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PHOSPHORUS AND MICRONUTRIENT METAL UPTAKE BY SOME TREE SPECIES AS AFFECTED BY PHOSPHATE AND LIME APPLIED TO AN ACID SANDY SOIL

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SUMMARY

The effects of added P and lime on Douglas fir and Scots pine seedlings, and poplar and willow cuttings growing in a podzolic soil (pH 3.8, 90 ppm total P) were studied in pot experiments. Conifer dry weights responded best to P applied in the absence of lime, whereas liming to pH 4.3 promoted the P response of the broadleaved species. Normal rates of P, and of lime (broadleaved species), by promoting growth, also raised total contents of P and metals (Zn, Mn, Cu, Fe) in the various plant parts (stems, foliage, roots), but generally lowered the metal concentrations. The results strongly suggest that P interfered with the root to shoot translocation of Cu, Fe and Al (Al only estimated in Scots pine), but not with that of Zn and Mn. It is postulated that internal plant tolerance (promoted by P) plays a more important part in neutralizing toxic metal concentrations (Zn, and possibly also Fe) in the soil than do exclusion mechanisms. High applications of P without Cu may depress growth, as demonstrated for willow. Water-soluble soil P data may be misinterpreted if other limiting soil factors (pH, Cu status) have not been eliminated.

INTRODUCTION

Conifer growth on a moist podzolic soil (pH-KCl 3.8; 3.4% organic matter) low in phosphorus (90 ppm total and 2.0 ppm water-extractable P, *cf* Van Goor[7 8]) near Someren, The Netherlands, has been poor for some time and fertilizer experiments have given inconclusive evidence as to the cause. High concentrations of zinc (150 ppm and higher) and iron (300 ppm and higher) in the needles of Scots pine (*Pinus sylvestris*) and Douglas fir (*Pseudotsuga menziesii*) suggested a possible role of these elements, *e.g.* in immobilizing soil phosphorus.

Interactions between phosphorus and zinc in soils have not been fully clarified (Keefer and Sing [12]), though those with iron and aluminium are well established. In acid soils phosphorus precipitation (fixation) can be decreased by raising the pH, which lowers the activity of iron and aluminium ions (Lindsay and Moreno [13]).

The purpose of the present study was to investigate the effect of various phosphorus rates, with and without added lime, on the growth and uptake of phosphorus and micronutrient metals of some tree species on this Someren soil. Information on metal uptake of tree species is also of interest in respect of the utilization of domestic and industrial waste in forestry. As optimum growth of conifer seedlings occurs within a narrow pH range (Benzian [5]) some broadleaved species were also included in the experiments.

Naturally, the results of pot experiments must be used with caution when predicting fertilizer responses under field conditions. Indeed, in the area referred to above, factors that are difficult to simulate in pots (soil density and structure, moisture regime) also play a part. Experiments on some of these factors are in progress.

EXPERIMENTAL METHODS

Pot experiments with Douglas fir (*Pseudotsuga menziesii*) and poplar (*Populus euramericana*, cv. Robusta), willow (*Salix alba*) and Scots pine (*Pinus sylvestris*) were conducted in an open cage with removable transparent plastic covers for protection against rain water. The (polythene) pots contained 11 kg of oven-dry 0–20 cm Someren top-soil (mixed A and B podzol horizons). Reagent-grade NH_4NO_3, K_2SO_4, $MgSO_4.7H_2O$, and $CuSO_4.5H_2O$, at rates (in mg/kg soil) of 140 N, 90 K, 30 Mg, 7 Cu (Douglas fir and Scots pine) or 230 N, 150 K, 60 Mg, 7 Cu (poplar and willow), were added 5–10 weeks prior to planting in each pot 9 (Douglas fir) or 5 (Scots pine) one-year-old seedlings or 1 cutting (poplar, willow). The experiments ran for 3 (willow), 6 (Douglas fir and poplar) or 18 months (Scots pine, repeating the basic NKMg dressing after 12 months). Pots were watered daily with deionized water to 60% of field capacity.

Each experiment consisted of 5 randomized blocks (= 5 replications per treatment) with the following treatments (applied at the same time as the basic dressing):

Douglas fir: 4 rates of P (0, 62.5, 125, and 250 ppm; 1 mg P/kg dry soil (= 1 ppm) is roughly equivalent to 1.75 kg P/ha) as reagent grade $Ca(H_2PO_4)_2.H_2O$, without lime added (pH 3.8);

Poplar: 4 rates of P (0, 62.5, 125, and 250 ppm) with 0 and 2.25 g CaO (as

reagent grade $CaCO_3$) per kg soil (pH 3.8 and 5.5 respectively), and 2 rates of P (0, 250 ppm) with 0.90 and 1.35 g CaO/kg soil (pH 4.3 and 4.7 respectively);
Willow: Experiment (a): 4 rates of P (62.5, 125, 250, and 375 ppm) with 0, 0.90, 1.50 and 2.40 g CaO/kg soil (pH 3.8, 4.3, 4.8, 5.7 respectively); treatment 0.90 g CaO at all P rates subdivided into + and − Cu; Experiment (b): 6 rates of P (25, 62.5, 125, 187.5, 250, and 500 ppm) with 0 and 0.90 g CaO/kg soil, 3 cuttings per pot;
Scots pine: 6 rates of P (12.5, 62.5, 125, 187.5, 250, and 375 ppm) with 0 and 0.90 g CaO/kg soil.

Stems, needles (leaves) and roots (thoroughly rinsed with deionized water) were oven-dried at 70°C, weighed and ground, and wet-ashed ($HNO_3/H_2SO_4/HClO_4$); samples were analysed for P, Cu, Fe, Mn (spectrophotometrically), Zn (atomic absorption), and in some cases for N (micro-Kjeldahl) and Al (spectrophotometrically).

