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Long-term trends of phosphorus nutrition and topsoil phosphorus stocks in unfertilized and fertilized Scots pine (*Pinus sylvestris*) stands at two sites in Southern Germany

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ABSTRACT

For two Scots pine (*Pinus sylvestris*) ecosystems in S Germany with different atmospheric N deposition (*Pfaffenwinkel*, intermediate N deposition; *Pustert*, large N deposition), the supply with phosphorus (P) has been monitored for unfertilized and fertilized plots over more than four decades by foliar analysis (1964–2007). Additionally, topsoil concentrations and stocks of total P and plant-available P (citric-acid-extractable phosphate) were quantified in 10-year intervals (1982/1984, 1994, 2004). At both sites, fertilization experiments, including the variants control, NPKMgCa + lime, PKMgCa + lime + introduction of lupine, corresponding to an addition of 75 and 90 kg ha^{-1} P in Pustert and Pfaffenwinkel, respectively had been established in 1964. Our study revealed different trends of the P nutritional status for the pines at the two sites during the recent four decades: At *Pustert*, elevated atmospheric N deposition together with small topsoil P pools resulted in significant deterioration of Scots pine P nutrition and in an increasingly unbalanced N/P nutrition. At *Pfaffenwinkel* a trend of improved P nutrition from 1964 to 1991 was replaced by an opposite trend in the most recent 15 years. For our study sites, which are characterized by acidic soils with thick O layers, the forest floor stock of citric-acid-extractable phosphate showed a strong and significant correlation with the P concentration in current-year pine foliage, and thus was an appropriate variable to predict the P nutritional status of the stands. Total P stocks as well as the concentrations of total P in the forest floor or in the mineral topsoil were poorly correlated with pine foliar P concentrations and thus inappropriate predictors of P nutrition. P fertilization in the 1960s sustainably improved the P nutritional status of the stands. At *Pfaffenwinkel*, foliar P concentrations and topsoil stocks of citric-acid-extractable phosphate were increased at the fertilized plots relative to the control plots even 40 years after fertilization; at *Pustert*, foliar P concentrations were increased for about 20 years.

1. Introduction

Phosphorus (P) is an essential nutrient element for all living organisms (Gilbert, 2009), and the relevance of a sufficient P nutrition for the growth of forest trees has been acknowledged already in the mid of the 19th century. Until recently, most forest ecosystems in Europe have been limited by the supply with N rather than P (Nave et al., 2009), except particular sites on calcareous or quartz-rich parent material. However, elevated atmospheric N deposition has strongly improved the N supply of many European forest stands (*e.g.* Mellert et al., 2004a), and N limitation nowadays is confined to very few particular sites. On the other hand, in recent years an increasing number of studies (*e.g.* Mohren et al., 1986; Polle et al., 1992; Houdijk and Roelofs, 1993; Wolff and Riek, 1997; Flückiger and Braun, 1998, 1999; Thomas and Büttner, 1998; Duquesnay et al., 2000; Jonard et al., 2009a) have reported a poor P nutritional status and/or decreasing foliar P concentrations and increasing foliar N/P ratios for European forests. At many sites, foliar P concentrations and N/P ratios nowadays indicate P deficiency and a disharmonic nutritional status according to conventional threshold values. Thus, a nation-wide German soil and stand nutrition inventory conducted in 1996 reported an insufficient P supply for the majority of spruce, pine, and beech forests in Germany (Wolff and Riek, 1997; Ilg et al., 2009). These stands are preferentially located on sites with P-poor parent material. Geologic substrates with low P content include (i) limestone or dolomite ("alkaline type"; *e.g.* Polle et al., 1992; Stefan et al., 1997), and (ii) quartz-rich substrates such as dune or alluvial sand, quartz-rich sandstone, or quartzite ("acidic type"; *e.g.* Fox et al., 2006; Achat et al., 2009; Trichet et al., 2009). Soils on such

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Table 1
Main properties of the soils at Pfaffenwinkel (Haplic Cambisol (Dystric, Greyic, Ruptic)) and Pustert (Albic Alisol (Ruptic, Endoclayic)). ECEC: effective cation exchange capacity, BS: base saturation, Fe_d: dithionite-extractable Fe (Holmgren, 1967), Fe_o: oxalate-extractable Fe (Schwertmann, 1964). NA: not analyzed. NC: not calculated.

Horizon	Depth [cm]	Coarse fragments [%]	Texture	C_{org} [g kg^{-1}]	Total N [g kg^{-1}]	C/N ratio [g g^{-1}]	ECEC [mmol$_c$ kg^{-1}]	BS [%]	pH ($CaCl_2$)	Fe_d [g kg^{-1}]	Fe_o [g kg^{-1}]
Pfaffenwinkel											
O	9–0	NA	NA	440.6	14.3	30.8	285	35	2.7	NA	NA
AE	0–4	0.5	Silt loam	37.5	1.6	23.4	94	11	3.0	17	1.8
Bw	4–17	10	Silt loam	15.8	0.94	16.8	55	8	3.7	28	1.6
Bw2	17–37	10	Silt loam	3.3	0.63	NC	29	14	4.0	28	0.3
Bw3	37–60	10	Silt loam	1.4	0.56	NC	27	16	4.0	25	0.3
BC	60–67	30	Silt loam	0.8	0.41	NC	16	23	4.0	31	0.1
2BC	67–73	5	Silt loam	0.9	0.35	NC	17	20	3.9	31	0.1
3BC	73–93	25	Silt loam	0.5	0.18	NC	12	30	4.0	35	0.1
4BC	93–113	70	Silt loam	0.2	0.25	NC	10	32	3.9	NA	NA
Pustert											
O	5–0	NA	NA	380.3	15.5	24.5	251	51	3.3	NA	NA
Ah	0–2	10	Silt loam	83.2	5.3	15.6	85	30	3.2	10	2.8
AE	2–4	10	Silt loam	33.7	3.1	10.9	56	16	3.3	10	2.2
E	4–27	15	Silt loam	8.1	0.84	NC	38	10	3.8	14	2.0
Bt	27–44	20	Loam	2.8	0.27	NC	78	14	3.8	18	2.5
2Btg	44–65	20	Clay	1.9	0.34	NC	119	47	3.9	25	3.9
2BC	65–80	25	Clay	1.6	0.28	NC	112	54	3.9	21	1.7

substrates often contain less than 2000 kg P ha^{-1} in the uppermost 1 m of the soil. At such sites, P shortage is expected to become an increasing phenomenon under conditions of elevated atmospheric N deposition (*e.g.* Mohren et al., 1986; Houdijk and Roelofs, 1993; Flückiger and Braun, 1998, 1999; Duquesnay et al., 2000). Causes may be (i) increased P sequestration in woody biomass of faster growing forests with increasing N supply (Spiecker, 1999; Mellert et al., 2008; Prietzel et al., 2008), (ii) increased export of P-rich biomass (*e.g.* tree tops, branches, foliage) as biofuel sources, and (iii) negative effects of atmospheric N deposition on mycorrhiza abundance and activity (Arnebrant and Söderström, 1992; Treseder, 2004). On acidic sites, progressive soil acidification might additionally reduce the P availability of forest stands by (iv) increased phosphate sorption to pedogenic Fe and Al oxyhydroxides, (v) precipitation as Al or Fe phosphate (Foy et al., 1978; Mohren et al., 1986), and (vi) decreased mineralization rates of organic P (Paré and Bernier, 1989; Carreira et al., 1997; Meiwes et al., 2002).

In contrast to agriculture, in European forestry and geobotany P has attracted much less attention as nutrient compared to N and base cations, particularly during recent times of elevated N and acid deposition, soil acidification, and eutrophication. Whereas recent changes of nitrogen and base cation stocks in European forest soils and the availability of these nutrients to the trees have been addressed and quantified in numerous studies (*e.g.* Wesselink et al., 1995; Meiwes et al., 2002; Mellert et al., 2004b; Prietzel et al., 2006), the available information concerning recent changes of soil P stocks and the P supply of forest stands is scarce. In this paper we present results of a study in which the P supply of two mature Scots pine (*Pinus sylvestris*) stands in S Germany as well as topsoil P concentrations and stocks have been monitored for 40 years. Both sites differ in the level of atmospheric N deposition. At both sites, amelioration experiments had been established; some plots had been fertilized with P-bearing fertilizer in the 1960s. The aim of our study was to address the following questions:

- Has the P nutritional status of the two stands with different N deposition changed systematically during recent decades?
- Can changes of Scots pine P nutrition be related to changes of concentrations and/or stocks of total P and plant-available P in the soil?
- Has the P fertilization 40 years ago resulted in sustained improvement of stand P nutrition?

