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Effects of aluminium on growth and nutrient uptake of small *Picea abies* and *Pinus sylvestris* plants

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Summary. The effects of aluminium concentrations between 0.2 and 30 m*M* at pH 3.8±0.2 on small plants of Norway spruce [(*Picea abies* (L.) Karst], Scots pine (*Pinus sylvestris* L.), and Scots pine infected with the ectomycorrhizal fungus *Suillus bovinus* (L. ex Fr.) O. Kuntze were investigated. The plants were grown at maximum relative growth rate (R_G % day^{-1}) with free access but very low external concentrations of nutrients. Steady-state conditions with respect to relative growth rate (R_G) and internal nutrient concentrations were achieved before addition of aluminium, which was added as $AlCl_3$ and/or $Al(NO_3)_3$. There were reductions in R_G at aluminium concentrations of 0.3 m*M* in spruce, 6 m*M* in pine and 10 m*M* in ectomycorrhizal pine, i.e. at aluminium concentrations considerably higher than those normally occurring in the top layer of the mineral soil where most fine roots are found. Nutrient uptake rate per unit root growth rate was calculated for different nutrient elements. The uptake rate of calcium and magnesium was reduced at aluminium concentrations of 0.2 m*M* (spruce), 1 m*M* (pine) and 3 m*M* (ectomycorrhizal pine), without influencing R_G. The results question the validity of the hypothesis of aluminium toxicity to forest tree species at low external concentrations.

Key words: Aluminium concentration – Nutrient uptake – *Picea abies* – *Pinus sylvestris* – Relative growth rate

Introduction

Background

Aluminium minerals are common in soils and aluminium solubility increases at pH below 4.5. Forest trees on acid soils are commonly exposed and probably adapted to root environments with Al^{3+} ions. With increasing anthropogenic acidification, toxic effects of increased Al^{3+} concentration may be expected.

Vast areas of conifer forests were damaged in central Europe and eastern North America during the late 1970s. Ulrich (1981) suggested that aluminium was one of the main factors concerned in the forest die-back. There have been several investigations of aluminium toxicity and tolerance of forest tree species (Humphreys and Truman 1964; McCormick and Steiner 1978; Steiner et al. 1980, 1984; Rost-Siebert 1983; Schier 1985; van Praag and Weissen 1985; van Praag et al. 1985; Göransson and Eldhuset 1987; Asp et al 1988; Godbold et al 1988). Growth response and different uptake mechanisms have also been reviewed by Pratt (1966), Foy (1974) and Schaedle et al. (1989).

Theory and hypothesis

Most of the cited investigations were made in uncontrolled conditions of nutrient availability. This could explain the large variations of growth response reported between different investigations of the same species, because effects of nutrient deficiencies can be confused with aluminium toxicity (Ingestad 1982, 1991; Ågren 1985).

Plants at steady-state growth must obtain nutrients in exponentially increasing amounts, as described by Ingestad (1982), Ågren (1985) and Ingestad and Lund (1986). They concluded that the relative growth rate (R_G) is linearly proportional to the internal nutrient concentration, which is stable with time at different stable R_Gs. Such plants have well-defined physiological and morphological properties (e.g. Ericsson 1981; Ingestad and Kähr 1985; Ingestad et al. 1986; Ericsson and Ingestad 1988).

The aim of the present investigation was to evaluate at which external aluminium concentrations growth of Norway spruce, Scots pine and ectomychorrhizal pine decreased and to estimate lethal concentrations. The hypothesis was that Al^{3+} in concentrations which are found in the fine-root layer in boreal forest ecosystems (Ulrich

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Table 1. Weight ratios (N = 100) of macro- and micronutrients in the different treatments. N concentration in the stock culture solution was 2.5 mg ml^{-1}

	N	K	P	Ca	Mg	S	Fe	Mn	B	Zn	Cu	Mo
Pregrowth All species	100	138	15	43	29	9	0.7	0.4	0.2	0.06	0.03	0.007
Experiments Spruce	100	50	16	5	5	9	0.7	0.4	0.2	0.06	0.03	0.007
Pine and ectomycorrhizal pine	100	45	15	6	6	9	0.7	0.4	0.2	0.06	0.03	0.007

1981; Nilsson and Bergkvist 1983; Berdén et al. 1987) do not cause decrease in growth if the plants are at steady-state nutrition and, in this case, at maximum R_G. Total aluminium concentrations of less than 0.1 m*M* (typically less than 0.1 m*M*) have been measure in lysimeter water and soil solutions from the B horizon in podzol soils (Abrahamsen 1983; Nilsson and Lundmark 1986). The parameters discussed in the paper are changes in R_G, biomass allocation and nutrient uptake rate per unit root growth rate of Norway spruce and Scots pine with or without the ectomycorrhizal fungus *Suillus bovinus*.

