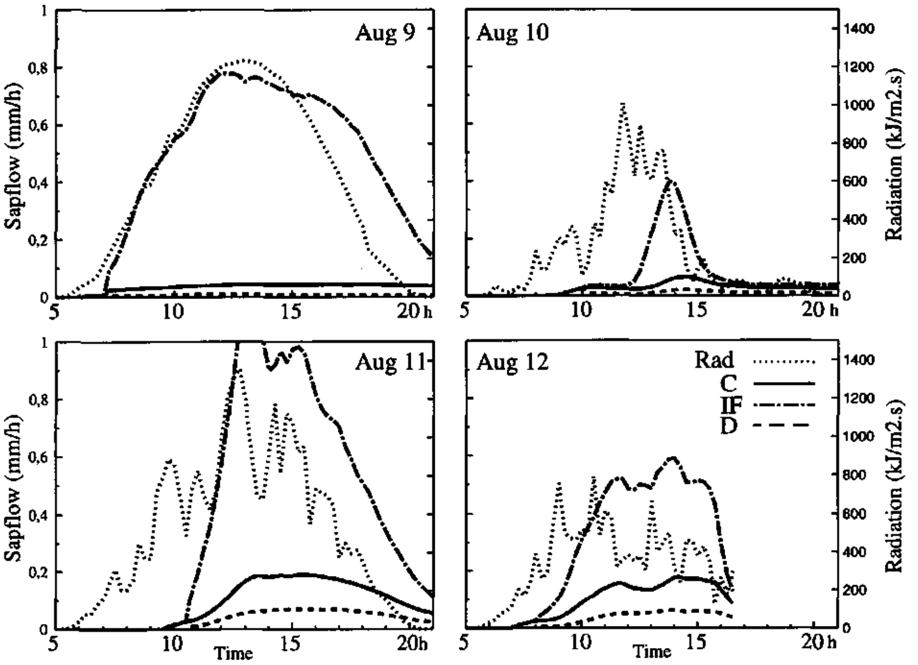


Figure 4. Diurnal course of tree transpiration (mm h^{-1}) according to sapflow in three treatment plots in August 1992. On August 12 at 16.30 h the measurements were stopped due to a technical failure.

In the two days that followed, 29 mm of rain and 22.5 mm of throughfall were registered. Radiation input was depressed by clouds from August 10 to 12. Nevertheless, on the rather sunny 11th of August, sapflow increased relative to that on August 9 at all treatments. Quite surprisingly, the fertigation tree was profiting from the extra water input, as did the other trees to a small extent. Transpiration in control (0.8 mm) treatment was still far from the calculated potential level (2.6 mm), despite the increased water availability. The roof cover did not intercept all throughfall water and a small transpiration increase was observed (0.6 mm) The trees' ability to respond on rain events has probably been lowered during summer and this can be illustrated by the transpiration in the control on two days at a equally high E_p (4.0 mm) subsequent to *ca.* 7 mm of throughfall: transpiration increased pronouncedly on June 1 (4.8 mm), but only moderately on July 15 (2.4 mm). Water uptake might have been restricted by a (reversible) decrease in xylem conductivity due to low water content, by cavitation (Breda *et al.*, 1993) or by a (irreversible) root dieback due to drought. This restriction was not apparent in the fertigated tree, which took advantage of the water from the recent rain showers. Field (Granier, 1987) and laboratory (Ciencela *et al.*,

1992) observations showed a rapid first response of sapflow upon rewetting, slowly further increasing in dependence of root resistance and xylem conductivity.

3.4. Driving variables of stand transpiration

3.4.1. Evaporative demand versus soil moisture

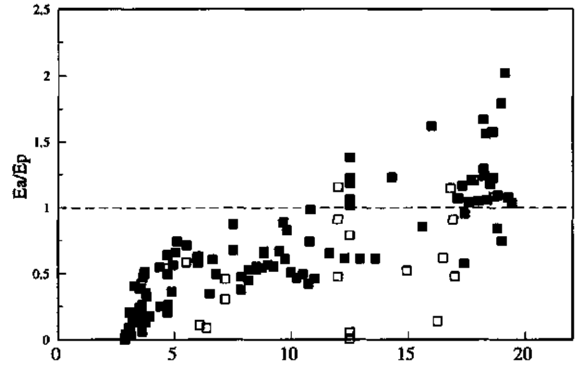


Figure 5. The ratio actual (E_a) versus potential (E_p) daily stand transpiration in relation to mean volumetric moisture content at 0 to 50 cm soil depth.

Daily stand transpiration E_a, as derived from sapflow measurements scaled to stand level, was compared to the potential forest transpiration E_p, calculated with the model FORGRO. The transpiration reduction was expressed as the ratio E_a/E_p. This reduction is plotted against the mean soil moisture content over the depth 0-50 cm during the research period (Fig. 5). During rain events transpiration was reduced due to a wet canopy. The ratio E_a/E_p decreased asymptotically from 10 % water content (v/v) towards a residual water content of 2.8%, equivalent to *ca.* -2 MPa according to soil retention curves. Above 10% soil moisture content the ratio scattered around 1, with some values above 1.2 in the fertigated tree and no apparent transpiration reduction. At dry soil conditions transpiration reduction was explained fairly well by soil moisture. The reduction is probably linear to the decrease in soil tension, as was shown by Bosveld *et al.*(1993), who found a 50% reduction at -0.6 MPa, *i.e.* 4.5% water content in our soil.

3.4.2. Weather conditions

Transpiration on days without rain could partly be explained by early-morning vapour pressure deficit (Fig. 6a). The best fit was found for the data of the control trees (R^2=22.2%, correlation coefficient= -0.47). Transpiration was clearly related to global radiation (Fig. 6b), and especially the data of the fertigated tree (R^2=72.0%, correlation coefficient=0.8486) seemed to show the same functional relation with radiation, as described by Jarvis (1976). For drought and control trees R^2 was smaller than 50% and transpiration was less due to the influence of a restricted root water uptake. No relation was found between transpiration and air temperature (data not shown). Actual daily transpiration was also calculated with FORGRO (see Mohren *et al.* (1992) for model description) on basis of the mentioned variables, including soil moisture and temperature and compared to transpiration, which was estimated from sapflow in the control trees (Fig. 7). During dry periods the simulation results agreed fairly well with the transpiration estimates, but in rainy periods differences upto 2 mm were probably related to local differences in water input (between the place of the sapflow trees and rainfall collectors).

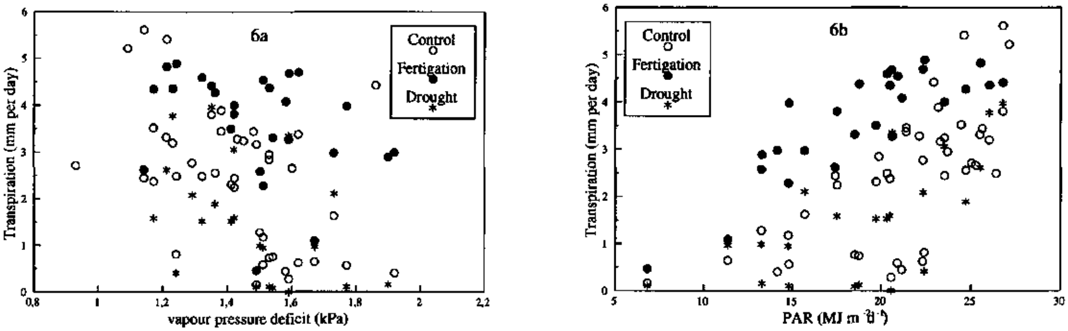


Figure 6. Daily transpiration (measured) *vs.* early-morning vapour pressure deficit (Fig. 6a) and *vs.* solar radiation (Fig. 6b).

Table 2. Predawn water potentials (Ψ), water contents (W_t) and osmotic pressure (π_{needle}) in cell sap of shoots sampled on four occassions.