2. Material and methods

2.1. Study sites

The study was conducted in the Scots pine (*P. sylvestris*) stands Pfaffenwinkel and Pustert in Bavaria, Germany. Important properties of the sites and stands have been described in detail by Prietzel et al. (2006, 2008); important soil data are presented in Table 1. At the beginning of the monitoring period in 1964, the sites were densely stocked with 86-year-old (Pfaffenwinkel) and 77-year-old (Pustert) Scots pine of poor quality. At Pfaffenwinkel, atmospheric S deposition in 1986 was 47 kg ha^{-1} yr^{-1}; N deposition was 10 kg ha^{-1} yr^{-1}. In 2004, the atmospheric S input was only 15 kg ha^{-1} yr^{-1}, but atmospheric N deposition has increased to 24 kg ha^{-1} yr^{-1} (Prietzel et al., 2006). At Pustert, atmospheric N deposition strongly increased in the mid 1970s from less than 10 kg ha^{-1} to 30 kg ha^{-1} (Prietzel et al., 2006) due to the establishment of a poultry farm in <1 km distance (Rodenkirchen, 1992). Cumulative N deposition fluxes for the period 1964–1985 were estimated to be 165 kg ha^{-1} at Pfaffenwinkel and 392 kg ha^{-1} at Pustert; the respective values for the period 1986–2007 are 397 kg ha^{-1} (Pfaffenwinkel) and 660 kg ha^{-1} (Pustert).

In 1964, at both sites amelioration experiments were established to compare several techniques to increase the poor stand productivity. The experimental setup is described in detail by Prietzel et al. (2008). All experimental variants, each represented by 3 replicate plots per site, have been studied intensively during the last 45 years. The investigation included (i) repeated assessment of the chemical status of the topsoil (forest floor, uppermost 30 cm mineral soil in 10-cm increments), (ii) annual or biannual assessment of the nutritional status of the Scots pines by foliage analysis, and (iii) forest inventories conducted in 3–7-year intervals. The results of the inventories are described in Prietzel et al. (2008). This paper presents results of long-term changes of Scots pine P nutrition and the soil P status in 2004 for the variants CON (control), FER (NPKMgCa fertilization, including application of 4000 kg $CaCO_3$ ha^{-1}), and LUP (combination of PKMgCa fertilization – again including the application of lime – with tillage and sowing of lupine). The fertilizer amendments, which are described in detail by Prietzel et al. (2008) resulted in addition of 95 kg P ha^{-1} (1964, 1967) at Pfaffenwinkel and 70 kg P ha^{-1} (1964) at Pustert.

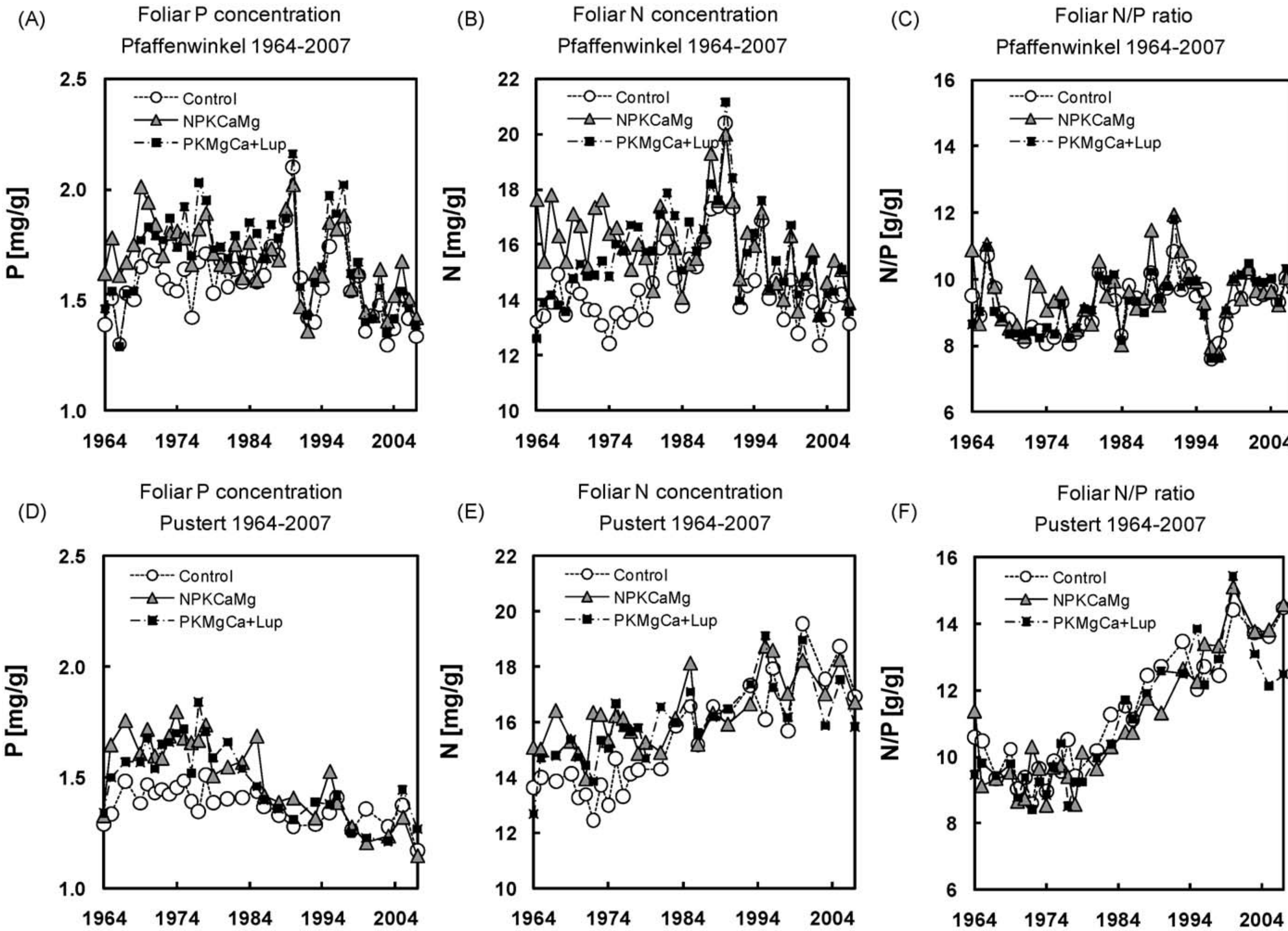

Fig. 1. Temporal courses and trends of (a and d) phosphorus (P) concentrations, (b and e) nitrogen (N) concentrations, and (c and f) N/P ratios in current-year foliage of Scots pines at control and fertilized plots of Pfaffenwinkel and Pustert. Concentrations are given as mg g^{-1} dry mass.

2.2. Assessment of topsoil P status and P nutrition of the forest stands

On all control and ameliorated plots at both sites, soil inventories were carried out in 1984 (Pfaffenwinkel: 1982), 1994, and 2004 with the method described in detail in Prietzel et al. (2006, 2008). The forest floor and the mineral soil down to 30 cm depth were sampled at 20 sampling points on each plot in 10-cm-sections. In order to yield samples which are appropriate for inventory and monitoring, a paired sampling technique was implemented (Lark, 2009): In the different inventories, always the same points were sampled. This was possible, because the boundaries of the plots (rectangles) are permanently marked and the sampling points can easily be identified. For each of the 20 sampling points on each plot, which are permanently marked by poles, soil samples were taken at four positions of a circle around the poles (radius: 0.5 m), with the bearings rotated systematically in each inventory (*e.g.* 1984: 0°, 90°, 180°, 270°; 1994: 45°, 135°, 225°, 315°; 2004: 30°; 120°, 210°, 315°). The samples taken at the four positions were pooled by depth increment to form the sample of a sampling point; subsequently, samples of five different points again were pooled by depth increment. Thus, for each study site and experimental variant, 12 samples per depth increment originating from three replicate plots were available.

