



## Root-induced increases in soil pH and nutrient availability to field-grown cereals and legumes on acid sandy soils of Sudano-Sahelian West Africa

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### Abstract

A field experiment with millet (*Pennisetum glaucum* L.), sorghum [*Sorghum bicolor* (L.) Moench], cowpea (*Vigna unguiculata* L.) and groundnut (*Arachnis hypogaeae* L.) was conducted on severely P-deficient acid sandy soils of Niger, Mali and Burkina Faso to measure changes in pH and nutrient availability as affected by distance from the root surface and by mineral fertiliser application. Treatments included three rates of phosphorus (P) and four levels of nitrogen (N) application. Bulk, rhizosphere and rhizoplane soils were sampled at 35, 45 and 75 DAS in 1997 and at 55 and 65 DAS in 1998. Regardless of the cropping system and level of mineral fertiliser applied, soil pH consistently increased between 0.7 and two units from the bulk soil to the rhizoplane of millet. Similar pH gradients were observed in cowpea, but pH changes were much smaller in sorghum with a difference of only 0.3 units. Shifts in pH led to large increases in nutrient availability close to the roots. Compared with the bulk soil, available P in the rhizoplane was between 190 and 270% higher for P-Bray and between 360 and 600% higher for P-water. Exchangeable calcium (Ca) and magnesium (Mg) levels were also higher in the millet rhizoplane than in the bulk soil, whereas exchangeable aluminium (Al) levels decreased with increasing pH close to the root surface. The results suggest an important role of root-induced pH increases for crops to cope with acidity-induced nutrient deficiency and Al stress of soils in the Sudano-Sahelian zone of West Africa.

### Introduction

On weakly buffered sandy soils of West Africa with cation exchange capacities often below 1 cmol kg<sup>-1</sup>, soil acidification is an on-going process which partly explains the low availability of phosphorus (P), a main limiting factor for plant growth in this region. The main cause of acidification is leaching of nitrate and cations with large rainfall events which is enhanced by the rapid decline in soil organic carbon (Corg) contents in cultivated land. The application of mineral fertilisers containing ammonium, can contribute to further pH decreases (Bationo and Buerkert, 2000). However, the present level of fertiliser use by the predominantly subsistence oriented farmers is too low to significantly contribute to soil acidification. Millet, the dominant

crop in local farming systems, is very well adapted to the low P and N availability due to formation of an extensive rooting system (Payne et al., 1996) and tolerance against free aluminium (Al; Kretschmar et al., 1991). From basic research under controlled conditions, it is well known that the dominance of anion uptake over cations leads to increases in rhizosphere pH of cereals and dicotyledonous plants, whereas excess uptake of cations stimulates proton release associated with rhizosphere acidification, which is also characteristic for N<sub>2</sub>-fixing legumes (Marschner, 1989; Marschner et al., 1986; Mengel and Steffens, 1982; Römheld, 1998). To our knowledge, however, these processes and their effects on nutrient availability have never been studied under field conditions with cereals and legumes in West Africa. This is surprising

since the yield increasing effects of crop residues (CR) have been partly attributed to pH increases and a subsequent rise in nutrient availability. In this context, it has been shown that an increase in topsoil pH by 0.4 units can lead to an increase in water soluble (P-water) by 41% (Buerkert et al., 2000). A similar magnitude of pH changes in the rhizosphere soil of cereals could, therefore, be important for their P nutrition.