Materials and methods

Plant culture

The seeds were collected in south Sweden: *Picea abies* (L.) Karst. from a maternal clone lat. 56°59′N, long. 14°18′E elevation 180 m; and *Pinus sylvestris* L. from a natural stand, lat. 57°45′, long. 15°15′E elevation 250 m. Pollination was not controlled. The seeds were sown in vermiculite or in a mixture of sand, perlite and vermiculite and germinated under continuous weak light approximately 50 μmol m^{-2}s^{-1}.

After approximately 2 weeks the plants were transferred to growth units with a complete culture solution for pregrowth at optimum conditions. The experiments began 2–3 weeks later. The composition of the culture solution was as described by Ingestad (1979), apart from the zinc concentration, which was doubled. The weight ratio of macro- and micronutrients in the pregrowth treatments and experiments are given in Table 1. All nitrogen was added as nitrate and the concentration in the stock solution was 2.5 mg N per ml.

Distilled water (5 dm^3) was recirculated and continuously sprayed on the roots at a flow rate of 10 dm^3/min. Into this, small and exponentially increasing amounts of the stock solution were added frequently, generally once every hour. The plants were growing at constant maximal R_G at very low external nutrient concentrations as the relative uptake rate (R_U) of nutrients equalled the relative addition rate (R_A). The conductivity was less than 100 μS cm^{-1} in the culture solution. The growth units and the principles of the technique have been described by Ingestad (1979), Ingestad and Kähr (1985) and Ingestad and Lund (1986).

Pregrowth

Pregrowth and experiments on spruce and pine seedlings were carried out in growth chambers with continuous illumination by 250 W lamps (Osram HQ-IR); photon flux density ≈300 μmol m^{-2}s^{-1}, 400–700 nm; air and solution temperature 20° C and relative air humidity 75%.

The seed germination, pregrowth and experiments on ectomycorrhizal pine were carried out in the phytotron in Stockholm with continuous illumination by 200 W lamps (ASEA-Scandia) and 215 W Grolux WR tubes, photon flux density ≈250 μmol m^{-2}s^{-1}, 400–700 nm; air temperature 20° C; solution temperature 24° C and relative humidity 75%. The seedlings were inoculated with a mycelium suspension of *Suillus bovinus* (L. ex Fr.) O. Kuntze and grown as described by Kähr and Arveby (1986). The pregrowth period lasted up to 3 weeks.

Experiments

After pregrowth, on the start day (D_0), 60 uniformly sized plants were selected and divided into 12 groups of 5 for each experiment. The fresh weight of each seedling was approximately 150 mg for spruce and 200 mg for pine. After an adjustment period of 2 weeks to steady-state nutrition and constant maximal R_G, the experimental period began. Three harvests of two groups on each occasion were made at intervals of 5–8 days. Directly after the third harvest, aluminium was added as equimolar ratios of aluminium chloride and aluminium nitrate, or, at low aluminium concentrations, as aluminium chloride alone. The concentrations in the different experiments were 0.2, 0.3, 1, 3, 6, 10 and 15 m*M* for spruce, 1, 3, 6, 10, 15 and 30 m*M* for pine and 3, 6, 10, 15, 30 m*M* for ectomycorrhizal pine. The experiments with 1 and 3 m*M* (spruce) and 10 m*M* (pine) were repeated once. The conductivity increased after the aluminium addition from less than 100 μS cm^{-1} to between 130 and 7750 μS cm^{-1}, depending on the concentration of the aluminium salt added. The remaining plants were harvested on three occasions of two groups each at an interval of about 1 week. To avoid chemical interactions between aluminium and nutrients, the R_A was adjusted after the aluminium addition if R_G decreased, but nutrient availability was never growth limiting. Conductivity and pH were measured at least once every day and, to maintain aluminium as Al^{3+}, pH was adjusted with HCl or NaOH to 3.8 ± 0.2 as often as necessary, although the aluminium salt normally buffered the system to a pH of approximately 3.8.

