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Response of a Scots pine (*Pinus sylvestris*) stand to application of phosphorus, potassium, magnesium and lime. 3. Foliar nutrient concentrations and stand development

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Abstract

The effects of liming and P, K and Mg fertilization in 1985-1988 on soil nutrient concentrations in the forest floor and mineral soil of a Scots pine stand were discussed in two previous papers. The present paper addresses the effects of these treatments on foliar nutrient concentrations and tree growth. Stem volume increments of individual trees were measured. Average volume growth was estimated to amount to approx. 16 m^3 ha^{-1} y^{-1}, which may be a slight underestimation. P and K showed increased foliar concentrations instantly after fertilization and were the only elements that significantly increased volume growth in the period 1988-1991. Additional volume growth of individual trees brought about by P and K corresponded with 0.9 and 2.2 m^3 ha^{-1} y^{-1}, respectively. Foliar Mg and Ca were increased later and insignificantly reduced and increased volume growth, respectively. Lime and Mg applications tended to lower foliar N. When absolute foliar concentrations and element ratios were compared to Dutch and German standards, it appeared that the application of some of these standards in present research would not always have given a fully correct prediction of growth responses to nutrient additions.

Keywords: fertilization, foliar diagnosis, liming, *Pinus sylvestris*, tree growth response

Introduction

Foliar analysis is a tool to assess nutrient requirements of crops (Walworth & Sumner, 1987) and forests (Van den Driessche, 1974; Evers, 1986). At present, the interpretation of total nutrient concentrations is well-documented, while alternatives are still developing. For the evaluation of foliar nutrient concentrations of Scots pine German standards are available (Hüttl, 1986). In the Netherlands, standards were developed later (Anon., 1990), based on both Dutch and Northwest European experiments. According to the latter standards, at a 'low' concentration stunted growth and visible deficiency symptoms may occur, and the trees have a low tolerance to stress (e.g. drought, frost, insects, diseases). At a 'normal' level the nutrient concentration is sufficient to support adequate growth, fertilization does not result in profitable additional yields and recovery may be expected after exposure to stress. If the concentration of a nutrient is 'high' a further increase in its concentration will not stimulate and may even reduce growth, while a reduced stress tolerance may result from an excess of this nutrient, or from induced deficiencies of other nutrients.

The extent to which nutrient availability is balanced can be assessed by considering nutrient ratios, rather than absolute concentrations (Walworth & Sumner, 1987). Ingestad (1979) reported optimum nutrient proportions in relation to N for several tree species. According to preliminary Dutch standards, partly based on Ingestad's, several nutrient ratios are classified as 'low', 'normal' or 'optimal', irrespective of species (Anon., 1990). The 'optimal' range of the mineral nutrient:nitrogen ratios approximately agrees with those proposed by Ingestad (1979). At an 'optimal' mineral nutrient:nitrogen ratio no growth response can be expected from addition of the nutrient.

In a previous paper (Arnold & van Diest, 1993), a forest fertilization experiment was described. The present paper evaluates to which extent Scots pine in this experiment could benefit from the fertilization and liming treatments and whether growth responses were correctly predicted by foliar analysis. The treatment effects on foliar nutrient concentrations, height-, basal area- and volume growth are discussed. Growth measurements were used to evaluate the effects of fertilization and liming on stand performance.

Materials and methods

Fertilization and needle analysis

The experimental area is a Scots pine stand, planted in 1960. In 1985, foliar nutrient concentrations were analyzed prior to fertilization (Table 1). P, Ca and Mg were rated 'deficient', K 'sufficient', and N more than 'sufficient' by German standards (Hüttl, 1986; Table 2A). By Dutch standards (Anon., 1990; Table 2B,C), initial foliar P and Ca would have rated 'low' and N, K and Mg 'normal'. The ratios of P, K and Mg to N and the K/Mg ratio were evaluated as 'normal', and the K/Ca ratio higher than 'optimal' (Table 2B,C). Zn, B and Cu were evaluated as 'sufficient'.

Table 1. Nutrient concentrations in 1985 autumn foliage of Scots pine (before starting the experiments).

Nutrient	Unit	Needle age	
		0.5 y	1.5 y
N	g kg^{-1}	17.9	18.5
P		1.13	1.07
K		5.49	4.73
Ca		1.11	2.36
Mg		0.76	0.54
Zn	mg kg^{-1}	47	43
B		18	28
Cu		3.7	3.6

Table 2. Evaluation of nutrient concentrations in Scots pine: German standards (Hüttl, 1986); Dutch standards (Anon., 1990); nutrient mass ratios according to Dutch standards (Anon., 1990).