Soil samples, for analysis of pH (in 1 *N* KCl, 1:5 suspension), total P, water-soluble P (according to Van der Paauw *et al.*[19] and NH_4OAc/dithizone (pH 7)–extractable Zn (according to Shaw and Dean [20] were taken after harvesting.

All data on dry-matter yields were subjected to an analysis of variance and Duncan's multiple range test.

RESULTS

Douglas fir

In a premilinary experiment dry weights of Douglas fir shoots had responded positively to added P (at the rates of 54 and 135 ppm) and negatively to added lime (final pH 4.3). Added P increased P and decreased Zn, Mn, Cu, and Fe concentrations, but the effect of lime was somewhat erratic. Trends for total P and metal uptake were very similar to those for dry weights.

The present, more detailed study of the P response confirmed the above results for both shoots (needles and stems) and roots. The highest rate of applied P (250 ppm), which doubled the main shoot length and produced an eight-fold increase in lateral shoot length (data not presented here), was still too low for optimum growth (Table 1). Top dry weight was affected much more than root dry weight.

Tissue P concentrations increased and metal concentrations diminished with increasing P rates (Table 1). However, it can easily

TABLE 1

Dry-matter yields an P and micronutrient metal concentrations in dry matter of Douglas fir seedlings as affected by various treatments (0, 62.5, 125, and 250 ppm P); dry weights are means of 5 replications (= 5 pots, 9 seedlings per pot). S = stems, N = needles, R = roots

	P_0			P_1			P_2			P_3		
	S	N	R	S	N	R	S	N	R	S	N	R
Dry weight (g)	4.0*	5.8	3.8†	6.0*	8.7	4.5†	9.3	13.2	6.1	21.0	25.9	10.9
P(%)	0.06	0.07	0.10	0.10	0.11	0.14	0.10	0.13	0.14	0.10	0.14	0.16
Zn (ppm)	190	245	564	169	255	502	137	232	273	113	179	384
Mn (ppm)	101	233	90	91	242	78	75	210	55	43	164	44
Cu (ppm)	12.2	10.6	37.5	10.9	9.8	30.0	11.2	9.2	25.2	8.8	7.2	23.1
Fe (ppm)	81	152	421	57	123	300	44	123	251	38	104	317

† Dry weights do not differ significantly for stems and roots† respectively ($P = 0.05$)

be calculated from the data that the *total* amounts in the various plant parts of both P and the metals increased. The enormous growth response to applied P and the resulting decrease in metal concentrations ('dilution)', masks any (inhibitory) effects of P on metal absorption.

The distribution pattern for P and Mn was similar to that for dry matter, *i.e.* with higher P rates an increasing accumulation in shoots relative to roots. This shows that P does not interfere with Mn translocation from roots to shoots. The roots had relatively high Cu, Fe, and Zn concentrations, but there was no definite trend for the distribution of these metals with the rate of applied P.

Poplar

Shoot length (not presented here) and dry weights of the various plant parts responded highly significantly to applied P, the largest rate (250 ppm) still being sub-optimal (Table 2). A significant P × lime interaction was also found, the P response showing a maximum at pH 4.3. In the presence of applied P liming to pH 4.3 promoted, but further lime additions depressed growth. Without applied P lime had no significant effect on stems and roots. The effects of the various treatments were most pronounced in top dry weights.

There was a general tendency for plant P concentrations to increase and for metal concentrations to decrease with increasing rates of applied P (Table 2). A notable exception is the treatment without

TABLE 2

Dry-matter yields and P and micronutrient metal concentrations in dry matter of poplar cuttings as affected by various pH and P treatments (0, 62.5, 125 and 250 ppm P); dry weights are means of 5 replications (= 5 pots; 1 cutting per pot)

	pH 3.8				pH 4.3		pH 4.7		pH 5.5			
	P_0	P_1	P_2	P_3	P_0	P_3	P_0	P_3	P_0	P_1	P_2	P_3
*Dry weight (g)**												
Stems	0.1^{a}	0.8^{ab}	1.5^{ac}	19.0^{dk}	2.6^{ae}	48.2^{f}	7.7^{ag}	27.7^{dh}	3.9^{ai}	9.9^{ij}	17.2^{k}	27.0^{dl}
Leaves	0.5^{a}	2.0^{ab}	2.8^{ac}	22.8^{dk}	4.8^{ae}	38.8^{f}	9.9^{egi}	26.0^{dh}	5.9^{ai}	12.7^{j}	19.6^{k}	26.3^{dl}
Roots	0.0^{a}	1.6^{ab}	2.3^{ac}	17.9^{dk}	2.6^{ae}	32.2^{f}	5.1^{ag}	15.9^{dh}	3.2^{ai}	8.6^{j}	13.4^{k}	18.0^{dkl}
P(%)												
Stems	0.13	0.07	0.07	0.13	0.11	0.10	0.07	0.11	0.07	0.10	0.08	0.07
Leaves	0.18	0.12	0.14	0.26	0.14	0.23	0.12	0.24	0.12	0.21	0.21	0.21
Roots	—†	0.14	0.16	0.24	0.17	0.20	0.17	0.22	0.17	0.18	0.21	0.20
Zn (ppm)												
Stems	—	138	181	142	257	131	218	170	177	132	118	108
Leaves	288	244	355	415	541	417	713	632	478	387	358	352
Roots	—	227	214	149	222	95	187	142	143	103	131	92
Mn (ppm)												
Stems	—	33	31	24	55	15	45	21	50	32	25	20
Leaves	—	—	94	94	124	98	169	124	119	115	103	95
Roots	—	—	38	29	57	23	79	61	142	86	77	57
Cu (ppm)												
Stems	—	—	6.5	4.1	12.4	3.6	7.4	4.7	9.6	5.6	5.0	3.5
Leaves	—	—	—	8.1	10.5	6.0	14.9	6.9	8.8	8.5	7.4	6.3
Roots	—	—	31.3	16.4	42.0	13.0	31.1	17.6	37.5	23.6	—	17.1
Fe (ppm)												
Stems	—	—	41	26	32	18	36	21	39	29	24	21
Leaves	—	—	85	74	83	70	90	81	85	91	84	81
Roots	—	—	518	200	621	211	505	316	562	372	398	293