All samples were dried to constant mass at 65 °C, and sieved (<2 mm). For each sample, the concentration of total P was analyzed by ICP-OES (Varian Vista Pro) after grinding and digestion with $HF/HClO_4$. Additionally, the concentration of citric-acid-soluble phosphate (P_{citr}), which is considered an estimate for plant-available P, was analyzed according to Schlichting et al. (1995) by extraction of sieved subsamples with 1% citric acid (soil:solution mass ratio 1:10; extraction time 23 h). The extracted phosphate was determined by colorimetry using the ascorbic acid method of Murphy and Riley (1962) as modified by John (1970). From ground samples, the concentration of total C and N was analyzed with a LECO analyzer CHN-2000.

From 1964 until 2007 the nutritional status of the stands at all plots was assessed annually (Pfaffenwinkel) or at least every second year (Pustert) by foliar analysis. To avoid confounding effects of bioelement translocation processes during the growing season on foliar bioelement concentrations (Wehrmann, 1959), needles were sampled during the period of winter dormancy from the uppermost crown of 12 dominant trees at each plot. From the pooled current-year needles of each plot, representative samples were ground and analyzed for P, N, and other nutrients. Until 1991, the foliar concentration of P was analyzed after combustion at 450 °C in a muffle oven and digestion of the residue in HCl by colorimetry (molybdenum-blue-method). From 1992 on, the foliage samples were subject to a 6 h pressure-digestion with concentrated HNO_3 at 160–180 °C; subsequently the P concentration in the digests was determined by ICP-OES (PerkinElmer Optima 3000). Until 1986, the N concentration was analyzed by the Kjeldahl method, later with a Heraeus Macro N analyzer (1987–1990) and a LECO analyzer CHN-2000 (since 1991). The comparability of data achieved with different methods during the 40-year investigation period was assured by repeated analyses of reference samples. In the following, all foliar concentration data are referred to foliage dry mass (dm).

2.3. Statistics

Significant trends of foliar nutrient concentrations and ratios for the different variants were identified by regression analysis. Differences between mean foliar nutrient concentrations among the different experimental variants at each site, which proved to be normally distributed according to Kolmogorov–Smirnov tests, were tested for statistical significance by one-factorial analysis of variance (ANOVA) followed by a post hoc least significant difference (LSD) test. Because the soil chemical data were not normally distributed, the Kruskal–Wallis *H*-test, followed by a post hoc Nemenyi test was used for testing the significance of differences between soil chemical features of a given horizon among sampling years and experimental variants. All statistics were calculated using the statistical software package SPSS for Windows, version 12.1.

3. Results

3.1. Comparison of the P status of the two study sites

As indicated by the P concentrations in current-year pine foliage (Pfaffenwinkel: 1.4 mg g^{-1}; Pustert 1.3 mg g^{-1}; Fig. 1a and d), the P supply of the stand at Pfaffenwinkel at the beginning of the monitoring period was low to intermediate and that of the stand at Pustert low according to the threshold values used in German forest nutrition assessment (Wolff and Riek, 1997). The poorer P status of Pustert is also reflected by smaller concentrations and stocks of total P and plant-available, citric-acid-extractable phosphate in the mineral topsoil (Fig. 2; Table 3).

3.2. Trends of Scots pine P nutrition and soil P status at the unfertilized plots

3.2.1. Scots pine P nutrition

At the unfertilized plots of the Pfaffenwinkel site, the P concentration in current-year foliage of the Scots pines decreased only slightly during the recent four decades (Fig. 1a), and the trend was not statistically significant (Table 2). For that site, the monitoring period can be distinguished into two different sub-periods: From 1964 to 1991, foliar P concentrations increased significantly, whereas a statistically significant decrease was noticed for the period between 1991 and 2007. At Pustert, foliar P concentrations decreased systematically (Fig. 1d) and significantly ($p = 0.002$; Table 2) during the 43-year monitoring period. Foliar N concentrations showed different patterns for the pines on the control plots of Pfaffenwinkel and Pustert: For Pfaffenwinkel, similar to P, foliar N concentrations increased significantly from 1964 to 1991, whereas a statistically significant decrease was noticed for the period between 1991 and 2007 (Table 2; Fig. 1b). For Pustert, a strong, systematic, significant ($p = 0.000$; Table 2)

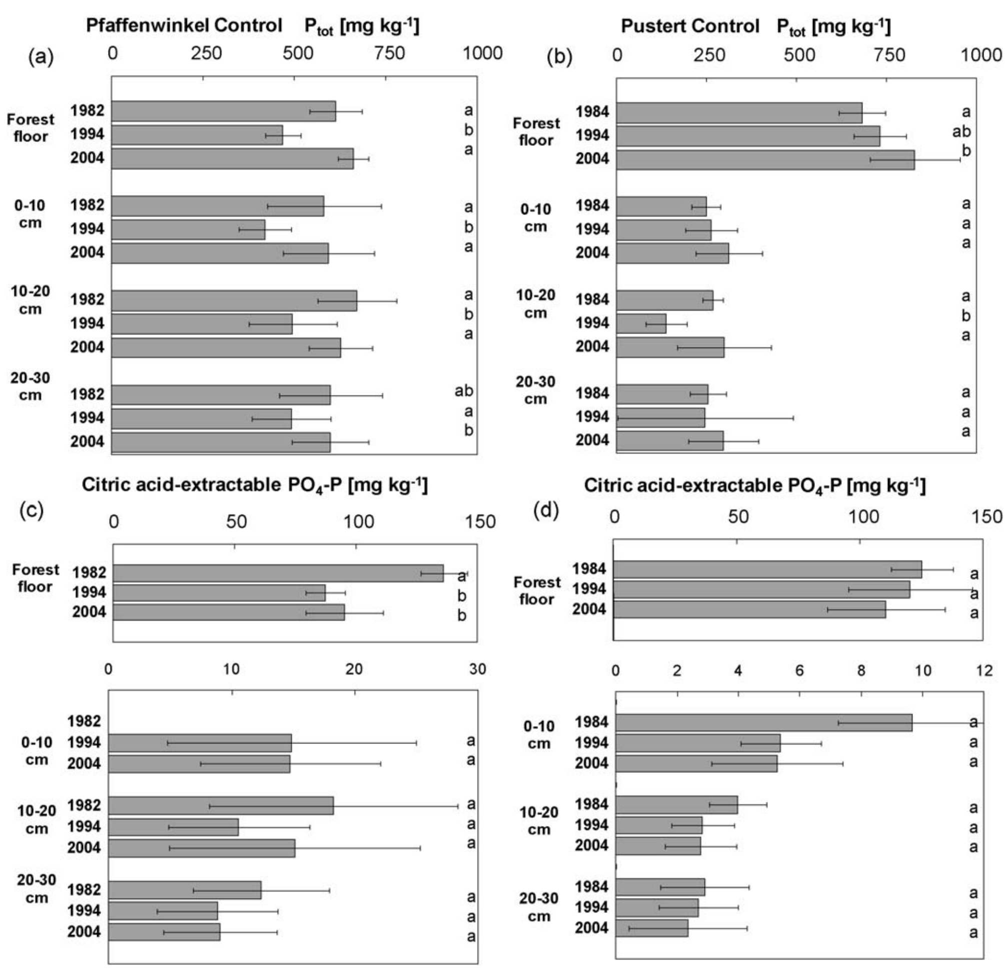

Fig. 2. Concentration of (a and b) total phosphorus (P_{tot}) and (c and d) citric-acid-extractable phosphate in the topsoil of the control plots at Pfaffenwinkel and Pustert in 1982/1984, 1994, and 2004. Different letters at right-hand side of the three bars shown for each depth increment indicate significant ($p < 0.05$; Kruskal–Wallis *H*-test) differences among years.

Table 2
Temporal trends of foliar nutrient concentrations in current-year needles of Scots pines at the control plots of Pfaffenwinkel and Pustert. Given are parameters for the regression equation: y (nutrient concentration in year x) = B + A × x (year). NC: not calculated.