Measurements and calculations

Harvests, R_G calculations and element determination were performed as described by Göransson and Eldhuset (1987).

Nutrient uptake of growing roots was calculated as nurient uptake rate per unit root growth rate, dn/dW_r [μmol h^{-1} (g root biomass h^{-1})$^{-1}$]. The uptake rate per unit root growth rate may be expressed as

$$\frac{dn}{dW_r} = \frac{n}{W_r} \cdot \frac{R_n}{R_{Wr}}$$

where n is the internal amount of nutrients (μmol), W_r is root biomass (g), R_n is relative ion uptake rate and R_{Wr} is relative root growth rate (Ingestad and Ågren 1988). The specific effect of aluminium on nutrient uptake was calculated as the ratio of dn/dW_r after aluminium addition to dn/dW_r before addition, dn/dW_r (Al).

At each harvest, the roots were rinsed in distilled water. Fresh and dry weights (65° C for 2 days) of roots and shoots were measured. Total carbon was measured in samples of the recirculating culture solution with a Carlo Erba NA 1500 (Carlo Erba Strumentatzione, Milan, Italy). Total nitrogen was determined by a micro-Kjeldahl method using a flow injection analysis apparatus (Bifok FIA 05, Tecator, Höganäs, Sweden) with

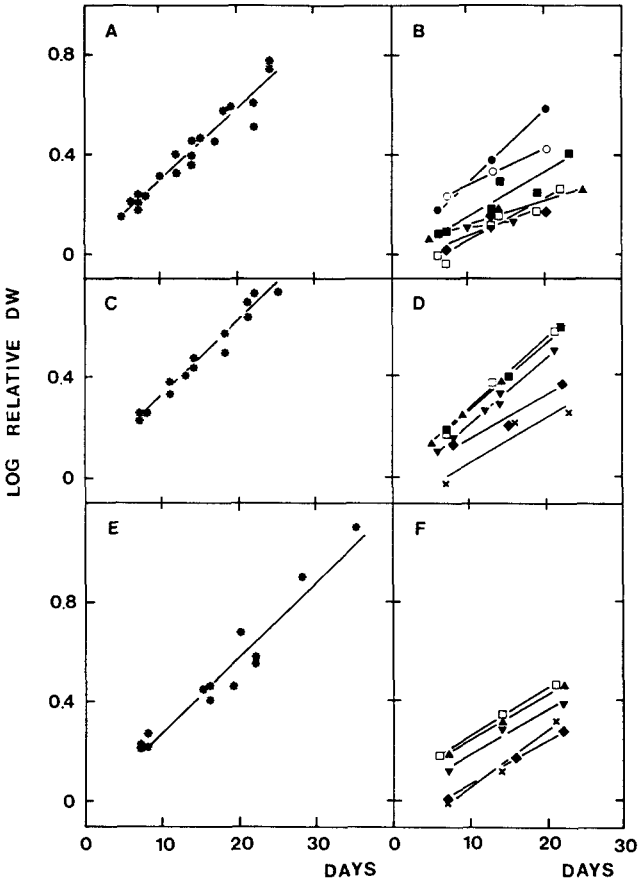

Fig. 1. Plant dry weight increase of small spruce, pine and ectomycorrhizal pine plants before (**A, C, E**) and after aluminium addition (**B, D, F**). The weight increase in **A, C** and **E** is the average of all pre-aluminium treatments and **B, D**, and **F** show the weight increase at different aluminium concentrations. The relative dry weight was set equal to 1 on day D_0 and day D_A. ✱, before aluminium addition; ●, 0.2 m*M* aluminium; ○, 0.3 m*M* aluminium; ■, 1 m*M* aluminium; □, 3 m*M* aluminium; ▲, 6 m*M* aluminium; ▼, 10 m*M* aluminium; ◆, 15 m*M* aluminium; and ✖, 30 m*M* aluminium

gas diffusion using phenol red as indicator. For analysis of other elements, samples were digested for 2 days in a 2.5 : 1 (v/v) mixture of nitric and perchloric acids. The analyses were performed by inductively-coupled plasma atomic emission spectrometry ICP-AES (IL P-200 Instrumentation Laboratory Andover, Mass. USA). For calibration purposes, the laboratory is connected to the IUFRO intercalibration network, forestry Commission of N. S. W., Australia.