A German standards	Nutrient g kg^{-1}	Deficient supply <	Sufficient supply	Good supply >
	N	13 - 14	14 - 16	16
	P	1.2 - 1.3	1.3 - 1.5	1.5
	K	4.0 - 4.5	4.5 - 6.0	6.0
	Ca	1.0 - 2.0	2.0 - 3.0	3.0
	Mg	0.7 - 0.8	0.8 - 1.0	1.0
B Dutch standards	Nutrient g kg^{-1}	Low <	Normal range	High >
	N	14.0	14 - 18	18.0
	P	1.4	1.4 - 1.7	1.7
	K	5.0	5.0 - 7.0	7.0
	Ca	(2.0)	(≥ 2.0)	
	Mg	0.7	0.7 - 1.0	1.0
C Nutrient mass ratios	Ratio	Low	Normal	Optimal
	P/N × 100	< 5	5 - <10	10-14
	K/N × 100	< 25	25 - <50	50-100
	Mg/N × 100	< 5	5 - <10	10
	Ratio	Low	Normal	Optimal
	K/Ca	< 0.5	0.5 - 1.0	1.0 - 3.5
	Ratio	Normal	High	Very high
	K/Mg	1 - 7 to 9	7 to 9 - 12	> 12

In two experiments P, K and Mg fertilizers and lime (Table 3) were applied: a 2^4 factorial experiment and an experiment with 5 liming rates (for details on design and application dates see Arnold & Van Diest, 1993).

In October or November, i.e. in the dormant season, of 1986 to 1989, needle samples were taken from the fifth whorl from the top, in the light-exposed part of the canopy. Per plot needles were collected from one dominant tree, and in 1989 from 10 dominant trees. The current year's and previous year's needles were sampled. These needles are denoted as 0.5 y and 1.5 y needles, respectively, corresponding with their approximate age at the time of sampling. Older needles were never found. The needle samples were dried in a forced-draft oven at 70 °C and ground. Subsamples were digested in a H_2SO_4, salicylic acid, H_2O_2 medium, catalyzed by selenium. In the digests N and P were measured colorimetrically, K, Ca and Na by atomic emission and Mg by atomic absorption spectrometry. Zn, B and Cu were determined occasionally

Table 3. Amounts and compositions of fertilizers and lime applied in the factorial experiment and at the 3tL level of the liming experiment.

Nutrient	Amount (kg ha^{-1})	Fertilizer	Date of first application
P	25	Rock phosphate	autumn 1985
	25	Triple superphosphate	autumn 1985
K	100[a]	Potassium sulphate	spring 1986
Mg	100[a]	Kieserite	spring 1986
Ca	1200	Calcium carbonate[b] (powder, 3000 kg)	autumn 1985

[a] K and Mg applications were split, with additional applications made in the springs of 1987 and 1988, to a total of 100 kg ha^{-1} each. [b] Contained 3.6% $MgCO_3$ (1% Mg).

and appeared to be unaffected by treatments. Therefore, these elements are not discussed in this paper.

Stand properties

In the autumn of 1985, thinning was carried out, aimed at an equal basal area per plot (23.4 m^2 ha^{-1} ± 10%). Thus, the factorial and the liming experiment were thinned to 2127 and 2324 trees ha^{-1}, respectively. In December 1991 the stockings had declined to 1762 and 2051 trees ha^{-1}, respectively, by natural mortality and mostly by storm damage (25 January, 1990) and subsequent thinning. The storm did not strike treatments selectively, which is evident from the fact that during the whole measurement period the reductions in number of trees did not significantly differ per treatment (tested with a binomial distribution). Average heights (and the averages of dominant height per plot) in 1985 were 10.3 (12.4) and 12.8 (15.0) m in 1991.

Starting in 1985, tree height and diameter at breast height (DBH) were measured every winter (November/December) until 1987 and 1989, respectively. In November/December 1991 both entities were recorded again. All trees within the net plots were measured. DBH was measured with a tree diameter tape. To prevent bias, each tree was marked at a 1.3 m height. If this was the position of an old whorl, the diameters 15 cm above and below that point were measured and averaged. Tree height was measured with a telescoping height pole (1985-1987) or with a Blume-Leiss altimeter (1991). Compatibility of both methods was checked. The highest point above the ground was measured, which, therefore, did not necessarily correspond to the actual stem length. Top shoot length in the years 1983-1985 was estimated in 1985 by measuring the heights of the three whorls below the top shoot. Total top growth from 1983 to 1985 was used as a covariate in testing treatment effects on height increment. In 1991 it was not feasible any more to infer the heights in 1988-1990, as the visibility of lower whorls was reduced by the increased tree height.