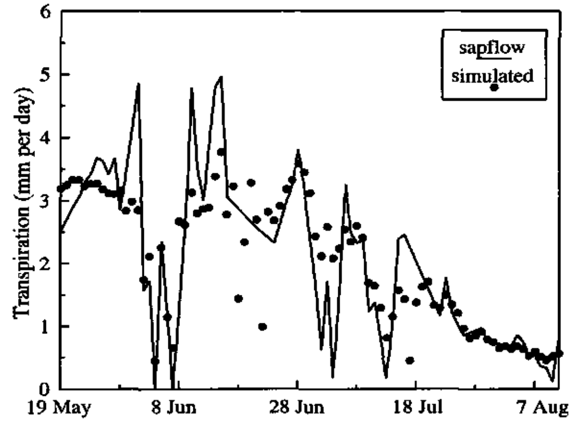
Sampling date	Treatment	Ψ_{shoot}	W_t	π_{needle}
		MPa	%H_2O (w/w)	MPa
Oct 16 1991	Control	-0.44 ± 0.02	153 ± 3	2.33-2.43 (8-13h)
	Fertigation	-0.40 ± 0.07	185 ± 12	2.04-2.31 (id.)
July 16 1992	Control	-0.38 ± 0.16	168 ± 15	2.4[#]
	Fertigation	-0.53 ± 0.20	196 ± 16	2.4[#]
July 31 1992	Control	-1.20 ± 0.08	173 ± 50	
	Fertigation	-0.86 ± 0.15	200 ± 26	
Aug 27 1992	Control	-1.02 ± 0.19	185 ± 2	
	Fertigation	-0.81 ± 0.21	194 ± 12	

[#], estimated from P-V curve (Fig. 8)

3.5. Impact of treatments on physiological parameters

3.5.1. Pressure-volume (P-V) relation

The relation between xylem potential and shoot water content was determined with the 'free-transpiration' method on samples collected on July 16 (Fig. 8). The fully hydrated shoots had a maximum water content (W_t or 100% relative water content) of 190 and 220% of dry weight in control and



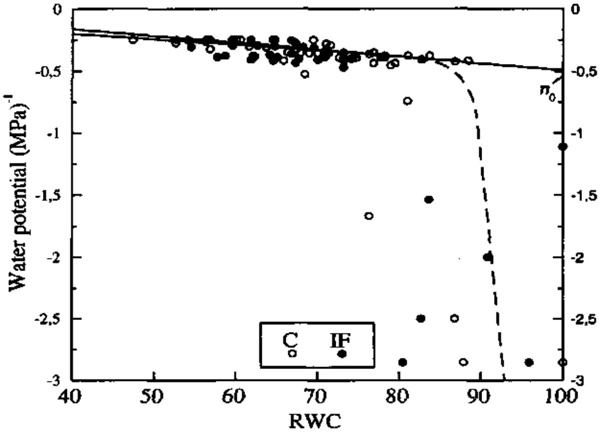


Figure 7 (above). Actual transpiration according to sapflow measurements (solid line) and calculated by FORGRO (filled circles).

Figure 8 (below). Pressure-volume (P-V) relation for control (C) and fertigated (IF) trees. At a relative water content (RWC) of 100% (full saturation) shoots of treatments C and IF contained 190 and 220% water (on dry weight basis) respectively. π_0, osmotic potential at full saturation, is 2 MPa.

fertigated trees respectively. Loss of water and turgor was apparent below -2.4 MPa (0.4 in MPa^{-1} in Fig. 8) in both treatments. The regression lines through the data points of the water potential below turgor was equal between the two treatments (R^2 ranged between 32 and 37%). The osmotic potential at full turgor π_0 was calculated from the intersection of the regression line with the Y-axis (at W_t)(Tyree and Hammill, 1972), giving approximately 1/0.5= 2.0 MPa for both treatments (Fig. 8). The similar π_0 and turgor loss point at approx. -2.0 MPa in both treatments indicates a lack of osmotic adjustment at water stress. The cell wall elasticity could not be calculated from the change of slope between between 1 and 2 MPa, because the number of points was limited. The significant difference in water content (WC) in turgid shoots of control and fertigated trees was found on other sampling occassions as well (Table 2). The fertigated trees seem to retain more water at approximately equal osmotic and turgor pressure (Oct. 16). This was also found by Jensen *et al.* (1993) in K-fed barley plants. They concluded that increased K availability had increased cell size. In the shoots we examined, K contents had raised from 0.7 to 1.0% by fertigation (Chapter 5). However, an increased cell elongation can also result from an improved water availability or a change in cell wall elasticity.

Table 3. Concentration of total water-soluble carbohydrates (WSC), starch and pyruvate in current-year needles of Douglas fir in 1992. Significant differences ($p<0.05$) within one column on one date are indicated by a different letter behind the mean (n = 3).

Date	Treatment	WSC	Starch	Pyruvate
		% of D.W.		mmol kg^{-1} D.W.
29-06	Control	6.94	2.75	1.08
	Fertigation	7.14	2.87	1.26
31-07	Control	5.28	2.78	1.63
	Fertigation	6.67a	2.96	1.46
27-08	Control	7.48a	2.10b	0.49b
	Fertigation	6.96ab	2.02b	0.48b
	Drought	5.79c	3.24a	1.34a
30-11	Control	5.16	2.24	1.51
	Fertigation	6.25	1.98	1.39

3.5.2. Organic compound) in needle tissue

A higher concentration of total water-soluble carbohydrates (WSC) was found in the fertigated trees on July 31 (Table 3) and a lower concentration in the water-stressed trees on August 27, relative to the control and fertigated trees ($P<0.05$). Starch concentrations were significantly increased due to drought on August 27, despite the high standard errors. The concentrations of pyruvate seemed to be equal for all treatments and sampling dates, except for two probably erroneous results on August 27.

A trend towards higher WSC concentration in the fertigated trees and a lowering at drought seemed to indicate less profitable conditions for carbon assimilation at water stress. The water potentials below -2.2 MPa found here, did not increase the WSC concentration as was found by Zwiazek and Blake (1990) below -2.3 MPa in black spruce. On the contrary, WSC levels were increased in the trees, that had shown an almost unconstrained water uptake. However, water potentials on bright, warm days were very low irrespective of treatment. The results suggest a decrease of WSC production with increasing stress. The control trees might have depleted some WSC during July, followed by a net increase during rewetting in August. During further stress in the drought trees the depletion of WSC might have continued. For some unknown reason the drought trees had accumulated some starch. However, more research is necessary to confirm that osmotic adjustment is not common in Douglas fir (Joly and Zaerr, 1987).

3.5.3. Tree growth

Diameter growth was approximately 2 mm until May 29 in all plots, afterwards DBH growth in the sapflow trees (n=2) was 5 mm in control, 3 mm in drought and 12.5 mm in the fertigated trees. On a plot scale the differences were less: annual growth was 6.0 mm in control, 4.6 mm in drought and 7.9 mm in fertigated plot. Growth in the control trees was almost 1 mm higher than in the three previous and mostly drier years. This might have been caused by the generally high temperatures during the season and the high rainfall amounts in June.

4. Conclusions

Stand transpiration decreases almost linearly during summer drought and transpiration reduction largely depends on soil moisture content. Occasional rain showers did hardly promote transpiration rate, unless soil conditions were moist beforehand. Stand transpiration can be simulated well, if the calculations comprise soil moisture content in addition to weather variables. Tree water uptake recovered (August 27) from water stress within 17 days after cessation of drought (August 10).

Stomatal closure occurs at shoot water potentials below -2.2 MPa in both control and fertigated trees and this is in accordance with the values on turgor loss point (*ca*. -2.4 MPa) and cell sap osmotic pressure (*ca*. -2.3 MPa). It is also in agreement with a -2 MPa soil suction at 100% transpiration reduction, indicating the maximum tree suction necessary for water absorption. No evidence was found for osmotic adjustment and carbohydrate accumulation despite transpiration deficits upto 90%. Diameter growth was not depressed relative to other years so water stress might have not been so severe, even at artificial drought. Yet the growth was considerably enhanced by fertigation and the daily transpiration rates, that were occasionally 6 mm, could hardly be met by the irrigation amounts of 4 mm day^{-1}.