At the end of each experiment, samples of the culture solution were analysed for total aluminium. Monomeric aluminium was measured according to the speciation principles outlined by Driscoll (1984), using a modification of the pyrocatechol violet method (Röyset 1986).

Results

Visual symptoms

In spruce, morphological changes in roots were seen at aluminium concentrations of 0.2 m*M* and above. A brown zone developed behind the apical root meristem. Aluminium concentrations of 3 m*M* and above caused discoloration and root necrosis, although new short lateral roots grew out behind the damaged or dead meristems. The needles became yellow to yellowish-red from the tips inwards at aluminium concentrations exceeding 1 m*M*.

Morphological changes in pine roots were similar to those in spruce and were observed at aluminium concentrations of 6 m*M* and above, for ectomycorrhizal pine at concentrations of 10 m*M* and above. The roots continued to grow but the new roots were thick and spotted brown and the growth pattern was disturbed, as the root tips bent to the sides and upwards. At aluminium concentrations of 15 m*M*, the root tips were dying and the new roots which grew out behind the dead root-tips were also thick and spotted brown and did not grow more than a few millimeters. The needles became yellow to yellowish-red from the tips at these concentrations.

Table 2. R_G (% d^{-1}) and coefficient of determination, r^2, in plants and roots before and after aluminium treatment

		Plant R_G				Root R_G			
	Al	before Al		after Al		before Al		after Al	
	(m*M*)	R_G	r^2	R_G	r^2	R_G	r^2	R_G	r^2
Spruce									
	0.2	7.2	0.99	6.7	1.00	7.2	0.99	7.8	0.96
	0.3	5.4	0.99	4.8	0.95	7.6	0.99	5.1	0.97
	1	7.4	1.00	4.3	0.98	7.4	1.00	4.3	0.95
	1	6.2	0.99	3.2	0.99	7.3	0.97	2.7	0.93
	3	7.1	0.99	3.1	0.85	7.7	0.92	2.9	0.89
	3	7.1	1.00	2.4	0.92	9.3	0.99	1.7	0.72
	6	7.7	0.99	2.8	0.89	11.7	1.00	2.7	0.96
	10	7.4	0.99	2.0	0.96	10.6	1.00	1.6	0.21
	15	6.3	0.99	2.3	0.89	6.8	0.98	2.7	0.87
Pine									
	1	7.1	0.99	6.2	1.00	7.4	0.99	6.1	0.99
	3	6.7	0.99	6.5	0.99	7.5	0.97	6.6	0.99
	6	7.2	1.00	6.3	1.00	7.5	0.99	6.6	0.99
	10	9.3	1.00	5.6	0.98	9.3	1.00	5.2	0.99
	15	7.6	0.99	3.8	0.97	7.8	0.99	3.3	0.97
	30	7.6	0.99	3.0	0.84	7.7	1.00	2.2	0.94
Ectomycorrhizal pine									
	3	5.6	0.99	5.1	0.99	5.5	0.99	5.3	0.99
	6	5.2	0.99	4.8	0.98	6.1	0.99	4.7	0.98
	10	5.4	0.99	4.2	0.99	6.3	0.99	3.9	0.98
	15	6.1	0.99	3.1	0.93	6.5	0.99	2.7	0.98
	30	7.3	0.99	3.5	0.84	7.3	0.99	2.8	0.91

Growth and biomass allocation

In each experiment, R_G was constant in the period before the aluminium addition. In each individual experiment the coefficient of determination, r^2, was 0.987 or better for all species before the aluminium addition. The dry weight increase of the plants before (A, C, E) and after (B, D, F) aluminium addition are shown in Fig. 1. The regression lines in A, C and E correspond to an average R_G in the period before aluminium addition of 7.2% day^{-1} for spruce, 7.8% day^{-1} for pine and 6.3% day^{-1} for ectomycorrhizal pine. By using a *F*-test, decrease in plant R_G ($P \leq 0.05$) was recorded at an external aluminium concentration of 0.3 m*M* and above for spruce, 6 m*M* for pine and

Table 3. Biomass allocation to roots as percent of plant weight at different aluminium concentrations

