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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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Abstract

Two pot trials 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 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 were studied, and in experiment II the 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 carbon 3.1% ; extractable P (H_2O) 25.6 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 (Table 1). In N100 and N300 10 mL of a 1000 times diluted N-serve solution (nitrification inhibitor) was added to each litre of fertilizer solution. Pots of the N0 treatment were

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 No.	Experiment duration	Code	NH_4-N	NO_3-N	F
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

not fertilized at all. With the other treatments respective nitrogen applications were (kg N ha^{-1}): 100 and 300 as $(NH_4)_2SO_4$ for N100 and N300, 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 as +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).

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 (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 moisture content of 22% (w/w), corresponding with –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 at 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 rate (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(–) $\cdot$ m^{-3}), but increased in treatment N300 (±10 mmol(–) $\cdot$ 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(+) $\cdot$ 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.

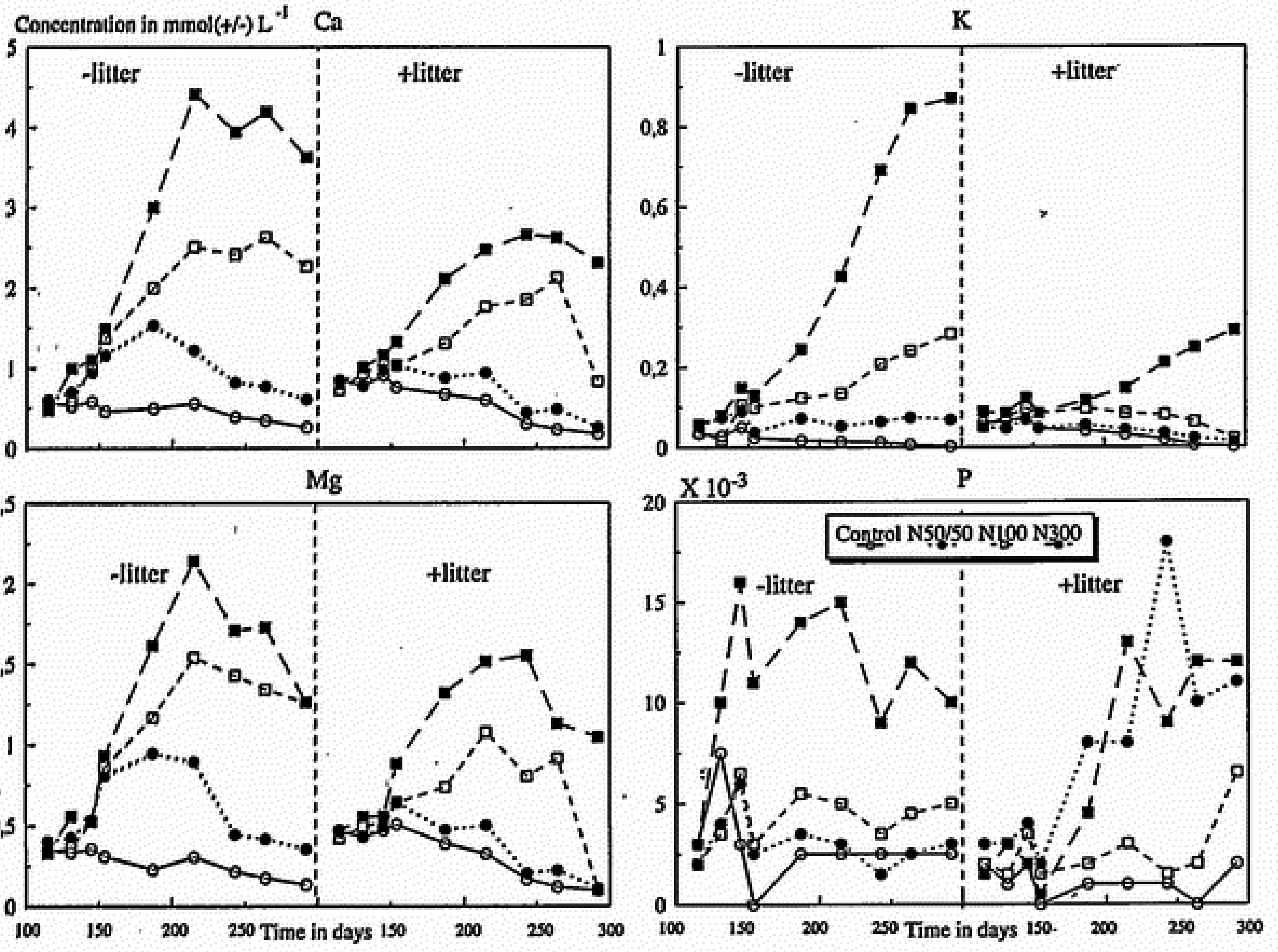

Fig. 1. Concentrations of Ca, Mg, K and H_2PO_4 in the soil solution (mmol(+/–) L^{-1}) at four treatments with and without a litter layer (Exp.I). Day 1 is 1 Jan 1989. The treatments were started on day 116.

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.