Shoot water storage capacity has increased by the combination of irrigation and nutrient applications, and this can be related to an increased cell size.

Acknowledgements

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CHAPTER 9

General discussion

General discussion

This chapter aims at answering the questions posed in Chapter 1, by discussing the results of this investigation with regard to existing knowledge. In addition the approaches and methods used in this research are discussed.

(i) Are growth and nutrition of trees influenced by ongoing soil acidification due to ammonium inputs ?

In addressing question *(i)*, the discussion will first focus on the soil acidification rates observed in this investigation, followed by an evaluation of the effects on trees, and finally the issue of excess NH_4 will be discussed.

(*i*-1) Soil acidification rates

The N supply in Dutch forests has increased in the last three decades due to increased atmospheric N deposition (Erisman, 1993; Heij and Schneider, 1991). All the three investigated forest ecosystems show a high N availability and a concomitantly high rate of soil acidification (Van Breemen *et al.*, 1986, Chapters 3 and 4). The loss of Acid Neutralizing Capacity (ANC) in the stands ranged from 2.14 in Scots pine (Chapter 4), 3.74 in Douglas fir (Van de Maas, 1990) and 4.3 (site C) to 12.3 (site A) kmol H^+ ha^{-1} y^{-1} in oak (Van Breemen *et al.*, 1986) . This acidification was mainly caused by N transformations and is largely buffered by Al dissolution in the top soil. Despite the observed differences in soil acidification rates, pH in the soil solution is rather similar between sites and treatments and fluctuates between 3.4 and 3.6 at 0 to 40 cm depth. One exception is the Scots pine stand, where all plots show pH values of *c.* 4.2.

The soil in the pine stand was further acidified by $(NH_4)_2SO_4$ applications and the pH-value decreased to 3.9 (Chapter 4). In this treatment soil acidification was predominantly increased by net NH_4^+ immobilization since nitrification was not strong: only a small increase in net NO_3 production was found (+0.3 $kmol_c$ H^+ ha^{-1} y^{-1}) compared to the control. The nitrification following $(NH_4)_2SO_4$ applications depends on the former use of the soil (Feger, 1992). Also NO_3 export may be much higher if a coniferous stand follows a rotation of a mixed stand (Kreutzer, 1989), yet this was not the case in the pine stand studied here. Despite the low nitrification rate, high Al soil solution concentrations, up to 60 mg L^{-1}, were recorded (Chapter 4). This probably caused root damage, although Scots pine seemed tolerant to Al concentrations upto 30 mg L^{-1} in hydroponic culture (Keltjens and Van Loenen, 1989).

Higher summer peaks and increased mean Al concentration in the soil solution were an adverse side-effect of fertigation (*i.e.* irrigation+nutrients, see Chapters 3, 4 and 5). This higher soil acidity was related to nitrification of added NH_4 and to adsorption to soil and tree uptake of applied base cations, releasing more protons and Al in the soil solution temporarily. This process was also observed by others after applications of K salts on acid soil (Matzner *et al.*, 1983; Tamm, 1991).

In the treatment where atmospheric deposition was excluded, Al concentrations decreased drastically in winter in all treatment years. In two treatment summers Al concentrations were raised due to the effects of fertigation, as mentioned above, combined with an occasionally dry soil despite water additions. The rapid decrease of soil acidity in winter in the absence of applied nutrients is in accordance with results of other deacidification experiments (Boxman *et al.*, 1994; Hultberg, 1992; Wright *et al.*, 1988).

(*i*-2) Effects of changes in soil acidification rate on trees

In two treatments the acid loads to the soil system were manipulated:

(*I*) $(NH_4)_2SO_4$ application: a depressed tree growth was observed after two years of growth enhancement. This growth decrease was probably related to the observed P deficiency, that may have been caused by increased Al-P precipitation in soil and roots due to higher Al activity and lower pH (Chapter 4). It is remarkable that the tree crowns showed no visual damage: tree characteristics as recorded in the routine vitality surveys probably fail to reveal the first effects of high soil acidity on trees.

(*II*) Withdrawal of atmospheric deposition: in this "soil reference plot", where effects of atmospheric deposition were excluded by the installation of a roof, soil acidification was only slightly decreased during a period of four years. Growth increased considerably (40%) and instantly. The growth enhancement might be attributed to a combination of factors: an increased water supply (1), a decrease of the NH_4/NO_3 uptake ratio (2) and a decreased nitrification (3), where (2) and (3) both decrease soil acidification. These factors probably favoured the growth conditions for roots, and could for instance increase root longevity, as was found by Murach and Wiedemann (1988) after liming. Van den Driessche (1978) also observed a growth enhancement in Douglas fir at an increased fraction of NO_3 in the N application to an acid soil. The small decrease in soil acidification is the only factor that differed from the plot receiving similar additions of nutrient and water, but without interception of atmospheric deposition. However, growth differences between trees in this roofed plot and those in the irrigated plot were quite small when compared to former growth levels (Chapter 5, Table 3), suggesting that any growth effect above that of irrigation alone might be insignificant.

(*i*-3) Is the N supply to trees excessive and, if so, to what extent ?
If the N concentration and the ratios P/N and K/N in needles are good predictors of excess N in trees, the studied stands can be judged likewise. For Scots pine critical upper needle concentrations of 1.8% (Aronsson, 1980), 2.0% (Focke, 1991) and 2.2% (Anon., 1990) have been reported. In the present study N concentrations in Scots pine needles vary between 1.6 and 2.3% (Chapter 3). In Douglas fir needles and oak leaves reported supra-optimal N concentrations, above 1.8% (Van der Eerden, 1992) and 2.8% (Anon., 1990) respectively, were observed only occassionally in the stands studied here. In these stand however, about 50% of the atmospheric N input is leached again from the soil (Van Breemen *et al.*, 1986; Chapter 5) and can be qualified nitrogen saturated according to the definition of Aber *et al.* (1989).

The observed N levels can be judged by relating the growth parameters to different N deposition rates. Three treatments presented in this thesis can be used for this purpose: (*I*) the $(NH_4)_2SO_4$ application in Scots pine; (*II*) the withdrawal of the atmospheric deposition in Douglas fir; (*III*) the application of NH_4NO_3 in the fertigation of the pine and fir stand. The response on these treatments is discussed below:

(*I*) The application of $(NH_4)_2SO_4$ (Chapter 4) resulted in a modest increase of both needle N concentration and growth during the first two years, followed by a drop in growth below the control level in the fifth treatment year. In the pot trial with Douglas fir a growth enhancement by $(NH_4)_2SO_4$ applications was also followed by growth depression, yet on a smaller time scale. The N nutrition was probably supra-optimal both in the adult pine trees and in the Douglas fir seedlings, since high concentrations of arginine were found in needles of both species (De Visser, 1990). In the $(NH_4)_2SO_4$ plot N uptake and leaching losses were increased by *c.* 10 to 15 kg ha^{-1} y^{-1}, indicating nitrogen saturation of the ecosystem, and almost 120 kg N ha^{-1} y^{-1} was retained in the soil. In acid soil in Germany Feger (1992) also found a high retention of NH_4 from $(NH_4)_2SO_4$ application, Meiwes and Beese (1992) however observed only 15 % retention and large nitrification rates at comparable application rates. Hofmann *et al.* (1990) calculated that N loads as used in this experiment, may cause dieback in Scots pine within five years, but he did not mention any distinctive mechanism.

(II) Withdrawal of atmospheric deposition clearly decreased needle N concentration (to 1.6%) and led to the highest tree growth of all treatments. Needle concentrations of other nutrients did not increase relative to those in the non-roofed fertigation treatment, where growth response was smaller (Chapter 5). An increase in growth after reducing N deposition was also observed in the Danish roof experiment (Chapter 3) and suggests that N

availability is still high enough to maintain high growth rates on the short term. The used N application rates in the roofed plot should even be further reduced to minimize N losses from the soil. On the longer term tree growth at lower N deposition levels might depend more on mineralization rate and nitrogen use efficiency.