	Al conc mM	root FW ±S.D.	root DW ±S.D.	n
Spruce				
	0	41.0±2.4	21.4±2.3	27
	0.2	43.6±3.6	21.6±2.5	3
	0.3	48.5±1.6	27.7±0.7	3
	1	40.9±2.2	21.0±2.0	6
	3	42.0±3.2	22.6±4.9	6
	6	40.3±1.5	22.8±0.8	4
	10	34.2±1.7	17.0±2.3	3
	15	38.6±0.9	19.8±0.9	3
Pine				
	0	57.1±3.3	33.1±4.0	16
	1	56.1±9.2	39.5±1.4	3
	3	37.8±0.6	35.8±0.9	3
	6	57.6±2.1	31.0±0.7	3
	10	53.1±5.7	27.7±4.6	6
	15	49.1±1.3	27.5±1.4	3
	30	46.6±3.7	23.6±2.2	3
Ectomycorrhizal pine				
	0	60.6±2.5	37.5±2.5	15
	3	63.9±1.5	37.8±0.6	3
	6	64.3±1.1	41.2±0.5	3
	10	61.3±0.2	39.7±1.3	3
	15	51.9±1.5	31.0±1.4	3
	30	45.4±2.4	23.2±1.7	3

Table 4. Aluminium concentration in roots and shoots on day D_E of spruce, pine and ectomycorrhizal pine seedlings grown at different aluminium concentrations

	Added Al mM.	Recovered Al mg (g DW)$^{-1}$	
		Roots	Shoots
Spruce			
	0.2	0.84	0.14
	0.3	0.53	0.19
	1	2.13	0.18
	3	2.96	0.20
	6	3.90	0.21
	10	5.31	0.23
	15	2.59	0.04
Pine			
	1	0.90	0.35
	3	1.79	0.20
	6	2.20	0.55
	10	5.86	0.54
	15	6.91	0.48
	30	6.05	0.95
Ectomycorrhizal pine			
	3	6.08	0.56
	6	9.11	0.55
	10	10.90	0.67
	15	15.34	0.18
	30	10.50	0.91

10 m*M* for ectomycorrhizal pine. The different R_Gs before and after aluminium addition are listed in Table 2.

Although root R_G decreased with increasing aluminium concentration, biomass allocation to roots was fairly constant up to 10 m*M* for spruce (Table 3), and to 15 m*M* for pine and ectomycorrhizal pine ($P \leq 0.05$). At 0.3 m*M* (spruce), 1 m*M* (pine) and 6 m*M* (ectomycorrhizal pine) the allocation to roots was greater than average.

Aluminium and nutrient dynamics

At the end of the experiments, more than 85% of the added aluminium was recovered in the culture solution and monomeric aluminium equalled total aluminium. The aluminium concentrations found in shoots and roots (Table 4) increased in roots with increasing external aluminium concentration up to 10 or 15 m*M*, but the concentrations in shoots were low. Total carbon concentration in the culture solution was less than 5 n*M* and the Ca/Al ratio in the nutrient solution was less than 0.2 in all treatments.

In spruce, there was no correlation between $dn/dW_r(Al)$ of the different macronutrients and increasing aluminium concentration (Fig. 2A) even if Ca and Mg uptake was reduced compared to the pre-aluminium treatment. The equations of regression for all elements and treatments are shown in Table 5. For pine, $dn/dW_r(Al)$ of N and K increased at the highest aluminium concentration ($P \leq 0.05$). Phosphorus, calcium, magnesium and sulphur (Fig. 2B, Table 5) were more or less uncorrelated with increasing aluminium concentration. In ectomycorrhizal pine, $dn/dW_r(Al)$ of Ca and Mg increased with increasing aluminium concentration ($P \leq 0.05$) (Fig. 2C, Table 5). The increase was from low values compared with the pre-aluminium treatment.

Discussion

Growth reductions in conifers have been found at different external aluminium concentrations. Tischner et al. (1983) and Abrahamsen (1984) found that growth of *Picea abies* was influenced by aluminium concentrations of 0.5–1 m*M*. Similar results were found by Godbold et al (1988) where root elongation in *P. abies* decreased by 63–73% at aluminium concentrations of 0.8 and 1.2 m*M*. Reductions in growth and root length elongation of different *Pinus* species occurred at aluminium concentrations of 3 m*M* but they were still growing at 9 m*M* (McCormick and Steiner 1978). Rost-Siebert (1983) recorded growth decrease in spruce at aluminium concentrations of only 0.04–0.15 m*M* depending on the Ca concentration in the nutrient solution. Traditional nutrient solution techniques with unquantified and uncontrolled conditions of nutrition and growth were used in these investigations. In the present experiments, growth was measured as R_G based on weight measurements of plants and plant parts. Growth reductions in plants were recorded at aluminium concentrations of 0.3 m*M* (spruce) and 6 m*M* and higher (pine and ectomycorrhizal pine). The swollen root tips and yellowing needles are symptoms similar to those described in other investigations. Tischner et al. (1983), van Praag et al. (1985) and Schier (1985) found that root-growth disturbances and damage may be a result of disturbed meristemic groth