The DBH and height data were used to estimate the stem volumes of individual trees according to

$$V = DBH^{1.82075} \times H^{1.07427} \times e^{-2.88085}$$

where V is the stem volume (dm^3), DBH the diameter at breast height (cm) and H the tree height (m) (formula from Dik, 1984). The results of these calculations were used to assess if, when, and to what extent fertilization effected an additional volume growth. For this assessment the annual basal area and volume increments per plot were to be calculated. However, this calculation was hampered by the fact that the amounts withdrawn in-between by (self-) thinning and the storm were not recorded. Therefore, when calculating volume growth as the difference in standing volume at the beginning and end of each time interval, the actually produced stem volume during that interval might be underestimated. To make a better estimation, only the trees remaining at the end of the considered time interval were used the growth calculations. The volume increments of these trees were added per plot. In fact, this approach implied the assumption that all trees that died or were thinned during the time interval were removed directly at the beginning of this interval. In doing so, the initial standing volume used in calculations was lower than the actual one, so that the calculated volume increments were higher than the actual increases in standing stem volume. However, this approach probably still calculated lower volume increments than a calculation in which the volume removed in-between could have been accounted for. Depending on the time of removal, this underestimation is more or less compensated for by an increased growth rate due to an increase in growth room per tree. In the growing seasons of 1986 and 1987 the calculated volume growth approximately equalled the increase in standing volume, because only few trees died.

Relative growth rates of the stem volume and basal area (denoted as rgr_v and rgr_b, respectively) of each time interval were also calculated on an individual tree basis, and averaged per plot.

Statistics

For calculations and statistical tests SAS software (SAS Institute Inc., 1990) was used. In the factorial experiment only effects with $P < 0.01$ were considered to be significant. Important interactions between treatments are mentioned in the text.

In the liming experiment effects with $P < 0.05$ were denoted as significant. If appropriate, results of repeated measures analysis of variance (RMAOV) of treatment effects will be presented (Moser et al., 1990), only if no significant year × effect interactions were found. (for more details see Arnold & Van Diest, 1993.).

Results

Foliar concentrations

Factorial experiment. The needle concentrations quickly responded to fertilization and liming (Table 4). Already in 1986, after the first fertilizer applications in spring, the P and K concentrations of the 0.5 y needles increased significantly. P in the 0.5 y

Table 4. Main effects of treatments on foliar nutrient concentrations in 0.5 y old and 1.5 y old needles of the factorial experiment (mg kg^{-1} DM).

Treatment	Year				Year			
	1986	1987	1988	1989	1986	1987	1988	1989
0.5 y needles	N				P			
Control	16.3	19.1	18.2	23.3	1.11	1.36	1.14	1.33
–P	16.2	18.2	18.1	20.9	1.05	1.37	1.20	1.40 ooo
+P	16.1	18.1	18.6	21.2	1.26 ***	1.66 ***	1.40 ***	1.69 ***
–K	15.7	18.1	18.3	21.5	1.16	1.53	1.30	1.56
+K	16.6	18.1	18.4	20.6	1.14	1.50	1.31	1.52
–Ca	16.3	18.3	18.7	21.5 o	1.23	1.52	1.32	1.52
+Ca	16.0	17.9	18.1	20.6	1.06 **	1.50	1.29	1.56
–Mg	16.5	18.3	18.6	21.4 oo	1.17	1.50	1.28	1.53
+Mg	15.9	18.0	18.1	20.7	1.14	1.53	1.32	1.56
	K				Ca			
Control	5.03	6.35	5.85	5.71	0.72	1.55	1.10	1.49
–P	5.52	6.52	6.02	6.24	0.95	2.17	1.87	2.03 o
+P	5.86	6.53	6.08	6.31	1.04	2.39	2.28	2.19
–K	5.32	6.13	5.58	5.75 ooo	0.94	2.18	2.08	2.06
+K	6.05 **	6.93 ***	6.52 **	6.81 ***	1.05	2.38	2.07	2.15
–Ca	5.77	6.70	6.35	6.50	0.94	1.92	1.60	1.36 ooo
+Ca	5.60	6.36	5.76	6.05 *	1.06	2.64 ***	2.55 ***	2.85 ***
–Mg	5.70	6.59	6.00	6.31	0.91	2.18	2.04	2.11
+Mg	5.67	6.47	6.10	6.25	1.09	2.39	2.11	2.11
	Mg							
Control	0.73	0.81	0.72	0.72				
–P	0.76	0.88	0.85	0.78				
+P	0.77	0.91	0.88	0.82 *				
–K	0.75	0.89	0.89	0.83				
+K	0.78	0.90	0.84	0.77 ***				
–Ca	0.75	0.90	0.86	0.75				
+Ca	0.78	0.90	0.87	0.86 ***				
–Mg	0.75	0.85	0.78	0.75 ooo				
+Mg	0.78	0.94 *	0.95 **	0.85 ***				
1.5 y needles	N				P			
Control	17.7	20.0	18.8	22.0	0.97	1.23	0.85	1.32
–P	18.0	19.0	16.1	20.1 ooo	1.01	1.19	0.83	1.41 ooo
+P	17.0	17.1 **	15.8	19.3 *	1.08	1.31 *	0.93 *	1.63 ***
–K	17.3	17.9	16.1	20.0	1.04	1.27	0.88	1.52
+K	17.7	18.3	15.8	19.5	1.04	1.23	0.88	1.52
–Ca	17.3	18.2	16.6	20.1	1.08	1.27	0.89	1.50
+Ca	17.7	18.0	15.3 *	19.3 *	1.01	1.23	0.86	1.53
–Mg	17.6	18.5	16.5	19.8	1.03	1.25	0.88	1.49
+Mg	17.4	17.6	15.4 *	19.6	1.05	1.25	0.87	1.54
	K					Ca		
Control	4.40	5.66	4.46	4.67	1.64	1.46	2.63	1.61
–P	4.98	5.37	5.00	5.33	1.99	2.10	3.61	3.04
+P	4.86	5.62	5.11	5.77 ***	1.84	2.24	4.03	3.47
–K	4.65	5.16	4.44	5.11 ooo	1.81	2.05	3.95	3.16
+K	5.19	5.83 *	5.68 ***	6.00 ***	2.02	2.29	3.69	3.35