Site (number of samples)	Element	Significant trend	Significance	*B* (intercept)	*A* (increment)	Beta (standardized *R*)	Adjusted R^2
Period 1964–2007							
Pfaffenwinkel (n = 44)	P	0	0.506	NC	NC	NC	NC
	N	0	0.457	NC	NC	NC	NC
	N/P	0	0.060	NC	NC	NC	NC
Pustert (n = 27)	P	–	0.002	1.447	−0.004	0.564	0.292
	N	+	0.000	12.73	0.128	0.876	0.758
	N/P	+	0.000	8.702	0.124	0.898	0.799
Period 1964–1985							
Pfaffenwinkel (n = 22)	P	+	0.034	1.488	0.007	0.455	0.168
	N	+	0.033	13.274	0.067	0.455	0.168
	N/P	0	0.903	NC	NC	NC	NC
Pustert (n = 16)	P	0	0.301	NC	NC	NC	NC
	N	+	0.008	12.896	0.107	0.639	0.365
	N/P	0	0.135	NC	NC	NC	NC
Period 1986–2007							
Pfaffenwinkel (n = 22)	P	–	0.002	1.804	−0.020	0.612	0.344
	N	–	0.001	17.220	−0.198	0.671	0.422
	N/P	0	0.817	NC	NC	NC	NC
Pustert (n = 11)	P	0	0.298	NC	NC	NC	NC
	N	0	0.068	NC	NC	NC	NC
	N/P	+	0.004	11.681	0.117	0.785	0.573

increase was noticed (Fig. 1e). The foliar N/P ratio, which reflects the relative availability of both nutrients, was similar for both study sites at the beginning of the monitoring period; it increased slightly (p = 0.06) at Pfaffenwinkel, and strongly (p = 0.000) at Pustert (Fig. 1c and f; Table 2).

3.2.2. Topsoil concentrations and stocks of total P and citric-acid-extractable phosphate

Total P concentrations in the topsoil of the unfertilized plots at Pfaffenwinkel did not change systematically between 1982 and 2004 (Fig. 2a). At Pustert, total P concentrations in the forest floor of the unfertilized plots at Pustert increased significantly between 1984 and 2004; no significant change was noticed for the total P concentrations in the mineral topsoil (Fig. 2b). At the control plots of Pfaffenwinkel, the concentrations of citric-acid-extractable phosphate (Fig. 2c) decreased significantly in the forest floor; also for the mineral topsoil a (statistically non-significant) decline was observed. For Pustert, a (statistically non-significant) decline was noticed for the concentrations of citric-acid-extractable phosphate in the entire topsoil (Fig. 2d).

At the control plots of Pfaffenwinkel, forest floor stocks of total P remained constant between 1982 and 2004; those of citric-acid-extractable phosphate decreased significantly (Table 3). For the mineral topsoil as well as for the entire topsoil, comprising the forest floor and the uppermost 30 cm mineral soil, a statistically insignificant tendency of decreasing pools of total P and citric-acid-extractable phosphate was observed. In contrast to Pfaffenwinkel, total P stocks of the forest floor and of the mineral topsoil at Pustert increased considerably between 1984 and 2004; for the forest floor, the increase was statistically significant. The stock of

Table 3
Stocks of total phosphorus and citric-acid-extractable phosphate (mean value ± standard deviation in kg P ha^{-1}; n = 12 samples per variant) in the topsoil (forest floor + uppermost 30 cm mineral soil) of the control (CON) plots of the experiments Pfaffenwinkel and Pustert in different years, and of the ameliorated plots FER (NPKMgCa fertilizer + lime) and LUP (combination of PKMgCa fertilization, liming, tillage, and lupine sowing) in 2004. Different letters indicate significantly different mean values (p < 0.05) among years or experimental variants (capital letters).

	Pfaffenwinkel		Pustert	
	Total P	Citric-acid-extractable PO_4-P	Total P	Citric-acid-extractable PO_4-P
Forest floor				
CON 1982/1984	62 ± 7 (a)	13.7 ± 0.9 (a)	40 ± 7 (a)	7.4 ± 1.3 (a)
CON 1994	53 ± 12 (a)	9.8 ± 2.0 (b)	41 ± 7 (a)	6.7 ± 2.4 (a)
CON 2004	66 ± 11 (bA)	9.5 ± 4.3 (bA)	59 ± 10 (bA)	7.1 ± 2.0 (aA)
FER 2004	71 ± 18 (A)	9.6 ± 1.6 (A)	32 ± 14 (B)	5.4 ± 9.1 (B)
LUP 2004	53 ± 12 (B)	7.7 ± 2.7 (B)	26 ± 7 (B)	4.7 ± 5.0 (B)
Mineral topsoil (0–30 cm)				
CON 1982/1984	1792 ± 222 (a)	ND	647 ± 58 (a)	13.7 ± 2.6 (a)
CON 1994	1505 ± 199 (a)	35.1 ± 12.0 (a)	698 ± 143 (a)	11.4 ± 1.9 (a)
CON 2004	1550 ± 178 (aA)	32.7 ± 14.4 (aA)	877 ± 187 (aA)	9.5 ± 3.3 (aA)
FER 2004	1528 ± 152 (A)	45.9 ± 28.2 (AB)	916 ± 151 (A)	12.5 ± 2.3 (A)
LUP 2004	1577 ± 122 (A)	51.5 ± 37.5 (B)	991 ± 208 (A)	11.1 ± 3.1 (A)
Forest floor + mineral topsoil				
CON 1982/1984	1854 ± 222 (a)	ND	687 ± 59 (a)	21.1 ± 2.9 (a)
CON 1994	1557 ± 199 (a)	44.9 ± 12.1 (a)	739 ± 143 (a)	18.1 ± 3.1 (a)
CON 2004	1616 ± 178 (aA)	42.3 ± 15.1 (aA)	936 ± 188 (aA)	16.7 ± 3.8 (aA)
FER 2004	1599 ± 153 (A)	55.6 ± 28.3 (B)	948 ± 151 (A)	17.9 ± 9.4 (A)
LUP 2004	1631 ± 123 (A)	59.1 ± 37.6 (B)	1017 ± 208 (A)	15.9 ± 5.9 (A)