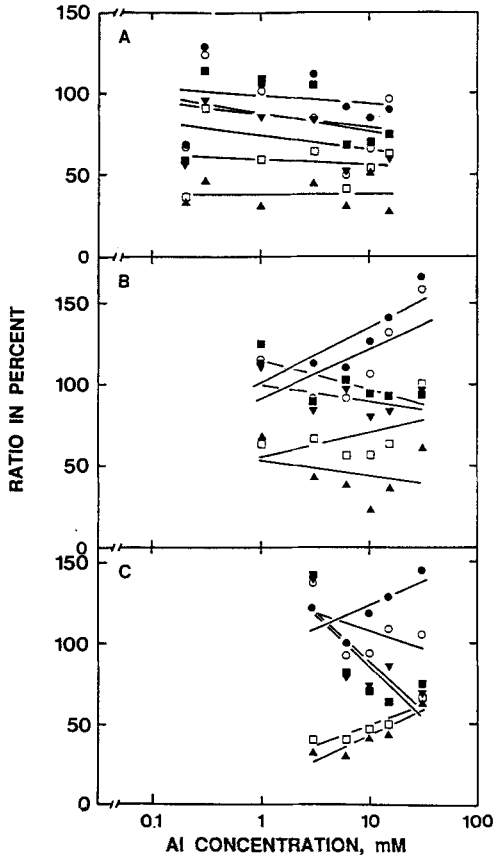

Fig. 2. Nutrient uptake rate per unit root growth rate [μmol (root dry weight)$^{-1}$] after aluminium addition as percent of the pre-aluminium value, $dn/dW_{r(Al)}$ in spruce (**A**), pine (**B**) and ectomycorrhizal pine plants (**C**). The Al concentrations are on a logarithmic scale and the corresponding equations of regression are given in Table 5. ●, Nitrogen; ○, potassium; ■, phosphor; □, calcium; ▲, magnesium; and ▼, sulphur

Table 5. Linear regression (y = a + bx) of $dn/dW_{r(Al)}$ versus aluminium concentration

	Element	a	b	r	r^2
Spruce					
	N	0.9853	−0.0452	0.1697	0.0288
	K	0.8820	−0.1141	0.3399	0.1155
	P	0.8801	−0.0831	0.2724	0.0742
	Ca	0.6014	−0.0321	0.1314	0.0173
	Mg	0.3848	−0.0038	0.0306	0.0009
	S	0.7421	−0.0924	0.3742	0.1400
Pine					
	N	1.012	0.3417	0.8273	0.6844
	K	0.9078	0.3032	0.6231	0.3883
	P	1.153	−0.1870	0.7744	0.5997
	Ca	0.5505	0.1530	0.4952	0.2452
	Mg	0.5398	−0.1022	0.3206	0.1028
	S	1.002	−0.1099	0.5047	0.2547
Ectomycorrhizal pine					
	N	0.9307	0.3009	0.6915	0.4781
	K	1.2940	−0.2249	0.4712	0.2220
	P	1.4980	−0.6409	0.7752	0.6009
	Ca	0.2322	0.2579	0.9083	0.8250
	Mg	0.1104	0.3189	0.9131	0.8337
	S	1.4920	−0.6118	0.7924	0.6279

patterns. In the present investigation, new fine roots developed at the highest aluminium concentrations even though these roots were badly deformed and fell off easily. The needles became chlorotic and necroses appeared at higher aluminium concentrations than those causing root damage.

Ectomycorrhizal fungi may protect plants against elevated concentrations of aluminium (Wilkins and Hodson 1989; Cumming and Weinstein 1990). In the pesent investigation ectomycorrhizal pine and pine responded in a similar way to increasing aluminium concentrations where R_G in ectomycorrhizal pine decreased at higher aluminium concentrations than in pine. The mycelium was well developed even at the highest aluminium concentrations.