* Figures in the same line having indices in common do not differ significantly ($P = 0.05$)

† Insufficient material for analysis

lime (pH 3.8) where P concentrations in stems and leaves diminished with the first additions of P fertilizer. This is an example of the well-known 'Steenbjerg phenomenon', typical of extreme nutrient deficiencies (Steenbjerg[23]; Steenbjerg and Jakobsen[24]. In the absence of lime, Zn concentrations in plant tops also deviated from the general pattern. Trends for total amounts of P and metals in the various plant parts (to be derived from Table 2), as affected by applied P, were very similar to those for dry weights. Evidently, the 'dilution effect', resulting from the large growth response to applied P, is predominant and no direct (inhibitory) effect of P on metal uptake can be demonstrated. If nutrient totals (or dry weights) are plotted against applied P, the curves for tops and roots will be found to diverge as P rates increase. It should be noted that Cu and Fe, in contrast to P, Zn and Mn, preferentially accumulate in the roots, expecially at the higher P rates.

The lime treatments showed no definite effect on plant metal concentrations, but P concentrations were mainly lowered. Total amounts of both P and metals in the various plant parts were raised by the lower but reduced by the higher lime levels, thus closely following the trends in dry weights. There is little evidence of lime directly interfering with uptake of the elements investigated, with a possible exception for P and Zn at the higher lime applications.

Willow

In the first experiment (Table 3) dry weights of stems and leaves were found to respond highly significantly to added P and lime, the P response being highest in the presence of applied lime (significant, positive interaction). At pH 4.3 or less, 250 ppm P proved optimal, the higher P rate (375 ppm) depressing yields somewhat in the absence of applied lime and copper (significant for stem dry weight). By contrast, the latter P rate turned out to be sub-optimal at pH values above 4.3. A well-defined pH optimum was found at 4.3 irrespective of P rate, but trees given only 62.5 ppm P did not respond significantly to lime. Omitting Cu from the basic nutrient dressing caused yields to decline, but only significantly so at the highest P rate.

Added P increased P and generally lowered metal concentrations in stems and leaves, but trends were less pronounced for Cu and Fe. With sub-optimal P rates, *i.e.* in the ascending part of the yield curve (Fig. 1), trends for metal concentration and total accumulation (also in Fig. 1) are opposite, masking any evidence of P inhibiting metal uptake. However, supra-optimum P rates are generally

TABLE 3

Dry-matter yields and P and micronutrient metal concentrations in dry matter of willow cuttings as affected by pH, Cu and P treatments (62.5, 125, 250, and 375 ppm P); dry weights are means of 5 replications (= 5 pots; 1 cutting per pot)

	Dry wt. (g)*		P(%)		Zn (ppm)		Mn (ppm)		Cu (ppm)		Fe (ppm)	
	Stems	Leaves	Stems	Leaves	Stems	Leaves	Stems	Leaves	Stems	Leaves	Stems	Leaves
pH 3,8												
P_1	0.3^{a}	0.5^{a}	0.11	0.12	–†	–	–	–	–	–	–	–
P_2	0.9^{ab}	1.7^{ab}	0.13	0.22	514	1085	70	206	14.5	–	–	–
P_3	5.0^{bc}	7.2^{cd}	0.22	0.44	357	1058	37	154	15.8	18.0	90	161
P_4	3.4^{abd}	6.1^{dln}	0.32	0.57	327	908	32	126	18.2	13.8	136	194
pH 4,3												
P_1	1.9^{abe}	1.9^{ae}	0.09	0.11	566	1973	99	404	6.7	–	128	145
P_2	8.8^{fj}	7.6^{df}	0.10	0.21	283	1364	51	257	9.0	14.3	245	135
P_3	$26.3^{gg'}$	$17.9^{gg'}$	0.17	0.33	178	929	28	165	6.7	11.2	42	156
P_4	$26.1^{g'h}$	$18.8^{g'h}$	0.17	0.38	141	761	25	125	7.1	11.2	34	153
pH 4,3 *minus Cu*												
P_1	$1.4^{abe'}$	$1.3^{ae'}$	0.09	0.11	749	2638	101	422	–	–	–	–
P_2	$9.0^{f'j}$	$8.2^{df'}$	0.12	0.22	427	1951	47	261	1.7	4.0	49	179
P_3	$22.6^{g'p}$	$16.2^{g'h'}$	0.16	0.34	259	1277	29	169	1.5	3.3	71	175
P_4	$18.6^{h'k}$	$13.7^{h'k}$	0.18	0.37	242	1050	32	143	1.5	2.8	55	179
pH 4,8												
P_1	2.6^{abl}	3.1^{al}	0.08	0.11	392	1461	105	400	5.4	11.7	88	150
P_2	7.9^{cj}	6.4^{djn}	0.11	0.20	248	1251	58	287	5.6	12.7	64	170
P_3	17.0^{k}	11.8^{k}	0.14	0.29	222	1180	35	232	6.1	11.2	30	172
P_4	$24.7^{g'l}$	$17.1^{g'l}$	0.17	0.35	143	848	27	184	6.0	11.0	40	160
pH 5,7												
P_1	2.6^{abm}	2.4^{am}	0.08	0.11	196	967	99	343	5.3	11.9	161	198
P_2	3.7^{abn}	3.7^{ain}	0.10	0.17	168	805	71	303	4.8	9.8	49	166
P_3	10.4^{jo}	8.1^{do}	0.12	0.27	135	665	41	225	5.6	10.7	35	155
P_4	19.4^{kp}	12.6^{kp}	0.14	0.33	92	558	26	175	5.3	9.7	39	160

* Figures in the same column having indices in common do not differ significantly ($P = 0.05$)

† Insufficient material for analysis

associated with decreases both in metal concentration and in total absorption, suggesting an adverse effect either on metal uptake by the roots or on translocation from roots to shoots.