(III) Fertigation with and without roof comprised, among other nutrients, an application of NH_4NO_3, that was reduced by 50% each year, starting at 78 and 31 kg N ha^{-1} in the Douglas fir and the Scots pine stand respectively. The high growth rate in 1989 in Douglas was not observed again in the following years and might be related to the N application that year. The needle N concentration suddenly rose relative to both the other treatments and the previous year, whereas in the two years that followed the N contents decreased and the needle concentration of other elements remained equal to those of 1989 (Chapter 5, Table 2). Above all, significant NH_3 immissions were registered above the forest floor (A. Vermetten, pers. comm.) in 1989. The Douglas fir is known to have a high capacity to absorb fertilizer N (*cf.* Van den Burg, 1988) and can store large amounts of N in needle tissue (upto 3.5%) without short-term damage. However, it may be too tentative, to generalize from a single treatment plot in a single year. Moreover, most of the applied N was lost again by leaching (Chapter 5).

(ii) What is the effect on growth of an improvement of the nutritional balance of trees at the present deposition rates ?

In the forest stands studied here, only mild deficiencies occur: in Douglas fir P and K are insufficient in some years, in Scots pine P is occasionally low, and in oak Mg seems insufficient according to Dutch standards (Anon., 1990) on one soil. Yet the Norway spruce stand in Solling showed pronounced deficiencies of N, P and especially Mg (Chapter 3). The element to N ratios can be regarded as unfavourable (Anon., 1990), and deviate strongly from optimal ratios according to Ingestad (1979). Nutrient applications have restored the balance between K and P to N, but since absolute concentrations of nutrients were never seriously limiting, this did not lead to growth enhancement, as shown by the results of the balanced fertilization trials (Chapter 3 and 4). However, possible growth effects could have been masked by the stronger response to irrigation, relative to the response observed in a fertilizer trial with K and P in a neighbouring Scots pine stand (Arnold and Van Diest, 1993).

The nutrition of trees can be out of balance due to traditional or pollution stress factors. Fertilizer application of deficient elements may rapidly alleviate nutrient limitations (Evers and Hüttl, 1990/91) and may exert its influence over decades (*cf.* Shepard and Mitchell, 1989). In Germany Mg deficiencies were mitigated by Mg hydroxide, Mg silica or dolomite applications (Zöttl, 1985). In Belgium Ca shortage was alleviated by lime applications (Nys, 1989). The shortage of base cations in these countries could be attributed to an almost exhausted soil due to former intensive management, in combination with leaching losses due to increased acid loads. In the Netherlands the most obvious element shortages nowadays have been induced by a high N availability, which increased above ground growth, thereby increasing the demand for other nutrients. In Douglas fir forests P deficiency is now more common than in the fifties (Mohren *et al.*, 1986) and Cu shortages have frequently been found in forests on former heathlands and in de "Peel" region (Van den Burg, 1988). In the forest stands studied here, the moderately low availability of P, and occasionally of K, were amended by nutrient applications within two years, as seen from the chemical composition of the needles. The better P and K status, which almost seemed "luxurious", may improve the resistance to drought (Larsen, 1983; see also question 3) and frost (Christersson, 1973). In the long run the added nutrients may result in a higher vitality and a possibly higher survival rate of trees. The nutrient applications have raised soil fertility, since a large fraction of the fertilizer was stored in the soil (Chapters 4 and 5). These soil nutrient pools may ensure an improved tree nutrient status for several years. For example an extra uptake 8 kg K ha^{-1} y^{-1} is sufficient to increase content of K in 4 Mg ha^{-1} new-formed needles from a low (0.6%) to an optimal (0.8%) value. Pot experiments with the forest soil of the Douglas stand showed that the nutrient pools can be rapidly exhausted (Chapter 6). Nutrient applications restored the seedling nutrient status, except for Ca and Mg. The Douglas fir stand in Kootwijk may probably benefit from higher Ca application rates as those, used here (5 kg Ca ha^{-1} y^{-1} during 4 years). The competition of Ca with Al at the root interface (Marschner, 1991) may be due to this Ca shortage, since the supply rate was based on levels used in hydroponic culture (Ingestad, 1979) without Al.

When nutrients are non-limiting but potential growth is not reached, an ecosystem disturbance might be present where either uptake or utilization of nutrients is hampered (Ingestad and Ågren, 1989), such a disturbance might be induced by acid deposition. The "optimal nutrition" approach becomes less useful, if the ecosystem disturbance is due to a fertilizer itself, *i.e.* ammonium deposition. Furthermore, the N nutrition may be supra-optimal and thus not further increase current annual production (Nilsson, 1986). This is very probably the case in the Dutch stands (see also below), even if all other nutrients and water are non-limiting.

(iii) To what extent is tree growth limited by drought, and are there interactions between water stress and soil acidification ?

Water stress reduced diameter growth of coniferous trees on sandy soils by as much as 40% (Chapter 3, 4 and 5). These growth reductions are larger than those observed in other temperate forests on sandy soil where irrigation experiments were conducted (Linder and Axelsson, 1982). The local weather conditions may affect the response considerably, yet tree response in Sweden was also less (Nilsson and Wiklund, 1992) in the years examined here. Of the two conifer species studied here, only in Douglas fir needle fall rates were clearly decreased by irrigation during 4 years. If we assume annual needle production did not decrease, this indicates an increase of canopy biomass. The extra biomass production of the irrigated trees may be related to several factors: needle fall was retarded by 1 to 2 months in autumn, thus the photosynthetic capacity was extended. Secondly, stomata were more open so that CO_2 uptake is facilitated (Chapter 8). Thirdly, less assimilates were supplied to the root system, since total root mass was less (Chapter 3) and root longevity was probably increased, and hence root turnover was diminished. The higher carbon availability decreased the concentrations of N and K in Douglas needles (Chapter 5) and changed the dominance of arginine in the free amino acid pool towards glutamine and others (Pérez-Soba and De Visser, 1994). The effects of irrigation and high N loads on trees are mutually linked: (1) N increases tree shoot growth and consequently water demand; (2) Irrigation stimulates growth and consequently dilutes excessive N loads in the needles, decreasing arginine concentration (De Visser, 1990).

In both Dutch forest stands the irrigation-enhanced growth did not result in increased N uptake. Instead, mineralization was stimulated by the moister soil conditions and N leaching from the soil increased (Chapter 4 and 5).

The high acidity of the soil from the Douglas fir stand impaired root growth and water uptake in a pot trial (Chapter 7). Specific root length (SRL) has often been used as an indicator of (physical and chemical) soil stress to roots. SRL is low in the soil below 20 cm depth (Chapter 3), where rooting is probably not impaired by physical constraints because bulk densities are rather low. This low root length may increase drought susceptibility in addition to the factors mentioned above. The poor root system in the control stand accounts to a certain extent for the positive growth response to irrigation. Persson (1980) found longer and thinner roots after fertigation. This is in accordance with observations in this study on specific root length, which increased by water additions (Chapter 3). Yet even in the irrigated plots water uptake and tree growth may not have been optimal due to the high Al concentrations (Chapter 5). Despite these acid soil conditions, high transpirations rates were recorded in the fertigated trees, coupled to high growth rates (Chapter 8). These trees were probably able to utilize the extra water of rain showers better than the control trees did. The causes for the constraint water uptake in the previously water-stressed trees are rather uncertain: without irrigation the root system might have been detiorated, the rewetting of conducting sapwood tissue is slow, or the rewetting of the rooting zone was not fully accomplished. Olsthoorn and Tiktak (1991) observed a considerable dieback of fine roots during drought in the same stand in 1989. These authors observed a lack of root growth response to a 64 mm rain event after drought and related this to a hampering of fine roots formation, due to the competition for assimilates with the extending shoots. The measurement of the sapflow in trees can indicate the water uptake by roots and thus the degree of root functioning (Cermák and Kucera, 1990), and this promising technique should be further applied to trees at different levels of soil-chemical stress.