## Materials and methods

### *Field experiment*

Cereal/legume rotation experiments established during 1995 in Niger, in Mali and in Burkina Faso were used to study root effects on pH and nutrient availability. Rainfed millet and cowpea were planted at the onset of the growing season 1997 and 1998 at Goberi (12° 58'N, 2° 50' E; 600 mm) and at Gaya (11° 59'N, 3° 32' E; 800 mm) in Niger and at Cinzana (13° 15'N, 5° 56' E; 650 mm) in Mali. The same trial was also conducted with sorghum and groundnut at Kouaré (11° 59'N, 0° 19' N; 850 mm) in Burkina Faso (Table 1). The soils ranged in pH-KCI between 3.9 and 5.3, P-Bray between 1.5 and 2.9 mg kg<sup>-1</sup>, mineral N (Nmin) between 5 and 11 mg kg<sup>-1</sup>, organic C between 1.5 and 5.8 g kg<sup>-1</sup> and cation exchange capacities between 0.9 and 3.5 cmol<sub>c</sub> kg<sup>-1</sup> (Buerkert et al., 1997). The experimental setup with two replications was a split-plot design with randomized main-plot treatments being factorial combinations of phosphorus (P) applied annually as broadcast single superphosphate (SSP) at 0 and 13 kg P ha<sup>-1</sup>, and as rock-phosphate at a three years' rate of 39 kg P ha<sup>-1</sup>, and calcium ammonium nitrate (CAN) broadcast into equal applications at 0, 30, 60 and 90 kg N ha<sup>-1</sup>. The four subplot treatments were: Continuous cereal, continuous legume and both phases of the cereal/legume rotation named 'rotation cereal' and 'rotation legume'. Crop residues were applied as mulch to the soil surface at a rate of 500 kg ha<sup>-1</sup> in the middle of the dry season from November to May. Single superphosphate was broadcast in early May at the start of the rainy season. In millet/cowpea cropping systems, millet was sown with the first major rain at the end of May or in early June, 15 days before the sowing of cowpea. For sorghum/groundnut cropping systems, both crops were sown simultaneously in June of each year. The planting geometry was 1 m × 1 m for millet, 1 m × 0.25 m for cowpea, 0.6 × 0.5 m for sorghum and

0.6 × 0.3 m for groundnut. At sowing, 25–30 viable seeds of cereals (millet and sorghum), 5–10 seeds of cowpea and 2–5 seeds of groundnut were placed at 50 mm depth in the soil. At thinning, about 25 days after sowing (DAS), seedlings were reduced to three plants per pocket (planting hole) for millet and sorghum, two plants per pocket for cowpea and a single plant per pocket for groundnut.

### *Rhizosphere soil studies*

The following procedure was used to obtain soil samples from the rooting zone of crops at 0–0.3 m for the determination of pH and mineral nutrients. After carefully removing plants from the soil, roots with attached soil were gently shaken to remove loosely attached soil particles which were labeled as 'rhizosphere soil'. Subsequently, the roots were vigorously shaken to obtain the remaining removable soil particles which were labeled as 'rhizoplane soil'. Finally at 0.5 m from the planting hole, composite samples were taken at 0–0.3 m depth and labeled as 'bulk soil'.

This operational method of soil separation was certainly too crude to allow a well defined compartmentalisation of the plant soil interface but given the sandy nature of all soils with only between 5 and 15% clay, there seemed little effect of the method on particle size distribution between 'rhizosphere', 'rhizoplane' and 'bulk soil'. Despite air temperature upto 35 °C, this method allowed field sampling within a few minutes before the plants showed any wilting symptoms. Treatments sampled at all locations in 1997 were continuous cereals, rotation cereals and rotation legumes at 0, 13 and 39 kg P ha<sup>-1</sup> and 0, 30, 60, and 90 kg N ha<sup>-1</sup>. In 1998, treatments sampled were continuous cereals and rotation cereals at 0 and 60 kg N ha<sup>-1</sup> and at 0 and 13 kg P ha<sup>-1</sup> (Table 1). For pH determination, 10 g soil was dissolved in 25 ml of 0.01 M KCI. The samples from Goberi were air-dried in the shade within 12 h, sieved to pass a 2 mm screen and analyzed for Bray-P (Olsen and Sommers, 1982), water soluble P (P-water; Sissin, 1971), Al and total acidity (Mc Lean, 1982). Exchangeable bases were extracted with 1 M NH<sub>4</sub>-acetate and cations determined by atomic absorption spectrophotometry (Ca and Mg) and flame emission spectrophotometry (K).