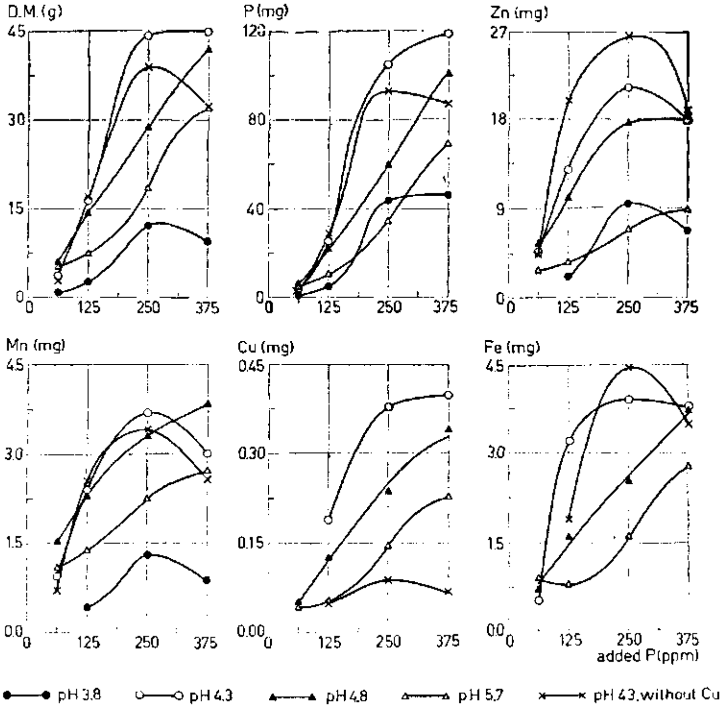

Fig. 1. Dry-matter production and total amounts of P, Zn, Mn, Cu and Fe in tops of willow cuttings as influenced by added P and lime.

Plants not given lime showed top chlorosis resembling iron deficiency. Lime depressed P and, generally, Zn, Cu, and Fe concentrations also. No definite trends were demonstrated for Mn. Unfortunately, the reference plant composition data (treatment without lime) are limited because of the small amounts of material available for analysis. Total P and metal accumulation increased with lime applications up to pH 4.3, but decreased at higher pH values, thus following trends in dry weights. The parallel downward trends in concentration and total absorption of P and metals (not distinct for Mn) indicate an adverse effect of lime either on root uptake or on translocation from roots to tops.

Without applied Cu, leaf Cu concentration fell to a low 2.8 ppm (at the highest P rate), but no symptoms of copper deficiency (*cf* Van der Meiden[17]) were observed. There was a steep rise both in Zn concentration and in total Zn accumulation in plant tops, but no similar effects occurred for the other metals.

TABLE 4

Dry-matter yields and P and micronutrient metal concentrations in dry matter of willow cuttings as affected by pH and P treatments (25, 62.5, 125, 187.5, 250, and 500 ppm); dry weights are means of 5 replications (= 5 pots; 3 cuttings per pot)

	pH 3.8						pH 4.3					
	P_1	P_2	P_3	P_4	P_5	P_6	P_1	P_2	P_3	P_4	P_5	P_6
*Dry weight (g)**												
Stems	0.4^{a}	0.5^{ab}	0.9^{ac}	1.8^{adg}	1.9^{aeg}	0.6^{af}	1.3^{ag}	5.8^{gh}	19.8^{i}	32.9^{j}	34.4^{jk}	22.4^{il}
Leaves	0.7^{a}	1.1^{ab}	2.0^{ac}	3.9^{ade}	3.8^{ae}	1.3^{af}	1.8^{ag}	6.6^{ah}	16.8^{i}	24.3^{ij}	25.9^{jk}	21.0^{i}
Roots	0.6^{a}	0.8^{ab}	1.6^{ac}	2.4^{acd}	2.5^{ace}	0.8^{af}	1.2^{ag}	3.5^{eh}	9.5^{ij}	12.2^{jk}	11.8^{k}	7.7^{l}
P(%)												
Stems	0.08	0.10	0.16	0.26	0.30	0.49	0.08	0.09	0.14	0.17	0.18	0.24
Leaves	0.10	0.12	0.24	0.52	0.62	0.55	0.10	0.16	0.29	0.35	0.38	0.45
Roots	0.20	0.23	0.28	0.34	0.42	0.51	0.15	0.18	0.22	0.29	0.34	0.45
Zn (ppm)												
Stems	225	290	274	338	301	211	629	463	292	205	172	214
Leaves	410	492	705	776	765	602	1873	1935	1329	1077	905	929
Roots	365	332	301	265	290	247	637	457	384	364	360	283
Mn (ppm)												
Stems	–†	71	58	51	47	34	108	70	38	30	29	33
Leaves	–	174	199	190	195	253	390	324	216	184	162	139
Roots	52	45	39	33	36	33	70	47	38	38	35	32
Cu (ppm)												
Stems	–	–	10	11	9	–	7	8	7	6	9	9
Leaves	–	–	15	26	17	10	16	14	13	12	14	13
Roots	–	–	99	124	141	58	270	484	379	312	281	370
Fe (ppm)												
Stems	–	105	104	112	89	85	78	–	34	36	50	40
Leaves	285	256	235	236	225	242	177	134	158	151	155	150
Roots	470	405	339	327	305	400	619	546	622	630	477	461