The increased drough sensitivity of trees, affected by high NH_4 loads, does not only relate to the size of root and shoot biomass. The trees' water economy may be affected by a poor K status in needles. Improvements of the K and P needle concentrations were shown to decrease transpiration rates in a pot experiment (Chapter 7). Larsen (1983) and Christerson (1973) also found lower transpiration rates in Douglas fir and Scots pine respectively, as long as the trees were winter hardened. If high concentrations of NH_4 are present in the soil solution, the ion antagonism of NH_4 with K might depress K uptake and, consequently, K/N ratios in tissue. No severe K shortages were reported for forests in the central part of the Netherlands (Oterdoom and Van den Burg, 1991), but low K and K/N ratios were observed in the "Peel" region (Van Dijk and Roelofs, 1988).

(iv) What is the effect of an increased supply of water and nutrients on the nutrient cycle in the forest ecosystem ?

The increased availability of water has increased the net retention of nutrients in stemwood at both experimental sites (Chapters 4 and 5), mainly through increase of growth. The retention of N, P and K was slightly higher in the plots where these nutrients were fertigated. The increased retention of N amounted maximally 8 (Scots pine) to 10 (Douglas fir) kg ha^{-1} y^{-1}. In young, aggrading forest stands fertilization can increase net nutrient uptake much more (*cf.* Ingestad and Ågren, 1989), because needle mass can increase considerably (Linder and Axelsson, 1982). The small increase in nutrient retention of trees was overshadowed by the mostly higher increase in leaching losses of N, K, and occasionally even Ca or Mg from the soil (Chapter 4 and 5). The more favourable soil conditions enhanced mineralization, nitrification and leaching of N. Arnold (1993) observed an increased NO_3 formation in the soil of plots fertilized with P, K and Mg applications, at a site comparable to the pine stand studied here. Kriebitz (1987) found a positive correlation between the NO_3 formation and the availability of P or K+Ca in acid forest soil. Even the N availability may limit NO_3 production, as was found by Mai and Fiedler (1986) after adding P and K to a Norway spruce forest soil. In our soils water additions alone enhanced mineralization and nitrification as well. The magnitude of the improved nutrient availability on NO_3 formation could not be quantified, since the fertigation comprised some N, part of which was taken up and part of which was leached as NO_3. In the Scots pine stand, mineralization may have been influenced by the abundant ground floor vegetation, through increased supply of easily decomposable litter (Chapter 4). Gross uptake in this vegetation was estimated *c.* 18 kg N ha^{-1} y^{-1} and some of the annual return might have added to the NO_3 leaching losses, that were 16 kg N ha^{-1} y^{-1}. Irrigation enhanced the cycling of K in the pine stand, as was shown by the K concentration increase in the forest floor percolate in winter, compared to that in the control (Chapter 4). This K mainly originated from litter return of the ground floor vegetation. The application of K had increased the K cycling in both stands, as was shown by the increased K fluxes with litterfall (Chapters 4 and 5). The Scots pine stand might have been saturated with K, given the leaching losses of approximately 16 kg K ha^{-1} in 1991. In the Douglas fir stand it seemed that the litterfall flux of N and P increased by fertigation as well. The results suggest that an improved supply of N and P from the soil to the new needles resulted in lower retranslocation from senescing needles. The decrease in N flux with litterfall at the improved water supply to Douglas fir does not indicate a stronger retranslocation of N, but is explained totally by the decrease in total litterfall. In the same treatment however, K concentrations in litterfall decreased due to an irrigation-induced K shortage (Chapter 5).

(v) To what extent pot trials and forest experiments can be compared ?

In Chapters 6 and 7 clear evidence was presented for depressed root functioning and nutrient status by high supply of $(NH_4)_2SO_4$ to Douglas fir. High levels of NH_4, that were occasionally found in forests in the "Peel" region, caused tree dieback within two years. During the first two years needle composition of seedlings was rather similar to those of adult trees (Chapter 6). Later P and K nutrition became much poorer in the pot trial, and N became limiting at a supply rate of 30 kg ha^{-1} y^{-1}, suggesting the juvenile trees had absorbed most of the easily accessible nutrients. As a result of these deficiencies, the growth of the young trees responded positively to the balanced nutrition, while adult trees did not, or only slightly so in case of pine. Although needle concentrations of P and K increased by application in the forest as well, the improved ratios to N did not increase growth. The absolute concentrations are probably more indicative for nutrient shortages, and which were hardly present at the sites, hence the increased P and K content might have been luxurious uptake. As long as the high N needle status does not depress absolute needle concentrations of P and K, the secondary effects of a high N content will be more important and may relate to fungus attacks, frost damage or increased needle senescence. In the pots of this study, Al as well as other elements showed quite high concentrations in the soil solution in the course of the experiment. These concentration increases were due to the accumulation of solutes upon application. Only a very low drainage was present in the pots and the soil solution could not be replenished. Although the study on water uptake at high Al concentrations was valuable (Chapter 7), the observed concentrations will hardly occur in a forest soil at ambient conditions.

Final conclusions

Effects of atmospheric deposition on the soil acidification rates and the soil solution chemistry were indisputable at the sites studied here and these effects can easily be enlarged or decreased experimentally. The impact on tree growth needs further quantification in future research, despite the clear tree reponse on a few treatments examined here. The nature of acid stress is not expressed in growth only, but one of its main causes, *i.e.* nitrogen deposition, has a large impact on growth, as was shown here. The detrimental effects of an increased N availability on nutritional balance and drought sensitivity were observed and experimentally alleviated in this investigation. The mechanisms that relate to root and tree dieback after prolonged stress in the forest, may be further elucidated by combining knowledge and experience from laboratory studies, with tree monitoring during experimental changes in exposition of trees to stress, as done in this study.

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Summary

Summary

The recent decrease in tree vitality has been related to increasing rates of soil acidification, that are due to increased acid atmospheric deposition in the last decades. The transformation of atmospherically deposited NH_4 plays a major role in the acidifying process. The nitrification of ammonium and the subsequent leaching of nitrate produces acidity. Also the net uptake of ammonium in the vegetation releases protons in the soil. In poorly buffered, sandy soils, where most of the Dutch forests are located, the high rates of soil acidification have resulted in a low pH and high concentrations of free Al, that both affect root growth and tree vitality to an unknown extent.

The loss of base cations from the soil due to soil acidification may result in nutrient deficiencies in trees. The nutritional balance of trees can be affected even further by preferential NH_4 uptake to supra-optimal levels and can be disturbed by the ion competition for uptake of ammonium , Al and H on the one hand and K, Mg and Ca on the other hand. Furthermore acid soils can have Ca/Al ratios that are unfavourable for roots. The high inputs of N can result in lower root/shoot ratios and may increase the drought sensitivity of trees.

This study deals with the growth and nutrition of three tree species, pedunculate oak (*Quercus robur*), Scots pine (*Pinus sylvestris*) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), under influence of acid soil conditions. The aim was to determine whether the nutrient supply is growth-limiting, under the constraint of Al stress and competition with NH_4, and how nutrition and root functioning are related to the water economy of the tree. Therefore, the effects on trees were quantified changing the input of water, nutrients and acidifying substances to the soil. Two experimental approaches were being used. Firstly (*I*), the cause of the increased rate of soil acidification was manipulated by either increasing or decreasing the atmospheric loads. This can reveal some mechanisms that are related to forest decline. Secondly, the effects of increased soil acidification on trees were 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. Restoring the nutritional balance of the trees may indicate whether growth is limited by nutrient imbalances relative to N.

First, the effect of natural variations in soil conditions on tree growth and nutrition were studied. Within one stand the elemental composition of pedunculate oak was examined on three distinctive soil types. Manganese concentrations in wood and leaves were related to concentrations in soil solution. Differences in dissolved Ca and Mg in soil were reflected in leaves as

well. Poor growth was observed at the site with the highest Mn concentrations, which however did not reach toxic levels. Tree ring analyses showed that at this site growth rates were depressed since 1961. The concentration of N, P, K, Mg and S in annual rings within the tree were higher in living sapwood than in heartwood. For N, P and S in sapwood a strong gradient towards higher concentrations in younger rings was found. The concentrations of N and S in biomass were high due to atmospheric deposition of these compounds.