### *Pot experiment*

A growth chamber study was conducted in 1996 to determine root-induced changes in pH and organic acid

Table 1. Summary of experiments conducted with soil and plant material from four West African sites

Experiment	Crops	Sites				Soil treatment <sup>d</sup>	Measurement	Data
		Goberi	Cinzana	Gaya	Kouaré			
Field	Millet	X		X	X	Continuous	pH	Figure 1, Tables 2 and 3
	Sorghum					Rotation		
Field	Cowpea	X	X		X	Rotation	pH	Figure 3
	Groundnut							
Field	Millet	X				Continuous	Available nutrients	Figure 4
						Rotation		
Nutrient solution	Millet		n.a. <sup>b</sup>			n.a.	pH	Figure 2
	Cowpea							
Nutrient solution	Cowpea		n.a.			n.a.	Exudates	Table 4
Soil incubation	n.a.	X				Bulk sample	Exudates	Table 5

<sup>a</sup> Averaged across several P and N levels (see 'Materials and methods' section).

<sup>b</sup> Not applicable.

Table 2. Cation exchange capacity (CEC), P-Bray and P-water in different soil fractions of continuous and rotation millet at 45 days after sowing; Goberi, Niger, 1997

Cropping systems (CS) Soil fractions (SF)	CEC	P-Bray	P-water
	cmol <sub>c</sub> kg <sup>-1</sup>	mg kg <sup>-1</sup>	mg kg <sup>-1</sup>
Continuous millet			
Bulk soil	0.77	3.43	0.130
Rhizoplane soil	0.55	4.49	0.580
Rotation millet			
Bulk soil	0.73	3.01	0.520
Rhizoplane soil	1.20	11.13	1.750
sed <sup>a</sup>	0.08	0.72	0.030
		P>F <sup>b</sup>	
SF	0.043	<0.001	<0.001
CS	<0.001	<0.001	<0.001
SF×CS	<0.001	<0.001	0.047

<sup>a</sup> Standard error of the difference.

<sup>b</sup> Probability of a treatment effect (significance level).

production during the growth of millet and cowpea in nutrient solution (Table 1). The composition of the nutrient solution was as follows: 0.7 mM K<sub>2</sub>SO<sub>4</sub>; 0.5 mM MgSO<sub>4</sub>; 2 mM Ca(NO<sub>3</sub>)<sub>2</sub>; 0.1 mM KH<sub>2</sub>PO<sub>4</sub>; 100 μM Fe-III-EDTA; 10 μM H<sub>3</sub>BO<sub>3</sub>; 0.5 μM MnSO<sub>4</sub>; 0.5 μM ZnSO<sub>4</sub>; 0.2 μM CuSO<sub>4</sub>; 0.01 μM (NH<sub>4</sub>)<sub>6</sub>Mo<sub>7</sub>O<sub>24</sub>. A P-free solution was prepared by removing KH<sub>2</sub>PO<sub>4</sub> from the complete nutrient solution. Ten pre-germinated seedlings were transferred into 3 l-pots containing the nutrient solutions. The temperature maintained during the growth period was 25 °C at 16/8 h light/dark. Nutrient solutions were changed every 3 days after measuring the pH. After 4 weeks of growth, root exudates were collected by placing

defined root zones between two layers of moist filter paper disks 0.4 mm thick, 5 mm diameter (Schleicher and Schüll, Dassel, Germany; no. 2992; Neumann and Römheld, 1999) on the root surface. After a 3 h collection period, aqueous extracts of the filter paper were analysed for organic acids by high pressure liquid chromatography (HPLC) according to Neumann and Römheld (1999).

#### Soil incubation at various pH levels

To determine the influence of pH on the availability of soil P, an incubation test was conducted on bulk soil sampled in plots of continuous millet, rotation millet and continuous cowpea at the Goberi site (Table 1). Five grams of soil were mixed with 10 ml of deionized water and the initial pH recorded. The pH was then adjusted to 4, 5, 6, 7 or 8 with 0.1 N NaOH or 0.1 N HCl. The pH, readjusted every 24 h was stable after 1 week of incubation 20 °C. A 2 ml aliquot of supernatant was centrifuged at 14 000 rpm (20,160 × g) and the water soluble P determined (Murphy and Riley, 1962). The remaining soil suspension was freeze dried and analysed for Bray 1 P (Olsen and Sommers, 1982).