* Figures in the same line having indices in common do not differ significantly ($P = 0.05$)

† Insufficient material for analysis

The second experiment was intended to study P effects in more detail, without and with (optimum rate) applied lime. The results (Table 4) largely confirm those of the first experiment. P and lime effects were highly significant and so was their interaction. Actually, no significant yield response to P was obtained in the absence of applied lime and, similarly, plants did not respond to lime at the lowest P rate (25 ppm). Applying 250 ppm P proved optimal and dry weights were significantly reduced when doubling this rate. Trends for stems, leaves, and roots were identical, being most pronounced in plant tops.

Trends for nutrient concentrations and totals (calculated from Table 4), as affected by applied P, correspond with those reported above. However, mainly at the lower P rates without applied lime, Zn (leaf and stem), Mn (leaf) and Cu (root) concentrations behaved differently. Generally, there was a concurrent decline in concentration and total accumulation of metals at P rates exceeding the optimum. Plotting nutrient totals (or dry weights) against P rates would show the curves for tops and roots to diverge as P increases and, eventually, to converge as P surpasses the optimum. In contrast to P, Zn and Mn, the metals Cu and Fe would be found to accumulate increasingly in the roots. These data do not suggest that P (at (sub) optimal rates) interferes with the translocation of metals other than Cu and Fe from roots to shoots.

Plants not receiving lime had chlorotic upper leaves, particularly so at the higher P rates. Liming (up to pH 4.3) generally lowered plant nutrient concentrations but increased their totals in the various plant parts. However, Zn (all plant parts), Cu (root) and Fe (root) concentrations increased rather than diminished with applied lime.

Scots pine

Dry weights of all plant parts (Table 5) were highly significantly increased by applied P and decreased by lime (pH 4.3), the P response being largest without lime added (significant negative interaction). P rates over 187.5 ppm (pH 3.8) and 250 ppm (pH 4.3) did not further significantly increase yields. Growth responses diminished in the order: needles, roots, stems.

Symptoms of phosphorus deficiency, characterized by dull, dark-green needles (often affected by black algae) turning brownish purple and dying (*cf* Baule und Frikker[3]; Van Goor[7]) occurred

TABLE 5

Dry-matter yields (g) and P and N concentrations (%) in dry matter of Scots pine seedlings as affected by various pH and P treatments (12.5, 62.5, 125, 187.5, 250, and 375 ppm P); dry weights are means of 5 replications (= 5 pots; 5 seedlings per pot)

	pH 3,8						pH 4,3					
	P_1	P_2	P_3	P_4	P_5	P_6	P_1	P_2	P_3	P_4	P_5	P_6
*Dry weight**												
Stems	3.1^{a}	10.4^{b}	22.7^{c}	33.7^{d}	34.9^{de}	34.4^{df}	2.1^{ag}	3.3^{ah}	9.0^{abi}	14.7^{bj}	23.4^{ck}	24.3^{cl}
Needles	4.7^{a}	26.4^{b}	55.6^{c}	78.6^{df}	77.5^{de}	86.8^{ef}	2.5^{ag}	6.5^{ah}	21.8^{bi}	36.8^{bj}	61.1^{ck}	66.3^{edl}
Roots	4.5^{a}	21.0^{b}	40.4^{ck}	54.7^{df}	55.3^{de}	60.8^{ef}	3.0^{ag}	7.4^{ah}	15.2^{abi}	26.9^{bj}	38.8^{cjk}	44.5^{dkl}
Phosphorus												
Stems	0.08	0.10	0.12	0.10	0.09	0.10	0.08	0.09	0.10	0.10	0.10	0.11
Needles	0.07	0.10	0.14	0.15	0.15	0.17	0.09	0.09	0.13	0.17	0.17	0.18
Roots	0.10	0.15	0.17	0.18	0.20	0.22	0.08	0.17	0.17	0.20	0.23	0.27
Nitrogen												
Stems	2.70	2.06	1.52	1.11	0.82	0.71	2.45	2.16	1.39	1.08	0.85	0.86
Needles	3.73	3.35	2.08	1.72	1.84	1.71	2.69	2.80	2.46	2.03	1.62	1.76
Roots	2.64	2.63	1.88	1.48	1.65	1.56	2.08	2.15	2.20	1.68	1.58	1.54

* Figures in the same line having indices in common do not differ significantly ($P = 0.05$)

at P rates up to 125 ppm. Affected plants contained 0.13 – 0.14 per cent P or less in the dry matter of needles.

Added P raised P and lowered N and metal concentrations in all plant parts (Tables 5, 6). However, in several cases the decline in metal concentrations was preceded by a (substantial) rise at the lower P rates. Curves representing dry weights and element totals as plotted against added P have the same shape (Fig. 2), contrasting with the descending trend in element (except P) concentrations. Again, 'dilution' appears to be predominant, obscuring a direct (inhibitory) effect of P on N and metal absorption. Some evidence of such a mechanism is shown at near-optimum P rates, in the form of concurrent declines in element concentrations and totals (Al, Zn, Mn). The divergence between corresponding curves for tops and roots with increasing P rates indicates that more N, P, Mn and, to a lesser extent Zn, accumulate in the tops relative to the roots, whereas the reverse holds for Cu, Fe and Al.