Tree growth at different rates of soil acidification

In a number of European coniferous stands, soil conditions were experimentally varied and response of tree growth and nutrient status was studied (Chapter 3). In view of the first approach (*I*), mentioned above, the rate of soil acidification was being increased or decreased in a number of experiments. Acid irrigation (4 kmol H^+ ha^{-1} y^{-1}) on a fertile soil in Höglwald (FRG) only slightly depressed element contents in needles of Norway spruce and no change in growth was observed. Lime applications in the same stand improved the Ca nutrition, but growth was decreased. Liming of another German stand in Solling had enhanced growth, due to the combination with N, K and Mg application, alleviating the strong Mg deficiency of the Norway spruce. The application of $(NH_4)_2SO_4$ during five years to a Scots pine stand in Harderwijk (NL) (Chapter 4) strongly increased soil acidification rates and resulted in Al concentrations up to 60 mg L^{-1} in soil solution from the third year onwards. Yet growth was first enhanced, probably by N-induced aboveground growth. In the fifth year growth was depressed and this coincided with P limitation, that might have resulted from $AlPO_4$ precipitates in soil and roots. Non of the mentioned acidifying treatments had changed the tree vitality. However, in a pot trial $(NH_4)_2SO_4$ applications first led to the same growth increase as mentioned above, but a decrease of root functioning was indirectly shown by depressed water uptake after 80 treatment days (Chapter 7). In the pots dissolved Al accumulated and this caused tree death after one year, when concentrations reached approximately 40 $mmol_c$ L^{-1}.

Rates of soil acidification were decreased not only by liming, but as well by exclusion of atmospheric loads. Roof constructions above the forest floor prevented the infiltration of throughfall water, being polluted with atmospheric substances, and clean rain was irrigated below. Tree growth increased drastically, but no instantaneous changes in nutrition were found. The growth increase at one site (Klosterhede, D) mainly resulted from the simultaneously increased water supply (Chapter 3). However, at the other site (Kootwijk, NL) at decreased rates of soil acidification, growth was increased in addition to the positive effect of water+nutrient applications (Chapters 3 and 5). 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 Al and H, hence soil conditions were probably more favourable for roots.

Tree growth and nutrition in relation to water and nutrient supply

Three out of four forest stands studied in this investigation (Chapter 3) showed a water-limited growth in the examined period. In the Dutch stands this was shown by an increase of 40% for Douglas fir (Chapter 5) to 50% for Scots pine (Chapter 4) in basal area growth upon irrigation of 3 to 4 mm day^{-1}. Differences in water storage capacity of the soil between foreign stands (Chapter 3) could explain the strong response on irrigation. In the Douglas fir stand the transpiration reduction in summer clearly depended on the decrease in soil moisture, as was demonstrated by sapflow measurements in trees (Chapter 8). No transpiration was detectable at a soil moisture content in the rooting zone of 3 % (v/v) and the corresponding soil suction was in balance with the lowest recorded shoot water potentials, *i.e.* approx. -2.2 MPa at stomatal closure. Yet in the irrigated trees equally low potentials were observed. Probably irrigation amounts were not always sufficient to keep pace with the water demand up to 6 mm day^{-1} and stomata closed. However, water uptake proceeded, while untreated trees were hardly able to absorb water after rewetting of the soil, probably due to root dieback and low sapwood conductivities. No osmotic adjustment to water stress was found in Douglas fir, but there was indirect evidence for an increased cell elongation upon fertigation, *i.e.* irrigation plus nutrient applications, indicating more profitable growth conditions. A dependence was found between transpiration and NH_4 supply (Chapter 7). It is a well-known fact that an increase in N availability stimulates shoot growth, thereby decreasing root/shoot ratios. Interestingly, after an initial increase due to an increased shoot size, transpiration at high NH_4 supply dropped below that of lower N supply level (Chapter 7). The high application doses of NH_4 had caused strong soil acidification and Al and H ions accumulated in the soil solution, affecting root growth and functioning and thus water uptake.

Fertigation consisted of a complete set of dissolved nutrients, given very frequently and in addition to irrigation during four growing seasons (Chapters 3, 4 and 5). The total annual application rate was equal to the estimated gross uptake in trees, and only for N the added amounts were adjusted for existing N sources in the ecosystem (mineralization and atmospheric inputs). P and K additions were quantitatively the most important and ranged from 13 (P) and 65 (K) in Scots pine to 36 and 60 kg ha^{-1} y^{-1} for Douglas fir respectively. Needle K and P content were raised in all treatment years by fertigation. Needle N remained stable and consequently K/N and P/N ratios increased, resulting in an improved nutritional balance in trees. 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. The lack of response did confirm that nutrient shortages were hardly present at the sites, although mass ratios to N seemed unprofitable. Input-output budgets suggested that applied nutrients were mostly retained in the soil, although more K was returned with needle fall and some K losses were observed in the Scots pine stand. Needle fall in the Douglas fir stand increased during the experimental period in the fertigated plots (Chapter 5). Fertigation did increase Al concentrations in soil solution in both stands and H concentrations in the pine stand by exchange of applied base cations with Al from soil and, only slightly, by increased root uptake and subsequent H extrusion. This effect was also observed on nutrient applications in a pot trial (Chapter 6) and this aggravated the effect of NH_4 additions, instead of ameliorating the soil. Yet the application of nutrients in addition to NH_4 in the pots did result in higher tree growth, since nutrient shortages of P and K were alleviated.

Fertigation, in combination with exclusion of atmospheric N and S loads by a roof, decreased soil acidification slightly and increased tree growth considerably relative to fertigation at ambient N and S loads (Chapter 5). The reduction in N loads had reduced leaching losses of NO_3 to the same extent, whereas all other fertigation treatments showed that increased N inputs of approximately 30 to 40 kg N ha^{-1} y^{-1} resulted in equally increased ouputs (Chapters 4 and 5), suggesting a N saturation of the ecosystems. It was discussed whether the high growth rates in the stand at low N loads may have resulted from a higher supply ratio of NO_3:NH_4, that can result in less acid soil conditions and can increase stem growth, as was shown in a pot trial (Chapter 6).

Samenvatting

Samenvatting

De recente vermindering van de bosvitaliteit wordt deels toegeschreven aan de indirecte gevolgen van atmosferische depositie ("zure regen") op de bodem-pH. De nitrificatie van het aangevoerde ammonium (NH_4) en het uitspoelen van het gevormde nitraat (NO_3) produceert veel zuur, dat leidt tot pH-verlaging, basenverlies of concentratieverhoging van potentieel toxisch aluminium. De opname van ammonium door de vegetatie produceert ook zuur, indien er weinig nitraat beschikbaar is. De meeste Nederlandse bossen bevinden zich op arme zandgronden met een laag zuurbufferend vermogen, waar hoge concentraties zuur en aluminium zijn waargenomen. Hoewel de bodems van oorsprong al arm waren aan nutriënten, worden de laatste tijd sterkere voedingstekorten in de bossen gevonden. Bovendien is er in vele gevallen sprake van een ongebalanceerde voeding met een onevenredig groot aandeel van stikstof. Deze verstoorde voeding kan leiden tot een verhoogde gevoeligheid voor droogte, vorst en insekten- en schimmelaantastingen. Ook ondergronds kan het door aluminium en zuur aangetaste wortelstelsel minder goed functioneren, met mogelijke gevolgen voor de water- en nutriëntenopname.

Deze studie heeft betrekking op de groei en voeding van Douglas spar, grove den en zomer eik in relatie tot bodemverzuring. Het doel van het onderzoek was te bepalen in hoeverre de boomvoeding groeibeperkend is als gevolg van Al stress en ion competitie met ammonium. Tevens was de vraag of de verstoorde voeding en de blootstelling van wortels aan lage pH en hoge Al concentraties invloed hebben op de waterhuishouding van de boom. De experimentele opzet betrof een verandering van de aanvoer van water, nutriënten en zuurlast naar de bodem. Twee benaderingen werden gekozen. In de eerste plaats de oorzaak van de toegenomen bodemverzuring werd aangepakt door verhoging danwel verlaging van de zuurlast. Hiermee kan bestudeerd worden welke mechanismen tot een effect in de bomen leiden en met welke intensiteit. In de tweede benadering werden de veronderstelde effecten tegengegaan van bodemverzuring en stikstofovermaat door optimalisatie van de water- en nutriëntenvoorziening. Door het aanbod van water te variëren kan het effect van droogtestress op het boomfunctioneren bepaald worden. De reactie van de groei op het herstellen van de nutriëntenbalans kan een groeibeperking aangeven.