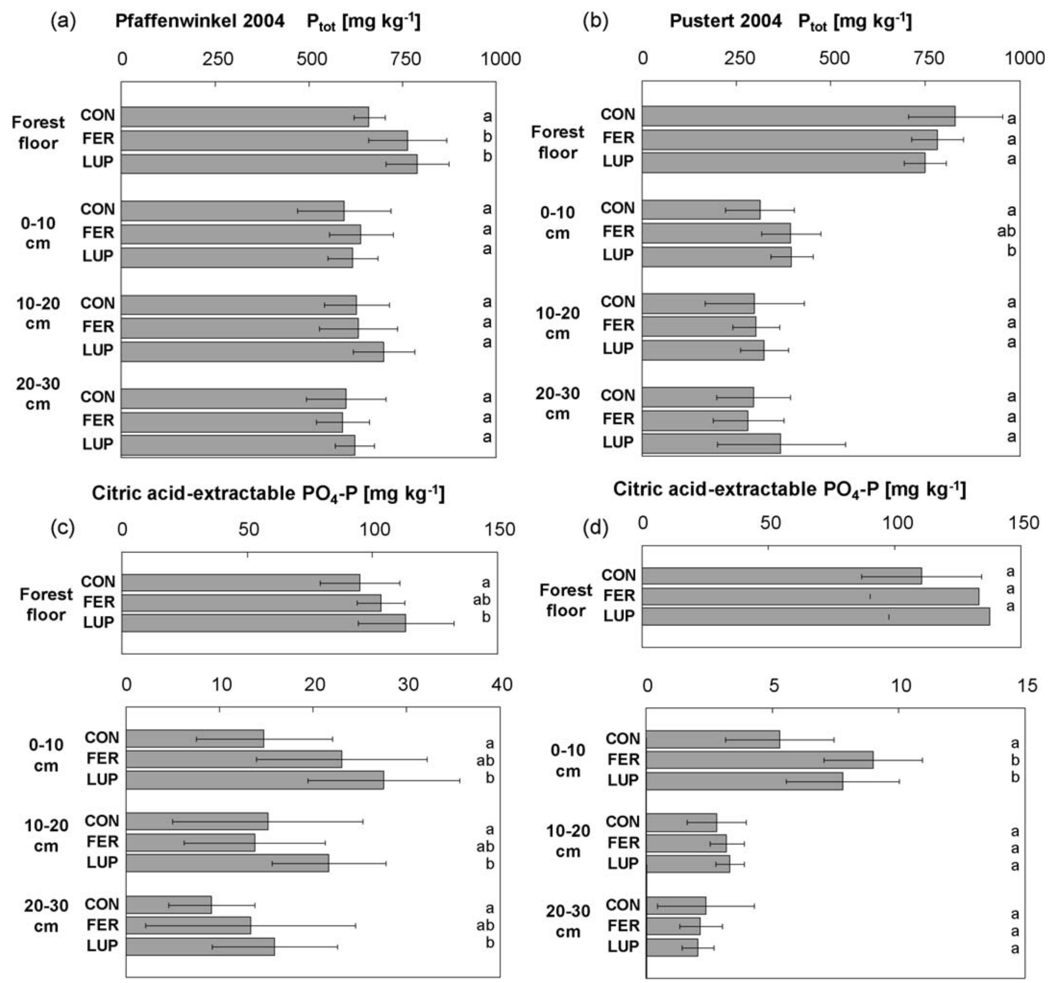

Fig. 3. Concentration of (a and b) total phosphorus (P_{tot}) and (c and d) citric-acid-extractable phosphate in the topsoil of control and fertilized plots at Pfaffenwinkel and Pustert in 2004. Different letters at right-hand side of the three bars shown for each depth increment indicate significant ($p < 0.05$; Kruskal–Wallis *H*-test) differences among experimental variants.

citric-acid-extractable phosphate in the forest floor and in the mineral topsoil of the control plots at Pustert decreased between 1984 and 2004; however, the decrease was not statistically significant due to a large variation among replicate samples.

3.3. Long-term fertilization effects on Scots pine P nutrition and soil P status

3.3.1. Scots pine P nutrition

At Pfaffenwinkel, application of P-bearing fertilizer in 1964 and 1967 (in total 95 kg P ha^{-1}) resulted in a sustainable (>40 years) increase of P (Fig. 1a) and N (Fig. 1b) concentrations in current-year Scots pine foliage. The differences to the pines on the control plots were particularly pronounced until 1980. During the entire 40-year monitoring period, foliar N/P ratios of the pines at Pfaffenwinkel were the same for the fertilized and the unfertilized plots (Fig. 1c). At Pustert, application of P fertilizer in 1964 (70 kg P ha^{-1}) resulted in markedly increased foliar P concentrations until 1983 (Fig. 1d). A small difference between the foliar P concentrations of the pines at the fertilized and control plots was present until 1995; in most recent years no systematic difference could be noticed any more. Foliar N concentrations were considerably elevated in fertilized compared to the control stands at Pustert only until 1977. The disappearance of a fertilization effect on foliar N concentrations in 1977 was accompanied by the inception of a systematic increase of foliar N/P ratios for all pines at Pustert, irrespective whether they had been fertilized or not (Fig. 1f). From 1965 to 1993, the fertilized pines showed smaller foliar N/P ratios than those at the control plots; in later years no difference could be noticed any more.

3.3.2. Topsoil concentrations and stocks of total P and citric-acid-extractable phosphate

Thirty-seven years after the last P amendment, the fertilized plots at Pfaffenwinkel showed significantly increased concentrations of total P (Fig. 3a) and significantly decreased C/P and N/P ratios (data not shown) in the forest floor. Total P concentrations in the mineral topsoil did not differ significantly among the experimental variants. For Pustert, P concentration changes as induced by P fertilization 40 years ago were in tendency negative in the forest floor, significantly positive in the 0–10 cm mineral soil, and absent in the mineral topsoil 10–30 cm (Fig. 3b). At that site, neither topsoil C/P nor N/P ratios were significantly affected by the fertilization. At Pfaffenwinkel, fertilization combined with introduction of lupine and tillage (LUP variant) resulted in a significant increase of the concentration of citric-acid-extractable phosphate (Fig. 3c) in all topsoil horizons. Concentrations of citric-acid-extractable phosphate increased also for the fertilization treatment without tillage (FER), but the increases were smaller and not significant. At Pustert, concentrations of citric-acid-extractable phosphate were significantly increased in the uppermost 10 cm mineral soil, and pronouncedly, but not significantly increased in the forest floor (Fig. 3d). Small increases were observed in the mineral soil 10–20 cm.

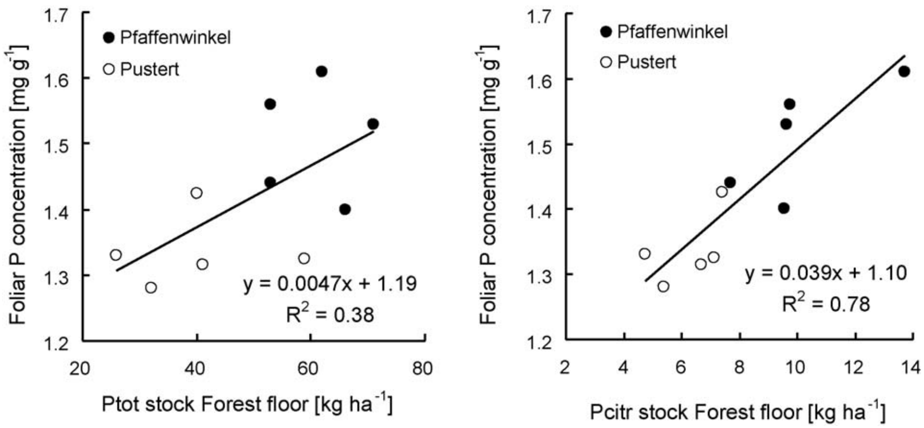

Fig. 4. Relationship between the stock of (a) total phosphorus (P_{tot}), (b) citric-acid-extractable phosphate (P_{citr}) and Scots pine foliar P concentration (mg g^{-1} dry mass; control and fertilized plots).

At Pfaffenwinkel, stocks of total P and of citric-acid-extractable phosphate were significantly depleted in the forest floor of the LUP plots compared to the other variants (Table 3). For the mineral topsoil and also for the entire topsoil (forest floor + uppermost 30 cm mineral topsoil) of Pfaffenwinkel, none of the fertilization treatments resulted in a sustainable change of total P stocks. In contrast to total P, the stocks of citric-acid-extractable phosphate were markedly (FER) or significantly (LUP) increased in the mineral topsoil and also in the entire topsoil of the fertilized compared to the control plots. At Pustert, the stocks of total P and citric-acid-extractable phosphate were significantly depleted in the forest floor of the ameliorated plots, and the respective stocks in their mineral topsoils were considerably increased. Both fertilization treatments resulted in a statistically insignificant increase of the topsoil stock of total P, whereas the topsoil stocks of citric-acid-extractable phosphate were similar for the different variants.

3.4. Statistical relationships between topsoil P variables and Scots pine foliar P concentration

Foliar P concentrations of the pines at Pfaffenwinkel and Pustert were significantly negatively correlated with the forest floor total P concentrations, and uncorrelated with forest floor concentrations of citric-acid-extractable phosphate. In contrast, significant positive correlations were present between the P concentrations in current-year Scots pine foliage on one hand and the forest floor stocks of total P (Fig. 4a) as well as citric-acid-extractable phosphate (Fig. 4b) on the other. The forest floor stock of citric-acid-extractable phosphate was a far better predictor of the P concentration in current-year foliage (R^2: 0.78) than the forest floor stock of total P (R^2: 0.38). The positive correlation patterns were present, irrespective whether only the pines at Pfaffenwinkel, those at Pustert, or those of both sites had been included in the analyses. In contrast to the forest floor, the stocks of total P and citric-acid-extractable phosphate in the mineral topsoil or in the entire topsoil (forest floor + uppermost 30 cm of the mineral topsoil) were poor predictors of the foliar P concentrations of the Scots pines at Pfaffenwinkel and Pustert (data not shown).