Table 4. Continued.

Treatment	Year				Year			
	1986	1987	1988	1989	1986	1987	1988	1989
–Ca	4.86	5.62	5.04	5.54	1.82	1.93	3.18	2.24 ooo
+Ca	4.99	5.37	5.07	5.57	2.01	2.41 *	4.46 ***	4.28 ***
–Mg	4.92	5.58	4.97	5.43	1.77	1.95	3.72	3.07
+Mg	4.92	5.41	5.15	5.68	2.06	2.39 *	3.92	3.44
	Mg							
Control	0.52	0.55	0.55	0.52				
–P	0.57	0.59	0.74	0.57				
+P	0.54	0.61	0.76	0.59				
–K	0.55	0.58	0.80	0.60				
+K	0.56	0.61	0.69	0.56				
–Ca	0.53	0.59	0.70	0.55				
+Ca	0.58	0.61	0.79	0.60 *				
–Mg	0.54	0.58	0.68	0.54 oo				
+Mg	0.57	0.62	0.82	0.62 ***				

[a] Symbols following a treatment pair of figures: ***, ooo = $P < 0.0001$, **, oo = $P < 0.001$, *, o = $P < 0.01$, for ANOVA (*) and Repeated Measures Analysis of Variance (o), respectively.

needles in 1986 was lowered by liming (Table 4). The effects of P and lime application on foliar P were not interactive, except for a significant P×Ca interaction on P in the 1.5 y needles in 1986, showing that P was raised only in the absence of lime.

In 1987, when the split dosages of K and Mg were not yet completed, all applied nutrients had significantly increased their corresponding nutrient concentrations in the 0.5 y needles. In 1989 these effects were strongly significant (Table 4).

Starting in 1987, P, K and Ca application significantly increased the concentrations of the corresponding nutrients in the 1.5 y needles. Only in 1989, Mg significantly increased in the 1.5 y needles by Mg application (Table 4).

The K concentration of the 0.5 y needles was significantly reduced by liming in 1989. This may be related with the observed lime-induced reduction in K concentrations (total and extractable) of the forest floor. However, K in the soil solution was not markedly influenced by liming (Arnold et al., 1993a). A K-Ca uptake antagonism may have played a role.

Ca in the 0.5 y needles was slightly raised by P (Table 4), which increase was significant ($P < 0.01$) in RMAOV only. This may be an effect of Ca being the accompanying cation of the applied P (Table 2).

Mg in the 0.5 y needles was influenced by the applications of all major nutrients in 1989: P, Ca and Mg applications significantly increased and K application significantly reduced foliar Mg concentrations (Table 4). The Mg increase effected by liming is easily explained by the Mg content of the applied lime (Table 2), thus compensating a possible Ca-Mg uptake antagonism.

N in the 0.5 y needles was not significantly affected by any treatment in individual years (Table 4). RMAOV, however, showed that N in the 0.5 y needles was significantly reduced by Ca and by Mg applications. Ca and Mg interactively lowered 0.5 y foliar N ($P = 0.008$, RMAOV). N in the 1.5 y needles was significantly reduced by P application in 1987 and 1989. In both needle classes foliar N gradually increased during the measurement period (Table 4). The ratio of N in 0.5 y over that in 1.5 y needles, which is usually > 1 if N supply is not excessive, increased in the control plots from 0.93 in 1986 to 1.07 in 1989. Each year, this ratio was increased by P and unaffected by K, Mg and lime, indicating that the P-supplied trees utilized N more efficiently.

Evaluation of nutrient concentrations in the 0.5 y needles by the standards given in Table 2 shows that N was 'high' since 1987. P in the 0.5 y needles was increased to 'normal' in the +P plots since 1987. K and Mg remained in the 'normal' range since 1986, both with and without fertilization. The Ca concentrations remained 'low' in the –Ca plots and were increased to 'normal' by liming since 1987.