Liming (pH 4.3) tended to reduce the concentrations of all ele-

TABLE 6

Concentrations of micronutrient metals in dry matter of Scots pine seedlings as affected by various pH and P treatment (12.5, 62.5, 125, 187.5 250, and 375 ppm P)

	pH 3,8						pH 4,3					
	P_1	P_2	P_3	P_4	P_5	P_6	P_1	P_2	P_3	P_4	P_5	P_6
Zn (ppm)												
Stems	152	177	135	115	97	92	148	112	102	96	90	86
Needles	217	238	199	163	169	162	171	256	265	247	207	202
Roots	380	461	331	234	210	205	343	576	640	460	488	363
Mn (ppm)												
Stems	152	169	92	61	41	37	94	82	80	53	44	36
Needles	246	311	189	154	142	130	182	279	285	236	196	169
Roots	119	91	28	21	20	18	56	82	93	43	31	27
Cu (ppm)												
Stems	10.2	9.2	9.4	7.0	5.9	5.6	13.6	8.0	7.0	6.7	7.2	5.9
Needles	7.7	6.9	6.2	5.2	5.2	4.9	4.8	5.0	5.8	5.8	5.4	4.9
Roots	35.5	44.5	34.7	28.8	25.7	27.1	37.2	47.6	41.7	28.8	37.2	34.9
Fe (ppm)												
Stems	178	141	170	105	126	76	311	116	80	89	68	80
Needles	210	148	124	121	116	130	158	152	123	132	110	114
Roots	815	605	535	519	512	475	628	1029	538	525	657	535
Al (ppm)												
Stems	565	242	252	228	168	135	452	273	146	158	138	129
Needles	671	367	315	298	257	240	244	219	185	244	218	199
Roots	2636	2537	2718	2547	1998	1797	3631	4890	2246	1898	2073	1562

ments investigated, except P. However, the trend was not distinct for needles, whilst root concentrations increased rather than decreased. Trends for totals were more definite, declining with lime applied. For some metals (Zn, Mn, Cu) this effect was small at the higher P applications. From these data there is little conclusive evidence that lime inhibited metal absorption by the roots.

In a supplementary pot experiment, Scots pine seedlings were grown on a podzolic soil (pH 4.3, 0.15 ppm water-extractable P) which had been exposed to Zn pollution from a Zn factory (Budel) for many years. The Someren soil was used as a reference. The largest amount of applied P (375 ppm) proved sub-optimal for the Budel soil, whereas 187.5 ppm P was found to be adequate for the Someren soil. This is in line with the plant P concentrations attained:

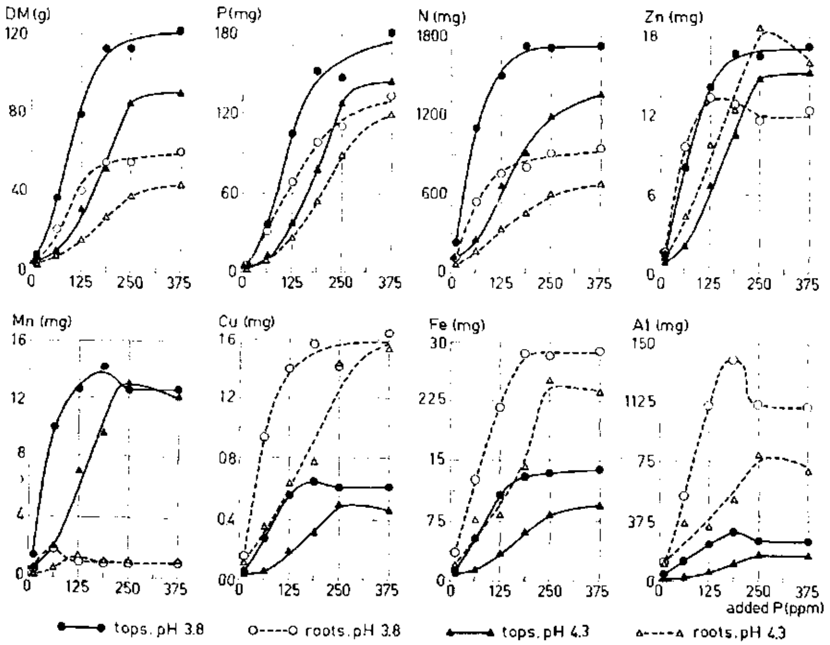

Fig. 2. Dry-matter production and total amounts of P, N, Zn, Mn, Cu, Fe and Al in tops and roots of Scots pine seedlings as influenced by added P and lime.

0.08, 0.13, and 0.14 per cent P (Budel soil) as against 0.10, 0.16 and 0.17 per cent P (Someren soil), for stems, needles and roots respectively. Plant Zn concentrations diminished with increasing rates of applied P and ranged from 286–156, 419–259 and 522–365 ppm Zn (Budel soil) as against 114–85, 161–126 and 262–136 ppm Zn (Someren soil), for stems, needles and roots respectively.

Soil analysis

Dithizone-extractable soil Zn (Table 7) as determined in the poplar experiment tended to decrease as more P and lime were added. The apparent P effect can be explained on the basis of a higher Zn uptake by the plant (*cf* p. 136), assuming that dithizone-extractable soil Zn is plant available (Massey [14]). Liming would appear to have a real depressing effect, the higher rates reducing both dithizone-extractable soil Zn and plant Zn. Supplementary analyses following

TABLE 7

Dithizone-extractable soil Zn (ppm) as influenced by various pH and P treatments (0, 62.5, 125 and 250 ppm P). Samples taken after harvesting the crop (poplar cuttings)

	pH 3,8				pH 4,3		pH 4,7		pH 5,5			
	P_0	P_1	P_2	P_3	P_0	P_3	P_0	P_3	P_0	P_1	P_2	P_3
Soil	9,2	9,7	9,4	7,3	8,2	6,6	6,4	7,5	8,3	6,8	4,6	4,6

extraction in 2.5% acetic acid produced soil Zn values in the 10–20 ppm range, irrespective of the amount of P and lime added. This is considerably less than in the nearby Budel area exposed to atmospheric Zn pollution, where levels of 40, 60, and 310 ppm acetic acid-extractable soil Zn were obtained at, respectively, 1500, 400, and 200 metres from the zinc factory.