4. Discussion

4.1. Long-term trends of pine P nutrition at the two sites—effect of atmospheric N input?

Our data set of continuous foliar nutrient analyses over 43 years enabled us to identify different long-term trends of P nutrition for two Scots pine ecosystems in Central Europe with different atmospheric N deposition. For the pines at *Pfaffenwinkel* (intermediate N input; cumulative N deposition estimate 1964–2007: 562 kg ha^{-1}), no systematic long-term (40 years) trend, but two different medium-term (20 years) trends were observed: The improvement of P nutrition between 1964 and 1991 can be assigned to site recovery from historic litter-raking (Prietzel et al., 2006), the deterioration in later years may have been caused by restricted P mineralization due to soil acidification (Paré and Bernier, 1989) and/or more frequent droughts (Mellert et al., 2004b). The systematic, statistically significant decrease of foliar P concentrations for the pines at *Pustert* (high atmospheric N input; cumulative N deposition estimate 1964–2007: 1052 kg ha^{-1}) was probably mainly an effect of the establishment of a large poultry farm in the vicinity to the site in the mid-1970s: At that time, the trend of a concomitant moderate improvement of P and N nutrition (likely the result of site recovery from litter-raking) changed to a trend of strongly improving N nutrition and concomitantly deteriorating P nutrition towards insufficiency (threshold according to Wolff and Riek (1997): 1.2 mg P g^{-1}) and unbalanced N/P nutrition (threshold: 10). The abrupt change of foliar N (strong increase) and P values (decrease) in the mid-1970s is unlikely to result from tree ageing effects like increased internal redistribution (Jonard et al., 2009a); neither an increased frequency of years with intensive fructification has been observed. More likely, similar to the effects of N-only fertilization (*e.g.* Teng and Timmer, 1995), continuing high N deposition at that site probably has resulted in gradual deterioration of the P supply of the pines due to progressive topsoil acidification (Prietzel et al., 2006), associated with increased soil P fixation (Foy et al., 1978; Mohren et al., 1986) and decreased mineralization of organic P (Paré and Bernier, 1989). Also the decrease of plant-available phosphate between 1984 and 2004 in the topsoil of Pustert may have been the result of reduced P mineralization, similar to the effect of N fertilization reported by Nohrstedt et al. (2000). In addition to the diminished topsoil pool of plant-available phosphate, decreased mycorrhizal P acquisition due to increased N saturation (Arnebrant and Söderström, 1992; Treseder, 2004) may also have contributed to the deterioration of pine P nutrition at Pustert. Besides the different N deposition levels at Pfaffenwinkel and Pustert, different initial soil P pool sizes may be responsible for the different trends of Scots pine P nutrition at both sites: The topsoil stocks of total P and of citric-acid-extractable phosphate were 2.5 times larger at Pfaffenwinkel compared to Pustert. Assuming a C/P ratio of 10,000 in Scots pine woody biomass (Kreutzer, 1976; Jacobsen et al., 2003), the annual net sequestration of C in accreting woody biomass, which had been calculated by Prietzel et al. (2006) as 2.7 and 2.2 Mg ha^{-1} for the pines at the control plots of Pfaffenwinkel and Pustert, respectively, was associated with an annual net P sequestration in woody biomass of 0.27 kg ha^{-1} (Pfaffenwinkel) and 0.22 kg ha^{-1} (Pustert). These rates are slightly smaller than the median value of 0.29 kg ha^{-1} reported by Ilg et al. (2009) for the 20 German Scots pine stands of the European Level II programme. Total net P sequestration during 40 years of stand development was 11.6 kg P (25% of the plant-available topsoil P stock) at Pfaffenwinkel, and 8.7 kg P (>50% of plant-available topsoil P) at Pustert. Phosphorus export with the seepage water (median value for German Scots pine stands: 0.01 kg ha^{-1} yr^{-1}; Ilg et al., 2009) can be considered negligible for the soils at the study sites which both are characterized by silt-dominated texture, large contents of pedogenic Fe and Al hydroxides, low pH, and slow seepage drainage. Even though the stocks of plant-available P are continuously replenished by atmospheric P deposition (median for German Scots pine stands: 0.15 kg ha^{-1} yr^{-1}; Ilg et al., 2009), mineral weathering, and mineralization of organically bound P, the different stand uptake: topsoil pool relations for both sites are striking.

4.2. Relationships between long-term trends of Scots pine P nutrition and tree growth

In principle, relationships between long-term trends of stand P nutrition and growth can be bi-directional: At P-limited sites, changes in P nutrition can affect stand growth (Mohren et al., 1986; Delzon et al., 2005; Trichet et al., 2009); increased stand growth at sites with poor P supply, but no P limitation can also result in deterioration of P nutrition due to increased P sequestration in woody biomass (Jonard et al., 2009a). At both study sites, tree growth has accelerated considerably between 1964 and 1990, followed by a decrease in later years, which was more pronounced at Pustert than at Pfaffenwinkel (Prietzel et al., 2008). The reason for the recent growth decline could be a natural age effect (Gower et al., 1996). However, the stand at Pustert is 9 years younger than that at Pfaffenwinkel; thus, an age effect should first occur at the latter site. The strong predictor effect of foliar P concentration on pine growth at Pustert (Prietzel et al., 2008) suggests that an insufficient P supply (Delzon et al., 2005) may have contributed to the growth reduction at that site since 1990. Contrariwise, increased stand growth may theoretically have contributed to the deteriorated P nutrition at the P-poor site Pustert due to increased P sequestration in woody biomass (Jonard et al., 2009a). However, the additional P sequestration in woody biomass caused by the growth increase since 1964 was only 1.1 kg P ha^{-1} or 6% of the topsoil pool of plant-available P. Thus, a significant contribution of that growth increase to the deterioration of P nutrition at Pustert seems to be unlikely.

4.3. Suitability of different soil P variables to describe the P supply of Scots pine stands—an indication for principal P uptake regions?

Our comparison of different soil variables which may characterize or predict the supply of P to forest trees (concentrations and stocks of total P and citric-acid-extractable phosphate in the forest floor, mineral topsoil, and topsoil, respectively) showed that (i) the forest floor was the most relevant soil compartment for the P nutritional status of the stands, (ii) forest floor P stocks were more relevant than forest floor P concentrations, and (iii) forest floor stocks of citric-acid-extractable phosphate were much better predictors of stand P nutrition than forest floor stocks of total P. At Pfaffenwinkel, root uptake of inorganic P from the acidic, Fe-oxide-rich (Table 1) mineral soil is probably restricted by strong phosphate fixation. At Pustert, stocks of inorganic phosphate in the subsoil are small. Moreover, stagnic soil conditions result in occlusion of phosphate in Mn and Fe-oxide concretions and restricted root penetration. Consequently, in the pine ecosystems of Pfaffenwinkel and Pustert, the forest floor is probably the principal location of tree P uptake, and microbial P mineralization probably is an important process in ecosystem P cycling. Unfortunately, root distribution and mycorrhiza studies have not been carried out at our study sites. However, several studies have shown that on sites with acidic, P-poor soils and thick O layers (i) the majority of fine roots, which are the most active organs for nutrient uptake, are located in the forest floor (*e.g.* Jackson et al., 1996; Brandtberg et al., 2004), and that (ii) fungal, microbial and enzymatic degradation of organically bound P located in the forest floor (Koukol et al., 2006; Achat et al., 2009; Jonard et al., 2009b), particularly by mycorrhizal symbiosis (Schachtman et al., 1998; Vance et al., 2003; Franco-Zorrilla et al., 2004) play a predominant role for the P nutrition of forest stands. According to a review of Attiwil and Adams (1993), much of the P demand of trees can be met by the cycling of organic residue P. Phosphorus uptake from the mineral soil might be more important at sites with less acidic soils on P-rich parent material. Such soils mostly lack thick forest floor layers and/or are characterized by (i) larger mineral soil P stocks, (ii) larger P input by mineral weathering, and (iii) less restricted plant availability of inorganic P. However, also at sites on calcareous bedrock, the turnover of organic P and the role of the forest floor seem to be crucial for the P supply of trees. Thus, the P nutritional status of beech stands in the Bavarian Alps was not correlated with their total soil P stocks (Ewald, 2000), whereas the P supply of Norway spruce and Scots pine regeneration on sites in the Limestone Alps was significantly better for sites with larger O layers compared to adjacent sites with smaller ones (Prietzel and Ammer, 2008). The coincidence of a deteriorating P nutrition of the pines at Pustert between 1984 and 2004 with increasing topsoil concentrations and stocks of total P in the same period supports the result of earlier studies (*e.g.* Ewald, 2000; Ilg et al., 2009) that total soil P stocks include biogeochemical P pools with slow release rates and thus are inappropriate to characterize the P supply of sites.