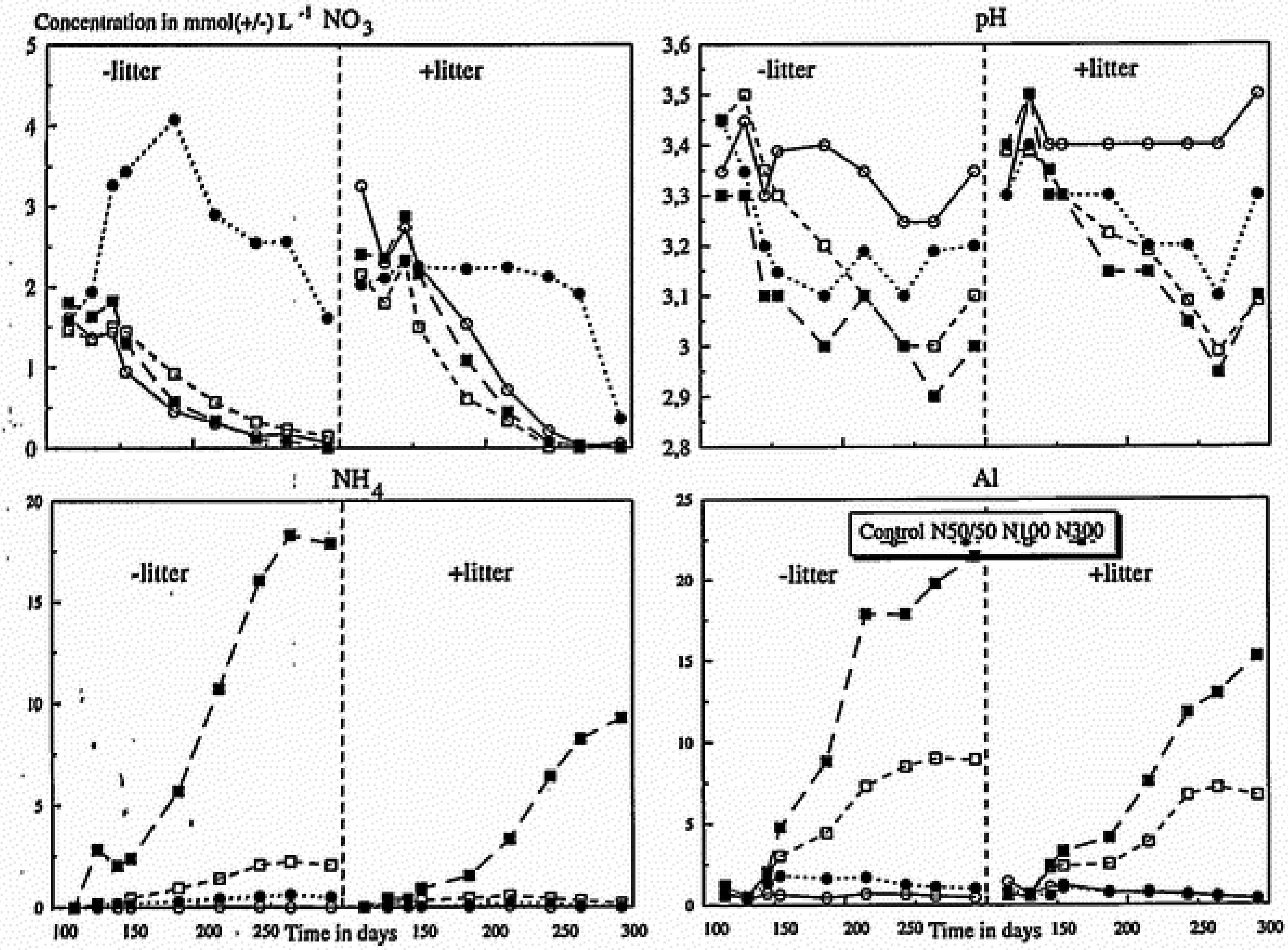

Fig. 2. Time course of pH and concentrations of NH_4, NO_3 and Al (mmol(+/–) L^{-1}) in the soil solution of pots of four treatments with and without a litter layer (Exp.I). Day 1 is 1 Jan 1989. The treatments were started on day 116.

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 experiment 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 ammonium-sulphate. 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

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×N-level	*	–	–	**	*
Balance×litter	–	–	–	–	–
Litter×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 value 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×N-level	**	*	–	–	*	–
Balance×litter	–	*	–	–	–	–
Litter×N-level	–	*	–	–	–	–

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

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 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 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.