The P/N and K/N mass ratios were always in the normal range, although each year the P/N ratio was significantly increased by P application and in 1987-1989 the K/N ratio by K application. The Mg/N ratio was significantly increased by Mg application in 1987-1989, but remained 'low', or at best reached the lower part of the 'normal' range. It was always < 0.06, which is the optimal Mg/N ratio according to Ingestad (1979). K/Ca was significantly reduced to the 'optimal' range by liming in 1987-1989. K/Mg was 'normal' or 'high' (but always < 9) throughout the whole period, although in 1987-1989 it was significantly reduced by Mg application and significantly increased by K application in 1988-1989.

Liming experiment. Also in the liming experiment the foliar concentrations quickly responded to the applications (Table 5). The Ca concentrations in 1986 were unusually low, as in the factorial experiment, and did not show treatment effects, but in 1987-1989 the Ca concentrations of the 0.5 y needles were increased by liming. In 1987 and 1989 the linear and quadratic components of the liming effect were significant, and polynomial models fitted better than exponential models (Table 6). In 1988 and 1989 the Ca concentrations of the 1.5 y needles were significantly increased by liming, also according to polynomials. From the fitted curves it could be inferred that 0.5 y foliar Ca concentrations peaked at 12 and 11 Mg lime ha^{-1}, in 1987 and 1989, respectively. For Ca in both needle classes RMAOV showed significant liming effects over 4 years.

There were only a few effects of liming on other nutrient concentrations. Any influence of the additional amount of Mg applied by liming was probably nullified by the standard Mg application. In 1987 liming significantly raised the N concentrations of the 1.5 y needles, but the effect was not consistent: the 9tL treatment had a relatively low N concentration (Table 5). Liming consistently reduced the N concentrations in 0.5 y needles, as was also observed in the factorial experiment. This effect was not significant in individual years, but RMAOV showed a significant liming effect over 4 years ($P = 0.02$).

In 1988 P in the 0.5 y and 1.5 y needles was linearly decreased by liming. In 1989 P in the 1.5 y needles was lowered by liming, with a linear and quadratic correlation with liming level (Table 5).

Table 5. Foliar nutrient concentrations in 0.5 y old and 1.5 y old needles of the liming experiment (g kg^{-1} DM).

Treatment	Year				Year			
	1986	1987	1988	1989	1986	1987	1988	1989
0.5 y needles	N				P			
Control[a]	16.1	18.1	20.1	21.2	1.35	1.64	1.57	1.71
3tL	15.5	17.1	17.2	20.5	1.16	1.54	1.29	1.64
6tL		17.6	17.5	20.3		1.56	1.37	1.58
9tL		17.2	17.6	21.3		1.85	1.28	1.61
18tL		17.7	18.2	20.3		1.64	1.24	1.57
	K				Ca			
Control	6.14	6.88	7.33	6.69	1.29	2.41	2.42	1.79
3tL	6.33	6.49	6.26	6.35	1.46	3.21	3.45	3.19
6tL		6.89	5.92	6.31		3.34	4.37	3.72
9tL		7.09	6.71	6.28		3.28	3.10	3.55
18tL		6.74	5.83	6.13		3.32	3.66	3.24
						*[b]		*
	Mg							
Control	0.81	1.04	1.05	0.86				
3tL	0.80	0.94	0.87	0.83				
6tL		0.94	1.11	0.90				
9tL		0.90	0.89	0.94				
18tL		0.97	0.83	0.88				
1.5 y needles	N				P			
Control	15.7	16.6	15.0	19.3	1.12	1.32	0.97	1.70
3tL	18.4	17.1	15.6	18.3	1.04	1.22	0.90	1.58
6tL		17.3	13.3	17.6		1.30	0.88	1.49
9tL		15.5	14.6	19.4		1.17	0.82	1.56
18tL		18.1	15.2	18.3		1.28	0.85	1.53
		*						*
	K				Ca			
Control	5.08	6.05	5.90	6.27	2.10	2.63	3.56	2.69
3tL	5.10	5.33	5.70	5.68	2.30	2.99	4.97	4.52
6tL		6.62	5.67	6.00		2.94	5.57	5.24
9tL		5.84	5.81	5.90		3.40	4.92	4.91
18tL		6.36	5.12	5.71		3.45	5.73	4.75
							**	**
	Mg							
Control	0.56	0.66	0.76	0.62				
3tL	0.53	0.58	0.62	0.57				
6tL		0.64	0.86	0.62				
9tL		0.66	0.83	0.66				
18tL		0.66	0.69	0.57				

[a] PKMg treatment of the factorial experiment. [b]** = $P < 0.01$, * = $P < 0.05$.

Table 6. All curve-fitting results with R^2 values > 50% of several response parameters vs. liming rate ($Mg\ ha^{-1}$) in the liming experiment. Element dimensions as used in previous tables.