4.4. Sustainable improvement of Scots pine P nutrition by P fertilization

At Pfaffenwinkel, the pines which had been fertilized with 95 kg ha^{-1} P (equal to 5% of the topsoil total P stock and 200% of the topsoil stock of plant-available P), showed a long-term (>40 year) increase of foliar P concentrations. Because the fertilization included an addition of N together with P, the P/N ratio remained constant and was always in the range of balanced N/P nutrition. At Pustert, where atmospheric N deposition has increased considerably after establishment of the poultry farm in the mid 1970s, the strong increase of foliar N/P ratios indicates N eutrophication for all experimental variants. Positive effects of fertilization with 70 kg P ha^{-1} (10% of the topsoil stock of total P and 400% of the topsoil stock of plant-available P) on foliar P concentrations became small after 1983 (20 years after fertilizer amendment) and disappeared completely after 1995 (32 years after fertilizer amendment). Fertilization resulted in smaller foliar N/P ratios, indicating a more balanced N/P nutrition compared to the control variant, until 1993. It thus mitigated negative effects of elevated N deposition for about 15 years. The stocks of citric-acid-extractable phosphate in the topsoil of both sites mirrored the foliar P concentrations: At Pfaffenwinkel, stocks of citric-acid-extractable phosphate in the topsoil of the fertilized plots in 2004 were still significantly larger (+15 kg P ha^{-1}; corresponding to 16% of the fertilized P amount) compared to the control plots, whereas at Pustert topsoil stocks of citric-acid-extractable phosphate did not differ among the experimental variants. This finding once more emphasizes the good predictor value of citric-acid-extractable phosphate stocks for the P nutritional status of the pines in our study. The lack of a significant difference among the topsoil total P stocks of the experimental variants at any of the two study sites can be explained by the fact that the amount of P added by fertilization was only 5 to 7% of the initial topsoil P stocks.

At both sites, the application of comparably small amounts ($<$100 kg ha^{-1}) of P resulted in marked improvements of the P supply of the stands for at least two up to more than four decades.

In several studies, long-term (20 up to $>$50 years) effects of P fertilization on soil P levels, P nutrition, and stand growth have been reported for pine stands also for single applications of 17–35 kg P ha^{-1} (*e.g.* Pritchett and Comerford, 1982; Comerford et al., 2002; Turner et al., 2002; Fox et al., 2006; Trichet et al., 2009; extensive compilation of additional references in Trichet et al., 2009). Generally, fertilization effects became small after 20–35 years, and were more effective and longer lasting at wetter than at drier sites (*e.g.* Pritchett and Comerford, 1982; Fox et al., 2006). Our results suggest that P fertilization may be an appropriate tool to counteract nutritional N/P imbalances induced by atmospheric N deposition. It must be, however, emphasized that this remedy only cures the insufficient P supply of the trees, but not any negative changes in mycorrhiza abundance and activity caused by increased N saturation of a forest ecosystem (Arnebrant and Söderström, 1992; Treseder, 2004). Intensified research on the latter topic is urgently needed to better understand P cycling in forest ecosystems with increasing N saturation in order to make sound predictions about the future P supply in Central European forests. Finally, our study emphasizes the necessity of long-term monitoring studies in forest ecosystems.

5. Conclusions

1. Long-term monitoring revealed a systematic deterioration of the P nutritional status and development of unbalanced N/P nutrition for a Central European Scots pine stand subjected to elevated atmospheric N deposition (Pustert) during the recent four decades. Another site with moderate N deposition (Pfaffenwinkel) showed two medium-term (10–20 years) periods with opposite trends of Scots pine P nutrition, emphasizing the necessity of long-term ($\gg$20 years) monitoring studies to correctly address long-term trends of P nutrition in forest stands.
2. For our study sites, the forest floor stock of citric-acid-extractable phosphate was an appropriate variable to characterize the P nutritional status of the stands, whereas total P stocks or concentration values of total P and citric-acid-extractable phosphate in the forest floor and the mineral topsoil were inappropriate. This finding emphasizes the crucial role of (i) the forest floor as key location and (ii) mineralization of organically bound P as key process for tree P nutrition at sites with acidic soils on parent material with poor P supply.
3. At our study sites, which are characterized by acidic, sesquioxide-rich soils, P fertilization resulted in long-term ($>$20 and $>$40 years) improvement of the P nutritional status of the pine stands.

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References

Achat, D.L., Bakker, M.L., Augusto, L., Saur, E., Dousseron, L., Morel, C., 2009. Evaluation of the phosphorus status of P-deficient podzols in temperate pine stands: combining isotopic dilution and extraction methods. Biogeochemistry 92, 183–200.

Arnebrant, K., Söderström, B., 1992. Effects of different fertilizer treatments on ectomycorrhizal colonization potential in two Scots pine forests in Sweden. For. Ecol. Manag. 53, 77–89.

Attiwil, P.M., Adams, M.A., 1993. Nutrient cycling in forests. New Phytol. 124, 561–582.

Brandtberg, P.O., Bengtsson, J., Lundkvist, H., 2004. Distributions of the capacity to take up nutrients by *Betula* spp. and *Picea abies* in mixed stands. For. Ecol. Manag. 198, 193–208.

Carreira, J.A., Harrison, A.F., Sheppard, L.J., Woods, C., 1997. Reduced soil P availability in a Sitka spruce (*Picea sitchensis* Bong.) plantation induced by applied acid-mist: significance in forest decline. For. Ecol. Manag. 92, 153–166.

Comerford, N.B., McLeod, M., Skinner, M., 2002. Phosphorus form and bioavailability in the pine rotation following fertilization: P fertilization influences P form and potential bioavailability to pine in the subsequent rotation. For. Ecol. Manag. 169, 203–211.

Delzon, S., Bosc, A., Cantet, L., Loustau, D., 2005. Variation of the photosynthetic capacity across a chronosequence of maritime pine correlates with needle phosphorus concentration. Ann. For. Sci. 62, 537–543.

Duquesnay, A., Dupouey, J.L., Clement, A., Ulrich, E., LeTacon, F., 2000. Spatial and temporal variability of foliar mineral concentration in beech (*Fagus sylvatica*) stands in northeastern France. Tree Physiol. 20, 13–22.

Ewald, J., 2000. Ist Phosphormangel für die geringe Vitalität von Buchen (Fagus sylvatica L.) in den Bayerischen Alpen verantwortlich? Forstwiss Cbl. 119, 276–296.

Flückiger, W., Braun, S., 1998. Nitrogen deposition in Swiss forests and its possible relevance for leaf nutrient status, parasite attacks, and soil acidification. Environ. Pollut. 102, 69–76.

Flückiger, W., Braun, S., 1999. Nitrogen and its effects on growth, nutrient status, and parasite attacks in beech and Norway spruce. Water Air Soil Pollut. 116, 99–110.

Fox, T.R., Allen, H.L., Albaugh, T.J., Rubilar, R., Carlson, C.A., 2006. Forest fertilization in southern pine plantations. Better Crops 90, 12–16.

Foy, C.D., Chaney, R.L., White, M.C., 1978. The physiology of metal toxicity in plants. Ann. Rev. Plant Phys. 29, 511–566.

Franco-Zorrilla, J.M., Gonzalez, E., Bustos, R., Linhares, F., Leyva, A., Paz-Ares, J., 2004. The transcriptional control of plant responses to phosphate limitation. J. Exp. Bot. 55, 285–293.

Gilbert, N., 2009. The disappearing nutrient. Nature 461, 716–718.

Gower, S.T., McMurtrie, R.E., Murty, D., 1996. Aboveground net primary production decline with stand age: potential causes. Trends Ecol. Evol. 11, 378–382.

Holmgren, G., 1967. A rapid citrate-dithionite extractable iron procedure. Soil Sci. Soc. Am. Proc. 31, 210–211.