Eighty-five percent or more of the added aluminium was recovered in the culture solution as monomeric aluminium at the end of the experiments. Total carbon in the solution was less than 5 n*M* and as the binding capacity of organic acids for aluminium is low (Hue et al. 1986), it may be concluded that the aluminium ion concentration in the solution during the experiments was virtually constant. Aluminium uptake into the shoots was restricted (Table 4) and most of the aluminium in the roots was probably precipitated or adhered to the cell walls of the cortex. The aluminium concentration of ectomycorrhizal roots was high compared with pine roots. A larger adsorbing area is the probable reason, as the aluminium concentration in the shoots was similar.

Disturbances of nutrient uptake caused by aluminium are commonly interpreted as antagonistic effets on cation uptake with detrimental effects on plant growth (Schier 1985; Jorns and Hecht-Buchholz 1985; Asp et al. 1988). In the present investigation uptake of Ca and particularly of Mg was influenced by aluminium. However, nutrient imbalances per se are not necessarily correlated with growth decrease (Ingestad and Lund 1986; Ericsson and Ingestad 1988). Ingestad and Ågren (1988) showed that there is a strong linear relationship at steady-state growth between the uptake rate of any nutrient per unit root growth rate, dn/dW_r[μmol h^{-1} (g root biomass h^{-1})$^{-1}$] and internal concentration of the limiting nutrient within the submaximum range. When added at free access FA, as in the present investigation, the uptake rate per unit of root growth rate of nutrients was higher than needed for maximal R_G and was thus defined as luxury uptake. In experiments with small birch plants, Ericsson and Ingestad (1988) showed that the internal concentration of phosphorus for constant maximal R_G was 60% of what was found at FA of phosphorus. The same pattern has been found for other elements at steady-state growth in the suboptimum range. The quantitative Ca and Mg demand for constant maximal R_G by small spruce and pine plants where R_A of Ca or Mg is the driving growth variable is unknown, but the demand of *B. pendula* is only 20% (Ca) and 50% (Mg) of what is taken up at FA (T. Ericsson, personal communication). The decrease in dn/dW_r of Ca and Mg was large even at low external aluminium concentrations, especially for Mg, but it is doubtful if it is large enough for growth disturbances, as both plant and root R_G were unaffected. The Ca/Al ratio in the nutrient solution was low in all experiments, indicating

that the external Ca concentration is of minor importance as long as the quantitative need of Ca for growth is fulfilled.

The present experiments were conducted at maximal R_G but the growth technique provided nutrients at low external concentrations, comparable to what is found in natural forest ecosystems. Göransson and Eldhuset (1987) showed that there was no difference in the response of growth and nutrient uptake to high external aluminium concentrations of *B. pendula* growing at near maximum R_G, 20% day^{-1}, and nutrient stressed birch plants at R_G 10% day^{-1}. As growth, allocation and nutrient uptake patterns were similar in birch, spruce and pine there is no reason to expect different reactions to aluminium in conifers growing at different availabilities of nutrients.

The reductions in growth occurred at aluminium concentrations which are high in comparison with those found in the fine-root zone of boreal forest soils. According to Roberts (1976), Persson (1980) and Murach (1984) approximately 80–90% of the fine-roots are normally present in the O and E horizon, where Al^{3+} concentrations are low compared with deeper soil layers (Ulrich 1981; Nilsson and Bergkvist 1983; Berdén et al 1987). Aluminium released from the B horizon is also likely to be more toxic than that released from the E horizon where organic complexes are dominant, as pointed out by Nilsson and Bergkvist (1983). It may be concluded that Al^{3+} ions as such, at concentrations found in the fine-root layers of boreal forest soils, do not decrease growth in Norway spruce and Scots pine. The most susceptible species was spruce which may suffer from root damage at Al^{3+} concentrations exceeding 0.3 m*M*, but the lethal concentration (8–10 m*M*) is high compared to those measured from soil layers penetrated by fine roots (<0.01 m*M*) (Nilsson and Bergkvist 1983). The results from the present investigation do therefore not support the hypothesis that inorganic aluminium as such is a major cause of forest die-back. However, in the fine-root layer of soils low in Ca or Mg and high in Al, antagonistic effects with aluminium may occur in the roots, thus causing Ca and/or Mg deficiency.

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