Foliar nutrient	Year	Needle age (y)	Exponential models		Linear and polynomial models			
			R^2	r value	R^2	intercept	linear component	square component
Ca	87	0.5	59.8	0.474	67.7	2.55	0.162	−0.007
Ca	88	1.5	59.1	0.615	79.6	3.87	0.269	−0.009
Ca	89	0.5	62.0	0.513	72.5	1.99	0.353	−0.016
Ca	89	1.5	63.5	0.529	89.1	2.98	0.443	−0.019
K	89	0.5			50.1	6.53	−0.026	
P	88	0.5			62.8	1.45	−0.014	
P	88	1.5			69.6	0.928	−0.006	
P	89	1.5			74.0	0.675	−0.030	0.001

The K/Ca mass ratio was lowered by liming in 1988 and 1989, with a reduction of the same magnitude for all liming rates. The K/Mg ratio was not influenced by liming.

Tree growth

The height measurement results are controversial for the factorial and liming experiment. In the factorial experiment a delayed treatment effect was observed (Fig. 1), whereas in the liming experiment there was an immediate response, that vanished after 1989 (Fig. 2). The height increments in the liming experiment had no apparent relationship with the liming levels, which hampers the interpretation of underlying mechanisms. In 1987 in the factorial experiment, height growth was significantly increased by P and in 1988-1991 by P, K and lime, with a significant P×K×Mg interaction. This interaction expresses that Mg caused an additional height growth only when both P and K were not applied.

The annual relative volume growth rate, rgr_v, in the factorial experiment was not significantly affected by any nutrient, up to and including the 1987 growing season (Table 7). In the period 1988-1991, P and K significantly increased rgr_v (Table 7; P = 0.006 and 0.003, respectively). There were no significant interactions between treatments. The volume increments of individual trees expressed on an area basis were 15.2, 16.3 and 17.5 $m^3\ ha^{-1}\ y^{-1}$ in 1986, 1987 and 1988-1991, respectively, and the additional volume growth brought about by P and K in 1988-1991 corresponded with 0.9 and 2.2 $m^3\ ha^{-1}\ y^{-1}$, respectively. In the latter period the actual increases in standing crop in the field were smaller, because of the storm and thinning in 1990. The actual standing stem volumes were 135, 150, 167 and 218 $m^3\ ha^{-1}$ in 1985, 1986, 1987 and 1991, respectively.

The annual relative basal area growth rate, rgr_b, was raised in the +K plots, which effect was significant in 1988 only (Table 7). The basal area is directly related to the stem volume, so it is likely that the strongest K effect on volume growth occurred in

Table 7. Annual relative growth rates (× 10,000) of basal areas (rgr_b) and stem volumes (rgr_v) in the factorial experiment.

Treatment	rgr_b per period					rgr_v per period		
	1986	1987	1988	1989	1990-1991	1986	1987	1988-1991
–P						1001	960	893
+P						996	1003	941 *[a]
–K	627	645	642	417	626	982	974	890
+K	661	655	691 *	422	657	1014	989	944 *
–Ca						984	979	898
+Ca						1013	984	936
–Mg						998	999	920
+Mg						999	965	913

[a] * = $P < 0.01$.

1988, two years after the first fertilizer applications. The other treatments did not significantly affect rgr_b.

There were no significant treatment effects on rgr_v and rgr_b in the liming experiment (Table 8). However, the rgr's usually declined above the 6tL or 9tL level.

Discussion

Needle concentrations

The reduced foliar N concentrations following liming may result from the lowered NH_4/NO_3 ratios of soil extractable N (Arnold & van Diest, 1993) and N in the soil solution at a 30-cm depth (Arnold et al., 1993a) in the limed plots of the factorial experiment. Scots pine absorbs NH_4 better than NO_3 from a mixed N source (Arnold, 1992).

The reduction in 0.5 y foliar P by liming which occurred in 1986 only (Table 4), corresponds with an initial liming-effected reduction of extractable P in the forest floor, gradually turning into higher extractable P concentrations in 1989 (Arnold &

Table 8. Annual relative growth rates (× 10,000) of basal areas (rgr_b) and stem volumes (rgr_v) in the liming experiment.

Treatment	rgr_b per period					rgr_v per period		
	1986	1987	1988	1989	1990-1991	1986	1987	1988-1991
Control[a]	632	608	658	425	634	976	954	977
3tL	692	661	783	431	701	1095	1044	977
6tL	702	705	691	488	680	1056	1051	979
9tL	634	761	729	419	685	1031	1123	970
18tL	672	655	711	482	652	1020	1006	954

[a] PKMg treatment.

van Diest, 1993). On the other hand, the lime-independent increase in foliar P by P application (Table 4) corresponds with the lime-independent increase in extractable (available) P by P application (Arnold & van Diest, 1993).

The Mg increase by P application cannot be attributed to soil processes (Arnold & van Diest, 1993). It may have a physiological basis (Truog et al., 1947). The reduced Mg concentration induced by K may be due to K inhibiting Mg uptake (Mengel & Kirkby, 1987) or to Mg being diluted by a K-induced additional volume growth (see below). However, such a dilution, if occurring, should probably have affected other nutrient concentrations as well.