Eerst werden de effecten van een natuurlijke variatie in bodemomstandigheden op de groei en nutriëntenstatus bestudeerd (Hoofdstuk 2). Binnen een opstand van zomereik werd de invloed van een drietal bodemtypen op de groei en de chemische samenstelling van de biomassa van de eik onderzocht. Mangaanconcentraties in hout en blad waren gerelateerd aan de bodemvochtconcentraties van mangaan. Verschillen in Ca en Mg in het bodemvocht werden ook weerspiegeld in de bladconcentraties. Een vrij lage boomgroei werd waargenomen op het bodemtype met de hoogste bodemvochtconcentraties van mangaan, welke echter nooit toxische waarden bereikten. Jaarringanalyse gaf aan dat deze groeireductie al aanving in 1961. De concentraties van N, P, K, Mg en S in jaarringen waren hoger in spinthout dan in kernhout. Voor N, P en S nam de concentratie sterk toe in jongere ringen van het spinthout. De relatief hoge N en S concentraties in de biomassa zijn waarschijnlijk gerelateerd aan de hoge atmosferische depositie.

Effecten op de boom van verandering in zuurlast

In een aantal Europese landen werden binnen bosopstanden de bodemomstandigheden kunstmatig gevarieerd (Hoofdstuk 3). Zoals vermeld bij benadering *I* werd de zuurlast, en hiermee de bodemverzuringssnelheid, verhoogd of verlaagd. Irrigatie van een zwavelzuuroplossing met een pH van 2.7 en een totale zuurlast van 4 kmol H^+ ha^{-1} j^{-1} op een rijke bosbodem in Höglwald (Duitsland) verminderde de elementgehalten in de naalden van fijnspar (*Picea abies*) slechts licht en de groei bleef onveranderd. Bekalking in dezelfde opstand verbeterde de calciumvoeding, maar de groei werd geremd. Toediening van dolomietkalk in een opstand van fijnspar in Solling (Duitsland) verhoogde de groei vooral door de combinatie met N, K en Mg toediening, waardoor de ernstige magnesiumtekorten in de bomen verlicht werden. In een opstand van grove den te Harderwijk (NL) werd de bodemverzuring sterk verhoogd door een frequente toediening van opgelost $(NH_4)_2SO_4$ gedurende een periode van vijf jaar (Hoofdstuk 4). De bodemvochtconcentraties van aluminium in de wortelzone liepen op tot waarden van *ca.* 60 mg L^{-1} in het derde behandelingsjaar. De eerste twee behandelingsjaren werd de boomgroei verhoogd door de stimulans van de stikstofgift en de verhoogde stikstofgehalten in de naalden gaven verzadiging aan. Vervolgens verminderde de groei weer, tot deze in het vijfde jaar lager was dan in de onbehandelde bomen. Deze groeiremming viel samen met een optredend fosfortekort in de naalden, en dit is een aanwijzing dat het fosfaat in de bodem verminderd beschikbaar was door P-precipitatie met vrij aluminium. In de zuurlast-verhogende experimenten werd geen merkbare vitaliteitsachteruitgang van het bos waargenomen. In een potproef met juveniele Douglas spar (Hoofdstuk 6) werd tijdens een hoge $(NH_4)_2SO_4$ toediening echter wel een sterk afnemende vitaliteit waargenomen naast een groeivermindering. Nadat eerst de groei was toegenomen, zoals ook boven werd vermeld maar dan in een ander tijdsbestek, verminderde reeds na 80 dagen de verdamping van de Douglas (Hoofdstuk 7) en een zichtbare achteruitgang leidde na 1 jaar tot boomsterfte. Deze achteruitgang werd toegeschreven aan wortelaantasting door de zeer hoge concentraties van zich ophopend aluminium (max. 360 mg of 40 mmol$_c$ L^{-1}).

Naast vermindering van de bodemverzuring door bekalking, werd dit ook beoogd met het wegvangen van de aanvoer van verzurende componenten. Dit werd bewerkstelligd door het plaatsen van een dak boven de bosvloer en het besproeien van de bodem met een schone oplossing. Hierop volgde momentaan een verhoogde boomgroei, die niet direct verklaard werd uit de nutriëntenstatus. De groei werd in de Deense proef (Klosterhede) vooral door de verbeterde watervoorziening gestimuleerd (Hoofdstuk 3). In de andere dakproef (Kootwijk, NL) was de verminderde zuurgraad en lagere aluminiumconcentratie in de bodem waarschijnlijk de reden voor de groeistimulans. Dit zou een gevolg kunnen zijn van een verbeterd wortelfunctioneren, maar ook hierbij werkte de verhoogde watertoevoer positief en was het onderscheid moeilijk te maken (Hoofdstuk 5). De berekende vermindering in bodemverzuringssnelheid onder dak kwam voort uit de verminderde aanvoer van ammonium en de verlaagde uitspoeling van nitraat. In een kasproef met bodemmateriaal van bovengenoemde boslocatie (Hoofdstuk 6) werd ook een verlaagde zuurgraad gevonden als de fractie ammonium in de N toediening werd verminderd ten opzichte van nitraat, en werd de Ca en P voorziening van Douglas verbeterd. Tevens werd waargenomen, dat een 100% NH_4 gift de wortelgroei, de specifieke wortellengte en de stamgroei onderdrukte ten opzichte van de toediening met 50% NO_3 en 50% NH_4.

Boomgroei in relatie tot de water- en nutriëntenvoorziening

In drie van de vier onderzochte bosopstanden was de groei gelimiteerd door de watervoorziening (Hoofdstuk 3). In de Nederlanse bossen werd dit aangetoond door een groeiverhoging van 40% in Douglas spar en van 50% in grove den (op basis van grondvlak) als reactie op een irrigatie van 3 tot 4 mm per dag. Verschillen in het waterbergend vermogen van de bodem tussen de buitenlandse bosopstanden verklaarde het verschil in respons op irrigatie. De naaldval in Douglas verminderde als gevolg van de watergiften en werd elk jaar met enkele maanden vertraagd. De door water gestimuleerde groei resulteerde bij de Douglas in verlaagde N en K gehalten in de naalden, maar niet bij grove den. In de niet geirrigeerde plot verminderde de transpiratie in de zomer als functie van de bodemvochtvoorraad en stopte bij *ca.* 3 % (v/v). De transpiratie werd gemeten met behulp van sapstroomsensors in het xyleem van de Douglas gedurende de zomer van 1992. Het verdampingsgedrag werd bestudeerd bij behandelingen controle, droogte en fertigatie. Het dagverloop van de transpiratie liet een reductie zien in alle behandelingen bij een takwaterpotentiaal van -2.2 MPa. Deze waarde kwam overeen met het verwelkingspunt, zoals vastgesteld met behulp van een druk-volume curve en zoals afgeleid uit osmotische potentialen van celsap. De gefertigeerde bomen, optimaal voorzien van water en nutriënten, konden meer water bergen bij gelijke waterpotentiaal. Tevens reageerden zij snel en efficient op verhoogde watertoevoer, terwijl uitgedroogde bomen daar, althans binnen enkele dagen, nauwelijks van profiteren. De sapstroommetingen bieden, door het directe verband met de actuele wateropname en door hun hoge tijdsresolutie, veel mogelijkheden om het wortelfunctioneren *in situ* te kwantificeren.