Some selected data on soil P, obtained in the experiment with Scots pine, are presented in Table 8. Water-soluble soil P was raised more than proportionally with increasing P rates, causing the ratio water-soluble over total P to rise. Considering the sigmoid shape of the P absorption curves (Fig. 2), and assuming that the absorbed P comes mainly from the water-soluble fraction, the effect may even be larger than would appear from Table 8. Simultaneous application of lime and P reduced the increase in water-soluble P. Because of the concurrent decline in plant P (Fig. 2), Table 8 probably gives too low an estimate of this effect. There is no evidence that lime affected

TABLE 8

Total and water-soluble soil P (ppm) as influenced by various pH and P treatments (0, 12.5, 62.5, 125, 187.5, 250, and 375 ppm P). Samples taken after harvesting the crop (Scots pine seedlings)

	P_0	P_1	P_2	P_3	P_4	P_5	P_6
pH 3.8							
Water-soluble P	1,6	2,2	6,2	13,1	24,3	40,9	68,9
Total P	90	90	130	220	220	310	440
pH 4.3							
Water-soluble P	1.6	1.9	4.4	8.7	16.2	28.1	50.9
Total P	80	90	130	220	260	350	440

the amount of native water-soluble soil P. In the poplar experiment (data not presented) water-soluble soil P also varied within narrow limits (1.6–2.2 ppm) in the P_0 treatments with pH ranging from 3.8 to 5.5.

DISCUSSION

Under the various conditions of P supply, varying from (extreme) deficiency to sufficiency, the broadleaved species accumulated more P per unit of dry matter than did the conifers. Maximum growth was associated with foliar concentrations of 0.14 (probably sub-optimal), 0.23, 0.35–0.38, and 0.15–0.17% P for Douglas fir, poplar, willow, and Scots pine, respectively.

The foliar Zn concentrations of all four tree species investigated appear abnormally high when compared with the data of Ahrens [1], Beaton and Brown *et al.*[4], Hacskaylo *et al.*[9], and Stone [25]. Poplar and willow attained much higher levels than did the conifers. This is in accordance with Stone [25], who, in his excellent review, lists *Populus* and *Salix* among the Zn-accumulator species and genera. Foliar Fe is also high, but Cu and Mn levels are more in line with the values quoted in the above reports.

Published data from the Netherlands [15 16 17 18] indicate that high fertilizer dressings of P, especially in the presence of N, may induce Cu deficiency in various tree species. However, leaf concentrations associated with deficiency symptoms, *i.e.* values lower than 4 ppm Cu (poplar) or 2.5 ppm Cu (willow and Douglas fir), were not encountered in the present study.

For lack of published (foliar) Al concentrations no evaluation of the Al levels can be given. Mean levels of 750 ppm Al for *Pinus radiata* growing on very acid soils are stated by Humphreys and Truman [11]. However, as work with nutrient solution culture showed, this species proved quite tolerant to Al provided ample P was available. This internal plant tolerance may also hold for other species and for other metals, as the results of the present work and the investigations on Zn/Cu/Fe-P inter-relationships in *Pinus elliottii* [27] and on Cu-P interactions in citrus seedlings [22] would suggest. Plants may also have a 'natural' mechanism of immobilizing Cu (in roots), and probably other (heavy) metals as well[2], as suggested by Dijkeman and De Sousa[6] reporting on the growth of *Betulus* sp. in a copper swamp forest.

It should be emphasized that the effects of P and lime on uptake and translocation of metals cannot be evaluated only on the basis of concentrations. Total uptake and distribution within the plant should also be assessed to obtain a proper insight into the nutritional status. Inadequate data in this respect probably explain discrepancies in the literature[26]. In the present work inhibition of metal absorption by the trees only seemed to occur with excessive rates, but not with normal additions of P, and of lime (broadleaved species). All tree species studied preferentially accumulated Cu and Fe, and conifers also Zn and Al (Scots pine), in the roots, and Mn in the foliage. This is in agreement with published data for *Populus deltoides* and Scots pine grown in nutrient solution culture[9]. There is a strong indication that P interfered with the root to shoot translocation of Cu, Fe, and Al, but not with that of Zn and Mn. Similar differences between Cu on the one hand, and Zn and Mn on the other, in their interaction with P, are described by Spencer[21] for citrus.

The dithizone-extractable soil Zn levels (Table 7) cannot be considered anomalously high when compared with the data reported by Massey[14] and Shaw and Dean[20]. Acetic acid-extractable soil Zn values too are considerably lower than those of Zn-polluted locations in the vicinity of Zn factories. Henkens[10] reports concentrations of 500–800 ppm acetic acid-extractable Zn in soils annually flooded by Zn-contaminated river (Dommel) water before 1960. However, since the plant metal concentration is more indicative than the metal concentration of the soil, it is postulated that besides P deficiency excess Zn might be an important factor in limiting tree growth on the Someren soil. On the Budel soil the extreme P deficiency would appear more clearly to be induced by Zn toxicity.