The Ca concentrations in both needle classes were extremely low in 1986 (Tables 4, 5). Re-analysis showed that these values were not due to inaccuracy. Moreover, the low values of the 0.5 y needles in 1986 are followed by low values in the 1.5 y needles in 1987. Annual variation in Ca concentrations is not uncommon. Variation of the same magnitude as found in the present experiment was found by e.g. Leaf et al. (1970) in red pine (*P. resinosa*) and by Atterson (as cited by Van den Driessche, 1974) in lodgepole pine (*P. contorta*). In the first case the variation was related to precipitation. Van den Burg & Kiewiet (1989) reported a steady decrease in Scots pine foliar Ca since 1956 in a high NH_x-deposition area in the Netherlands and Sauter (1991) since 1978 in northern Bavaria (with rapidly increasing foliar N since ca. 1980). In the latter case foliar Ca showed a minimum value in 1984, with a gradual increase until 1988. In the Netherlands foliar Ca levels were low in the same period, which was possibly caused by root damage (J. van den Burg, pers. commun.).

The responses of foliar concentrations to the various liming rates were always better described by polynomial than by exponential models (Table 6). The Ca concentrations showed negative quadratic responses to liming rate, with maxima at 11 to 12 Mg lime ha^{-1} for the 0.5 y needles. The decline of foliar Ca concentrations at higher lime applications can not easily be explained. Liming lowered H^+ and Al in the forest floor and mineral soil (Arnold & van Diest, 1993), so the circumstances for root growth and, thus, Ca uptake by young root tips (Mengel & Kirkby, 1987) were increasingly favourable at higher liming levels. At the recommended lime application of 1,5 Mg ha^{-1} (Anon., 1990) the 0.5 y foliar Ca concentrations would have been 2.8 and 2.5 g kg^{-1} in 1987 and 1989, respectively, which is sufficient for Scots pine (Table 2).

Tree growth

The controversial findings concerning the height increments in the factorial and the liming experiment may be related to the higher stem density of the latter (possibly stimulating height growth and its responses). However, the inconsistent relationship with liming rates, and the absence of any response in 1988-1991, when the first liming response was observed in the factorial experiment, suggest that the observed differences are not related to the treatments.

The use of rgr values assumes exponential growth. Exponential growth of individual trees was likely, as (1) diameter growth from 1985 to 1991 was highly linear (87 % of the trees had R^2 values > 0.90 in linear regression of DBH on year, R^2 increasing with DBH); and (2) rgr_b and rgr_v had been reasonably constant throughout the measurement period (Tables 6, 7).

After canopy closure a stand is less responsive to fertilization than before. However, thinning can be seen as a temporal return to the stage before canopy closure. In that stage biomass aggradation is not completely balanced by litter fall and there is greater competition for soil nutrients (Miller, 1981). The 1985 thinning, therefore, probably enabled the stand to respond to fertilization more clearly. Such a reasoning is supported by the rgr being essentially constant throughout the measurement period. Trees in a fully occupied stand would exhibit a more linear, or even declining, annual volume increment.

Theoretically, a second growth response could have been expected after the storm and thinning in 1990 when part of the canopy was opened. However, as shown, the data indicate that the strongest response occurred in 1988 (Table 7), i.e. before thinning. Spiecker (1991) found that the greatest fertilization and liming responses occurred in favourable years. 1988 was a very favourable year for Scots pine, with a cool and cloudy summer probably preventing drought stress. This is reflected in a relatively high rgr_b, especially in the fertilized plots (not the control plots). The low rgr_b in 1989 is probably due to the extremely dry and sunny weather in May, followed by a relatively dry summer.

In the period 1990-1991, rgr_b recovered from the depression in 1989, despite very dry periods in both summer seasons. However, no fertilization effects were observed. Probably, the 1990 thinning stimulated basal area growth, in spite of the unfavourable weather conditions. The absence of any significant fertilizer effect on basal area growth after canopy opening in 1990 might suggest that at that time the growth potential was governed more by light interception than by nutrient availability.

In the present experiment there was no obvious relationship between foliar nutrient concentrations in any year and the rgr_v in 1988-1991 (as examined by selection of multiple regression models). In the liming experiment, foliar Ca concentrations and the relative growth rates showed similar optimum curves versus liming rate, but there was no positive correlation between foliar Ca and growth rates. Rgr_v and rgr_b in 1986 were negatively correlated with the 1.5 y foliar Ca concentrations of that year. This suggests that high growth rates in the previous year reduced foliar Ca by dilution. After the start of the experiment such an effect was eliminated by an increased Ca availability.