Fertigatie, *i.e.* irrigatie, aangevuld met een nutriëntengift, welke is afgestemd op de bruto groei, gaf nauwelijks een additionele groei te zien ten opzichte van irrigatie, hoewel reeds in het eerste toedieningsjaar de naaldgehalten aan kalium en fosfor stegen. Alleen in het vierde behandelingsjaar was bij grove den de groei significant verhoogd ten opzichte van irrigatie (Hoofdstuk 3). De stikstofvoorziening in de Deense fertigatieproef was vermoedelijk nog beperkend, ondanks de sinds jaren toegenomen atmosferische N depositie.

De beperkte groeireactie op fertigatie in de Nederlandse opstanden wijst op de afwezigheid van een voedingsgebrek. De stikstofvoeding van de bomen was reeds optimaal en de voeding van de overige nutriënten was slechts licht gebrekkig, m.n. P in grove den en K en Ca in sommige jaren in Douglas. Toch leidt de in sommige jaren overmatige stikstofvoorziening tot een onbalans met andere nutriënten, maar de herstelde balans als gevolg van fertigatie uit zich kennelijk niet in de groei.

In de bodem van zowel irrigatie- als fertigatie-behandeling werd een verhoogde zuurproductie gevonden, die werd gebufferd door vrijkomend Al. Dit aluminium spoelde vervolgens uit met nitraat als begeleidend anion. In de fertigatie-experimenten ging de kleine gift van ammoniumnitraat (NH_4NO_3) vrijwel geheel verloren door uitspoeling en dit duidt op stikstofverzadiging van de opstanden, hoewel de gehalten aan stikstof in de bomen nog licht stegen. De verlaging van de stikstofaanvoer onder dak, verminderde de uitspoeling van nitraat evenredig, hetgeen ook duidt op een overmatige stikstofvoorziening. Het N gehalte in de naalden nam af door de verlaagde N voorziening en vermoedelijk door verhoogde groei.

De fertigatie, zoals toegediend in de boslocaties, werd in een aantal potproeven herhaald met bodemmateriaal van de boslocatie Kootwijk als substraat (Hoofdstuk 6). De grond, inclusief strooisellaag, bleek na twee jaar te weinig N, K, P en Mg meer te leveren voor optimale groei van jonge Douglas. Fertigatie met een complete set nutriënten bevorderde de groei. Deze voeding verhoogde de naaldgehalten van P en K, maar versterkte de bodemchemische stress door verhoging van de Al-concentratie en een hoog zoutnivo in de bodemoplossing.

De interactie tussen NH_4 gift en transpiratie werd in dezelfde potproef bestudeerd (Hoofdstuk 7). Gedurende de eerste 3 toedieningsmaanden bleek de boomtranspiratie hoger bij hoge dan bij lage NH_4 gift door een grotere bovengrondse biomassa. Daarna zakte de transpiratie, totdat deze in het tweede jaar onder het nivo van de met lage doses gevoede bomen lag. De jonge bomen met de lage N-voorziening doorstonden een korte, opgelegde droogteperiode goed, waarbij een gebalanceerde, additionele voeding de transpiratiecontrole vergrootte. De vitaliteit ging verder achteruit bij de hoge N-behandeling tijdens de droogte, maar verzuring leek de uiteindelijke doodsoorzaak.

Curriculum vitae

Pieter Huibert Bram de Visser werd geboren op 6 juni 1958 te Bergen op Zoom. In 1976 behaalde hij het Atheneum diploma aan het Protestants Lyceum te Eindhoven. Vervolgens begon hij de studie Biologie aan de Rijksuniversiteit Utrecht die hij afrondde in februari 1984 met als hoofdvak Botanische Oecologie, als bijvak Bodemkunde en als nevenvakken Milieukunde, Ontwikkelingssamenwerking en Vakdidaktiek.
In datzelfde jaar begon hij als gastmedewerker van de vakgroep Bodemkunde en Geologie van de Landbouwuniversiteit te Wageningen aan de modellering van watertransport in de bodem. Spoedig volgde daar voor hem een functie als toegevoegd onderzoeker met als opdracht het kwantificeren van groei en elementenopname van eik. Na een korte werkopdracht in 1986 bij het Staringcentrum te Wageningen ten behoeve van de modellering van bodemverzuring op regionale schaal, kwam hij in 1987 weer in dienst bij bovengenoemde vakgroep, echter gedetacheerd bij de vakgroep Bodemkunde en Plantevoeding. Zijn onderzoeksopdracht betrof de kwantificering van de effekten van zure depositie via de bodem op groei en voeding van bossen, welke hij afrondde met dit proefschrift.

APPENDIX

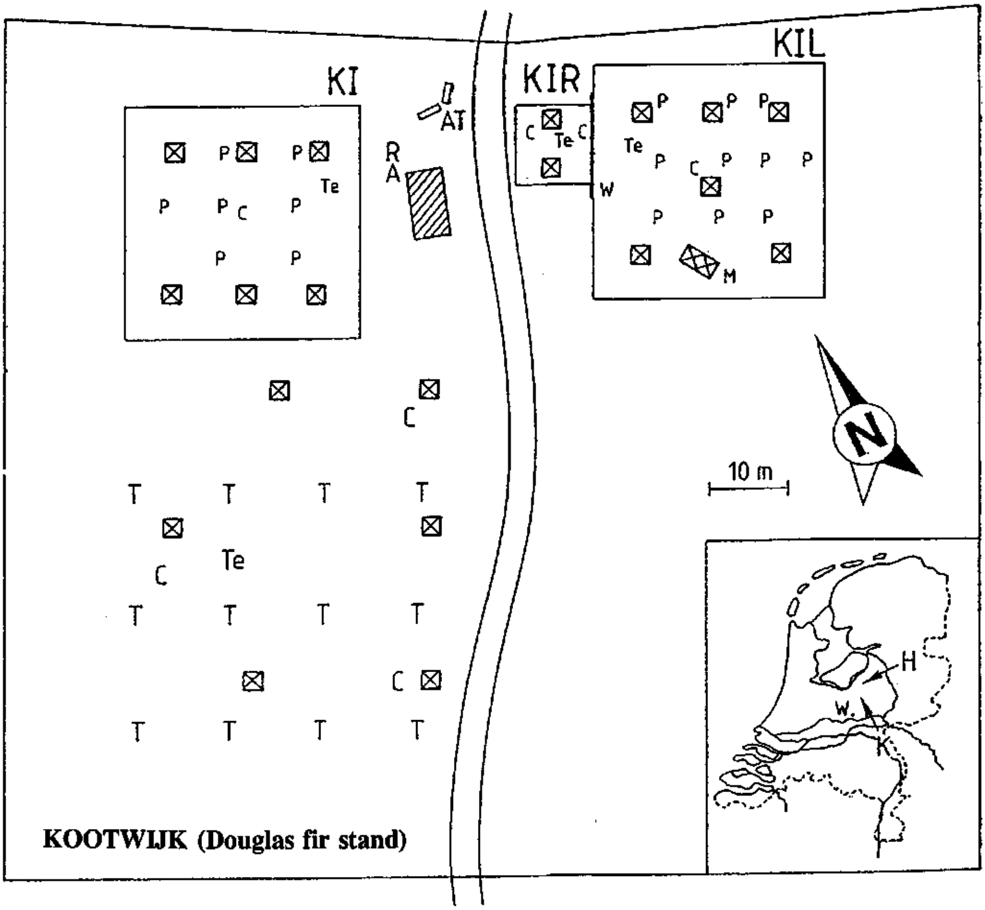
Site maps and location of equipment

Situation of the experimental sites in the Netherlands and the exact location of the equipment in the Douglas fir stand at Kootwijk.

Meaning of the abbreviations and symbols used:

KI, irrigation plot **I**; KIL, fertigation plot **IF**; KIR, fertigation plot under a roof, **IF+R**;
AT, automatic throughfall registration; R, radiation sensor; A, air temperature; C, soil chemical monitoring; M, measuring tower (23 m high); P, ceramic cups for pooled samples at 20 cm soil depth; T, throughfall funnels; Te, tensiometer systems; W, PVC wall in the soil (90 cm deep). ⊗, ☒ ,litterfall collector.

Codes on the country map: K, Kootwijk; H, Harderwijk; W, Wageningen



HARDERWIJK (Scots pine stand)