The relationship between water-soluble soil P and added P (sigmoid curve) and also the sigmoid shape of the P absorption curves (Figures 1, 2) suggest P fixation. In this study trends in water-soluble soil P were not necessarily reflected in plant P uptake. Raising soil pH from 3.8 to 4.3 did not affect the (very low) level of native water-soluble P and reduced the increase in water-soluble P following P application (p. 144). However, the broadleaved species absorbed more, and the coniferous species less native and applied P when limed. Apparently liming, by vigorously stimulating (root) growth, improved the utilization of soil P by the broadleaved species. Similarly, the decrease in P absorption of the coniferous trees given lime may be explained on the basis of impeded (root) growth. It is suggested that water-soluble soil P levels should be interpreted with caution if other limiting soil factors (pH) have not been eliminated.

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REFERENCES

1 Ahrends, E., Untersuchungen über den Gehalt von Blättern und Nadeln verschiedener Baumarten an Kupfer, Zink, Bor, Molybdän und Mangan. Allgemeine Forst und Jagdzeitung **135**, 8–16 (1964).

2 Antonovics, J., Bradshaw, A. D. and Turner, R. G., Heavy metal tolerance in plants. Advances Ecol. Research **7**, 1–83 (1971).

3 Baule, H. und Fricker, C., Die Düngung von Waldbäumen. Bayerischer Landwitschaftsverlag GmbH, München (1967).

4 Beaton, J. D., Brown, G., Speer, R. C., Mac Ray, I. *et al.* Concentration of micronutrients in foliage of three coniferous tree species in British Columbia. Soil Sci Soc. Am. Proc. **29**, 299–302 (1965).

5 Benzian, B., Nutrition experiments in forest nurseries. Quart. J. Forestry **60**, 94–100 (1966).

6 Dykeman, W. R. and De Sousa, A. S., Natural mechanisms of copper tolerance in a copper swamp forest. Can. J. Botany **44**, 871–878 (1966).

7 Goor, C. P. van, Bemestingsvoorschrift voor naaldhoutculturen. Korte Meded. Bosbouwproefst. **56**, 16 pp., (1967).

8 Goor, C. P. van, Kriterien zur Feststellung des Düngungsbedürfnisses in der Forstwirtschaft. Proc. 5th Colloq. (Forest Fertilization) Intern. Potash Inst. Finland. 55–64 (1967).

9 Hacskaylo, J., Finn, R. F., and Vimmerstadt, J. P., Deficiency symptoms of some forest trees. Ohio Agr. Research and Development Center, Research Bull. **1015**, 68 pp. (1969).

10 Henkens, Ch. H., Zinkovermaat op bouwland. Landbouwk. Tijdschr. **73**, 917–926 (1961).

11 Humphreys, F., and Truman, R., Aluminium and phosphorus requirements of *Pinus radiata*. Plant and Soil **20**, 131–134 (1964).

12 Keefer, R. F., and Singh, R. N., The mechanism of P and Zn interaction in soils as revealed by corn growth and composition. Trans. 9th Intern. Congr. Soil Sci. Adelaide **II**, 367–674 (1968).

13 Lindsay, W. L., and Moreno, E. C., Phosphate phase equilibria in soils. Soil Sci. Am. Proc. **24**, 177–182 (1960).

14 Massey, H. F., Relation between dithizone-extractable zinc in the soil and zinc uptake by corn plants. Soil Sci. **83**, 123–129 (1957).

15 Meiden, H. A. van der, Die Wirkung der Phosphatdüngung auf Pappelpflanzungen. Phosphorsäure **21**, 39–50 (1961).

16 Meiden, H. A. van der, Kopergebrek bij populier. Ned. Bosbouw Tijdschr. **34**, 29–33 (1962).

17 Meiden, H. A. van der, Kopergebrek bij wilg. Ned. Bosbouw Tijdschr. **36**, 24–29 (1964).

18 Oldenkamp, L. and Smilde, K. W., Copper deficiency in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Plant and Soil **25**, 150–152 (1966).

19 Paauw, F. van der, Sissingh, H. A., and Ris, J., Een verbeterde methode van de fosfaatextractie van grond met water: het Pw-getal; *with a summary*: An improved method of water extraction for the assessment of availability of soil phosphate: Pw value. Verslag. Landbouwkund. Onderz. **749**, 64 pp. (1971).

20 Shaw, E., and Dean, L. A., Use of dithizone as extractant to estimate the zinc nutrient uptake of soils. Soil Sci. **73**, 341–347 (1952).

21 Spencer, W. F., Effect of heavy applications of phosphate and lime on nutrient uptake, growth, freeze injury, and root distribution of grapefruit trees. Soil Sci. **89**, 311–318 (1960).

22 Spencer, W. F., Effect of copper on yield and uptake of phosphorus and iron by citrus seedlings grown at various phosphorus levels. Soil Sci. **102**, 296–299 (1966).

23 Steenbjerg, F., Manuring, plant production and the chemical composition of the plant. Plant and Soil **5**, 226–242 (1954).

24 Steenbjerg, F., and Jakobsen, S. T., Some approaches to experimental investigations into the correlation between the slope and the sigmoidal shape of yield curves. Plant and Soil **10**, 284–295 (1959).

25 Stone, Earl L., Micro element nutrition of forest trees: a review. *In*: Forest Fertilization, Theory and Practice, p. 132–175, Tennesse Valley Authority (1968).

26 Stukenholtz, D. D., Olsen, R. J., Gogan, G., and Olson R. A., On the mechanism of phosphorus-zinc interaction in corn nutrition. Soil Sci. Soc. Am. Proc. **30**, 759–763 (1966).

27 Van Lear, D. H., and Smith, W. H., Relationships between macro-and micronutrient nutrition of slash pine on three coastal plain soils. Plant and Soil **36**, 331–347 (1972).