Foliar analysis and fertilizer requirements

Van den Driessche (1974) stated that in silviculture annual variations in nutrient concentrations may limit the value of foliar analysis as a diagnostic tool, because the situation in any one year may not be representative. In the present research, the 1985 foliar analysis correctly reflected the trees' nutritional status, because throughout the experimental period the foliar nutrient concentrations in the control plots remained in the same ranges as found in 1985. Only the rating for N changed, as it increased to > 18 g kg^{-1} (i.e. 'high') after 1986. Also, the nutrient ratios in the control plots remained in the same ranges as in 1985. However, the classification of the ranges may have to be reevaluated. German (Hüttl, 1986) and Dutch (Anon., 1990) standards agreed upon foliar K being sufficient, leaving room for growth responses, and P and Ca deficient. Mg was rated deficient by the former and normal by the latter. Most remarkably, the K/Ca ratio was very high. In view of these classifications it may be surprising that in the factorial experiment K increased volume growth to such an extent, and that lime did not. However, in 1985 the N/K ratio was not higher than 'normal', leaving room for a growth response to K application. Moreover, foliar K and P concentrations were the first to increase after fertilization, while Ca and Mg responded later (Table 4). This suggests that there was a crop demand for P and K, which was correctly predicted for P, but not consistently for K. The fact that a highly mobile and a highly immobile nutrient showed the first responses does not support the assumption that mobility determines the response time.

Additional volume growth due to liming is usually to be expected after a few years. Spiecker (1991) reports a long-lasting effect of liming on volume growth of Norway spruce starting about 5 years after lime application. Growth responses to liming of Scots pine can be negative or positive, but are usually small (Van den Burg, 1985, 1986). Ca deficiency is usually not caused by a deficient Ca bioavailability, but by a disability of the plant to absorb Ca. The elimination of this disability, e.g. root damage due to acidification, will take longer than the actual improvement in Ca availability.

The lack of growth response to Mg application suggests that in the present situation the Dutch standards are more valid than the German ones. Mg in the soil solution at a 30-cm depth was most significantly increased by Mg application until the final measurements in spring 1992 (Arnold et al., 1993a). However, the consistently 'low' Mg/N ratio would indicate that Mg sufficiency was not evident. Mg uptake may have been hampered by drought occurring in the growth seasons of 1989, 1990 and 1991. Al may also have inhibited Mg uptake. In the unfertilized plots it may have done so by a low Mg:Al ratio and in the fertilized plots by an increased absolute Al concentration (Arnold et al., 1993a). Huang & Bachelard (1993) found that *Pinus radiata* shoot and root concentrations of Mg decreased with increasing Al concentrations in nutrient solutions.

Conclusions

Nitrogen is usually the nutrient limiting plant growth most. In a situation of ample nitrogen supply through atmospheric deposition, growth rates may be high in spite of developing deficiency syndroms or malfunctioning (Nihlgård, 1985). Consequently, growth responses to fertilization with mineral nutrients may be small, and not necessarily indicative of tree vitality.

Assuming that growth responses to nutrient additions are related to nutrient demand, evaluation of foliar nutrient concentrations in 1985, according to standards listed in Table 2, did not always lead to correct conclusions regarding the forest's nutritional status. In the present experiment the largest increase in volume growth, 2 m^3 ha^{-1} y^{-1}, was observed after K application, although foliar K concentrations of unfertilized trees were rated 'sufficient'. However, the K/N ratio was 'normal', while only at an 'optimal' ratio no fertilization effects are to be expected. This shows that nutrient ratios may more precisely indicate nutrient deficiencies than do concentrations. Foliar P and Mg ratings correctly predicted that the stand's growth would increase after P and not after Mg application, respectively. However, the additional growth caused by P application was small: 0.9 m^3 ha^{-1} y^{-1}, while the rating 'low' suggested that fertilization was likely to result in a profitable growth increase. From this short-term experiment it can not be judged whether such growth increases are profitable.

Liming did not give a growth response, in spite of a rating 'deficient' for foliar Ca and improved Ca concentrations after liming. This does not necessarily mean that the rating for Ca should be corrected, since the response may be delayed. It may be deemed positive that liming reduced foliar N concentrations in this area with high N deposition, because such a reduction may lower the susceptibility to plagues and diseases (Nihlgård, 1985). The reduction in foliar N is likely associated with a lowered NH_4/NO_3 ratio of total available N (Arnold & van Diest, 1993; Arnold et al., 1993a). Such a lowering may inhibit N absorption by pine trees absorbing NH_4 better than NO_3 from a mixed N source (Arnold, 1992). However, liming did promote N mineralization (Arnold et al., 1993b), and thus the possibility of NO_3 leaching. A reduced N accumulation in biomass will further corroborate this effect.

The present experiment was conducted in an area with high atmospheric N inputs and high growth rates for Scots pine. It was shown that nutrient imbalances, possibly caused by an excessive N availability, can be corrected with the addition of minerals. However, a restored nutrient balance does not necessarily result in significant growth increases.

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