Houdijk, A.L., Roelofs, J.G., 1993. The effects of atmospheric nitrogen deposition and soil chemistry on the nutritional status of *Pseudotsuga menziesii*, *Pinus nigra*, and *Pinus sylvestris*. Environ. Pollut. 80, 79–84.

Ilg, K., Wellbrock, N., Lux, W., 2009. Phosphorus supply and cycling at long-term monitoring sites in Germany. Eur. J. For. Res. 128, 483–492.

Jackson, R.B., Canadell, J., Ehringer, J.R., Mooney, H.A., Sala, O.A., Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108, 389–411.

Jacobsen, C., Rademacher, P., Meesenburg, H., Meiwes, K.J., 2003. Gehalte chemischer Elemente in Baumkompartimenten Ber. Forschungs zentr. Waldökosyst. B 69, 81.

John, M.K., 1970. Colorimetric determination of phosphorus in soil and plant material with ascorbic acid. Soil Sci. 109, 214–220.

Jonard, M., Andre, F., Dambrine, E., Ponette, Q., Ulrich, E., 2009a. Temporal trends in the foliar nutritional status of the French. Walloon and Luxembourg broad-leaved plots of forest monitoring. Ann. For. Sci. 66, 412.

Jonard, M., Augusto, L., Morel, C., Achat, D.L., Saur, E., 2009b. Forest floor contribution to phosphorus nutrition: experimental data. Ann. For. Sci. 66, 510.

Koukol, O., Novak, F., Hrabal, R., Vosatka, M., 2006. Saprotrophic fungi transform organic phosphorus from spruce needle litter. Soil Biol. Biochem. 38, 3372–3379.

Kreutzer, K., 1976. Effect on growth in the next rotation (regeneration). In: ECE symposium Harvesting of a larger part of the forest biomass. pp. 78–90.

Lark, R.M., 2009. Estimating the regional mean status and change of soil properties: two distinct objectives for soil survey. Eur. J. Soil Sci. 60, 748–756.

Meiwes, K.J., Meesenburg, H., Bartens, H., Rademacher, P., Khanna, P.K., 2002. Accumulation of humus in the litter layer of forest stands at Solling: possible causes and significance for the nutrient cycling. Forst und Holz 57, 428–433.

Mellert, K.H., Prietzel, J., Straussberger, R., Rehfuess, K.E., 2004a. Long-term nutritional trends of conifer stands in Europe—results from the RECOGNITION project. Eur. J. For. Res. 123, 305–319.

Mellert, K.H., Prietzel, J., Straussberger, R., Rehfuess, K.E., 2004b. Statistical assessment of relationships between recent changes of tree growth in two Bavarian Scots pine stands and changes of stand nutrition and climate. Austrian J. For. Res. 121, 141–166.

Mellert, K.H., Prietzel, J., Straussberger, R., Rehfuess, K.E., Kahle, H.P., Perez, P., Spiecker, H., 2008. Relationships between long-term trends of air temperature, precipitation, nitrogen nutrition and growth of coniferous stands in Central

Europe and Finland—first results from the RECOGNITION Project. Eur. J. For. Res. 127, 507–524.
Mohren, G.M.J., van den Burg, J., Burger, F.W., 1986. Phosphorus deficiency induced by nitrogen input in Douglas fir in the Netherlands. Plant Soil 95, 191–200.
Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27, 31–36.
Nave, L.E., Vance, E.D., Swanston, C.W., Curtis, P.S., 2009. Impacts of elevated N inputs on north temperate forest soil C storage C/N, and net N-mineralization. Geoderma 153, 231–240.
Nohrstedt, H.-Ö., Jacobson, S., Sikström, U., 2000. Effects of repeated urea doses on soil chemistry and nutrient pools in a Norway spruce stand. For. Ecol. Manag. 130, 47–56.
Paré, D., Bernier, B., 1989. Phosphorus fixing potential of Ah and H horizons subjected to acidification. Can. J. For. Res. 19, 132–134.
Polle, A., Mössnang, M., von Schönborn, A., Sladkovic, R., Rennenberg, H., 1992. Field studies on Norway spruce trees at high altitudes 1. Mineral, pigment, and soluble protein contents of needles as affected by climate and pollution. New Phytol. 121, 89–99.
Prietzel, J., Ammer, C., 2008. Montane Bergmischwälder der Bayerischen Kalkalpen: Reduktion der Schalenwilddichte steigert nicht nur den Verjüngungserfolg, sondern auch die Bodenfruchtbarkeit. Allg. Forst- und Jagdztg. 179, 104–112.
Prietzel, J., Stetter, U., Klemmt, H.J., Rehfuess, K.E., 2006. Recent carbon and nitrogen accumulation and acidification in soils of two Scots pine ecosystems in Southern Germany. Plant Soil 289, 153–170.
Prietzel, J., Rehfuess, K.E., Stetter, U., Pretzsch, H., 2008. Changes of soil chemistry, stand nutrition, and stand growth at two Scots pine (*Pinus sylvestris* L.) sites in Central Europe during forty years after fertilization, liming, and lupine introduction. Eur. J. For. Res. 127, 43–61.
Pritchett, W.L., Comerford, N.B., 1982. Long-term response to phosphorus fertilization on selected southeastern coastal plain soils. Soil Sci. Soc. Am. J. 30, 509–512.
Rodenkirchen, H., 1992. Effects of acidic precipitation, fertilization and liming on the ground vegetation in coniferous forests of Southern Germany. Water Air Soil Pollut. 61, 279–284.
Schachtman, D.P., Reid, R.J., Ayling, S.M., 1998. Phosphorus uptake by plants: from plant to cell. Plant Physiol. 116, 447–453.
Schlichting, E., Blume, H.P., Stahr, K., 1995. Bodenkundliches Praktikum. Pareys Studientexte 81, 295.
Schwertmann, U., 1964. Differenzierung der Eisenoxide des Bodens durch Extraktion mit Ammoniumoxalat-Lösung. Zeitschr. Pflanzenern. Bodenkde. 105, 194–202.
Stefan, K., Fürst, A., Hacker, R., Bartels, U., 1997. Forest foliar condition in Europe. In: Results of a Large-scale Foliar Chemistry Survey 1995, Forest foliar Coordinating Centre, Vienna, p. 207.
Spiecker, H., 1999. Overview of recent growth trends in European forests. Water Air Soil Pollut. 116, 33–46.
Teng, Y., Timmer, V.R., 1995. Rhizosphere phosphorus depletion induced by heavy nitrogen fertilization in forest nursery soils. Soil Sci. Soc. Am. J. 59, 227–233.
Thomas, F.M., Büttner, G., 1998. Nutrient relations in healthy and damaged stands of mature oaks on clayey soils: two case studies in northwestern Germany. For. Ecol. Manag. 108, 301–319.
Treseder, K.K., 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytol. 164, 347–355.
Trichet, P., Bakker, M.R., Augusto, L., Alazard, P., Merzeau, D., Saur, E., 2009. Fifty years of fertilization experiments on *Pinus pinaster* in Southwest France: The importance of phosphorus as a fertilizer. For. Sci. 55, 390–402.
Turner, J., Lambert, M.J., Humphreys, F.R., 2002. Continuing growth response to phosphorus fertilizers by a Radiata pine plantation over fifty years. For. Sci. 48, 556–568.
Vance, C.P., Uhde-Stone, C., Allan, D.L., 2003. Phosphorus acquisition and use—critical adaptations by plants securing a nonrenewable resource. New Phytol. 157, 423–447.
Wehrmann, J., 1959. Methodische Untersuchungen zur Durchführung von Nadelanalysen in Kiefernbeständen. Forstwiss. Cbl. 78, 77–97.
Wesselink, L.G., Meiwes, K.J., Matzner, E., Stein, A., 1995. Long-term changes in water and soil chemistry in spruce and beech forests, Solling, Germany. Environ. Sci. Technol. 29, 51–58.
Wolff, B., Riek, W., 1997. Deutscher Waldbodenbericht 1996–Ergebnisse der bundesweiten Bodenzustandserhebung im Wald von 1987-1993 (BZE). Ed. Bundesministerium für Ernährung, Landwirtschaft und Forsten, Germany. Band 1.