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).

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).

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

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] Estimated from ionic charge balance. Missing values are indicated by –.

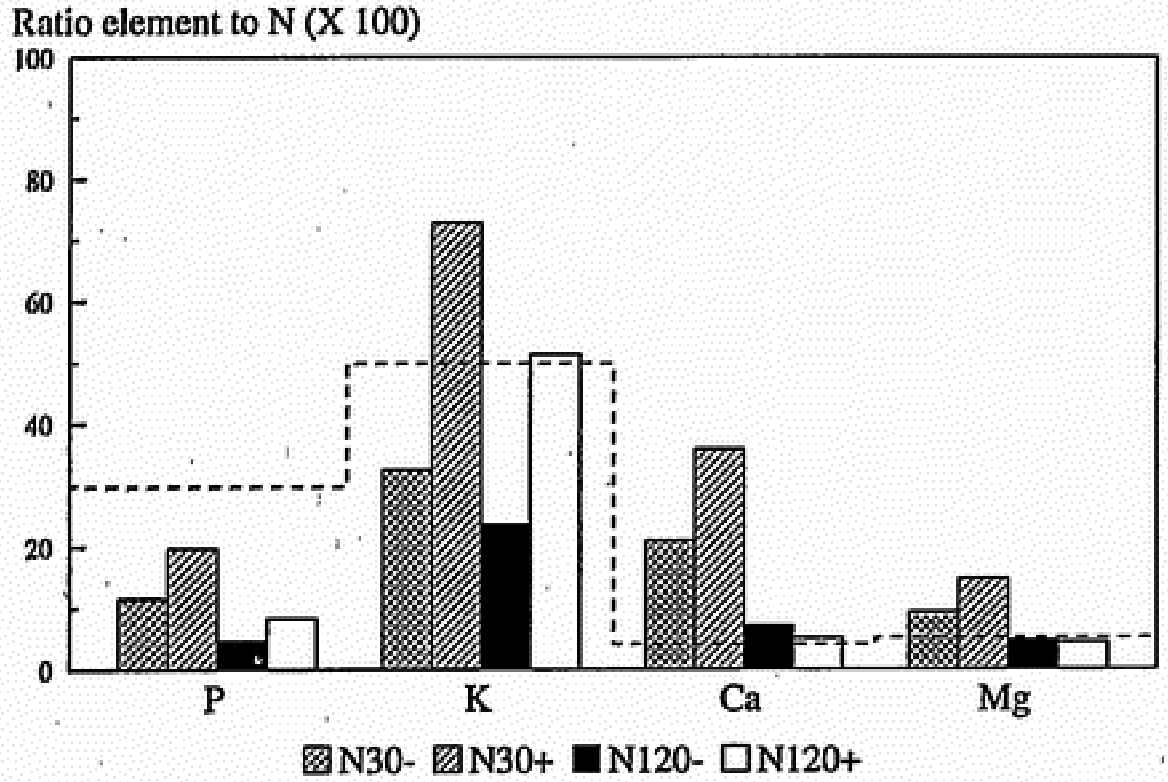

Fig. 3. Element/Nitrogen weight ratio (×100) in current-year needles in Experiment II. The broken line indicates the optimal ratio of the specific element relative to N (Ingestad, 1979).

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 most 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 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 (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, or severely decrease. 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.
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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