#### Data analysis

All data were subjected to analysis of variance or regression analysis using GENSTAT release 3.2 (Lawes Agricultural Trust, 1995). Since changes in rhizosphere pH and nutrient levels were similar for all levels of applied mineral P and N fertilisers, data were averaged across fertiliser treatments. Means, standard errors of the difference (sed) and *F*-values were

Table 3. Nutrient availability in the rooting zone of continuous and rotation millet at 65 days after sowing, Goberi, Niger, 1998

Cropping systems (CS)	P-water	P-Bray	NH <sub>4</sub> -N	NO <sub>3</sub> -N	CEC	K	Mg	Al	Ca
Soil fractions (SF)	mg kg <sup>-1</sup>			cmol <sub>c</sub> kg <sup>-1</sup>		cmol kg <sup>-1</sup>			
Millet continuous									
Bulk soil	0.246	3.2	0.5	7.4	0.879	0.120	0.091	0.257	0.227
Rhizosphere soil	0.489	5.7	1.4	16.3	0.900	0.094	0.136	0.117	0.336
Rhizoplane soil	0.529	7.0	5.0	23.3	0.860	0.142	0.153	0.064	0.316
Millet rotation									
Bulk soil	0.229	3.4	0.6	6.3	0.836	0.107	0.091	0.243	0.223
Rhizosphere soil	0.554	5.5	1.2	14.7	0.844	0.090	0.127	0.115	0.315
Rhizoplane soil	0.617	6.9	2.8	20.8	0.857	0.130	0.150	0.080	0.319
sed <sup>a</sup>	0.050	0.36	0.42	0.98	0.029	0.008	0.008	0.018	0.018
	P>F <sup>b</sup>								
SF	<0.001	<0.001	<0.001	<0.001	0.050	<0.001	<0.001	<0.001	<0.001
CS	0.275	0.857	0.037	0.043	0.728	0.145	0.529	0.973	0.631
SF × CS	0.541	0.827	0.024	0.789	0.398	0.796	0.859	0.659	0.801

<sup>a</sup>Standard error of the difference.

<sup>b</sup>Probability of a treatment effect (significance level).

Table 4. Rates of carboxylate exudation in 4-week old cowpea roots grown in nutrient solution without (-P) and with phosphorus (+P). Data represent means and one standard error of the mean (in parentheses) of measurements conducted with three representative roots

Treatments	Malate	Malonate	Citrate	Fumarate	cis-Aconitate	trans-Aconitate
Root parts	pmol s <sup>-1</sup> m <sup>-1</sup> root length					
-P						
5 mm apical	25.3 (3.7)	26.9 (3.0)	6.4 (1.5)	0.58 (0.2)	0.19 (0.1)	0.33 (0.1)
20 mm subapical	Traces	Traces	0	0.25 (0.1)	0	0
+P						
5 mm apical	15.3 (3.8)	0	0	0.17 (0.1)	0	0
20 mm subapical	5.8 (1.8)	0	0	0.22 (0.1)	0	0

reported to indicate the significance of treatment effects. Standard errors of the mean (se) were reported whenever data for a single treatment at different time intervals were used.

## Results

### *pH changes in millet and sorghum*

In millet/cowpea systems at Goberi, the pH in the rhizoplane was 1.9 units higher than in the bulk soil 45 DAS and 1.2 units 75 DAS. Respective differences were 0.6 units 50 DAS and 0.4 units 80 DAS at Gaya (Figure 1). At all sites, pH levels followed

the pattern rhizoplane>rhizosphere>bulk soil. With the exception of the early sampling at Goberi, the root-induced increases in soil pH were independent of cropping system. Large plant-induced pH increases were also observed in millet grown in nutrient solution (Figure 2). With sorghum at Kouaré (Figure 1), pH increases towards the rhizoplane reached a maximum of 0.3 units, much smaller than in millet and not statistically significant.

### *pH changes in cowpea and groundnut*

In 1997, early sampling 35–45 DAS at Cinzana and Goberi showed increases of 1.6–2.4 pH units from bulk to rhizoplane soil in cowpea. However, at Goberi,

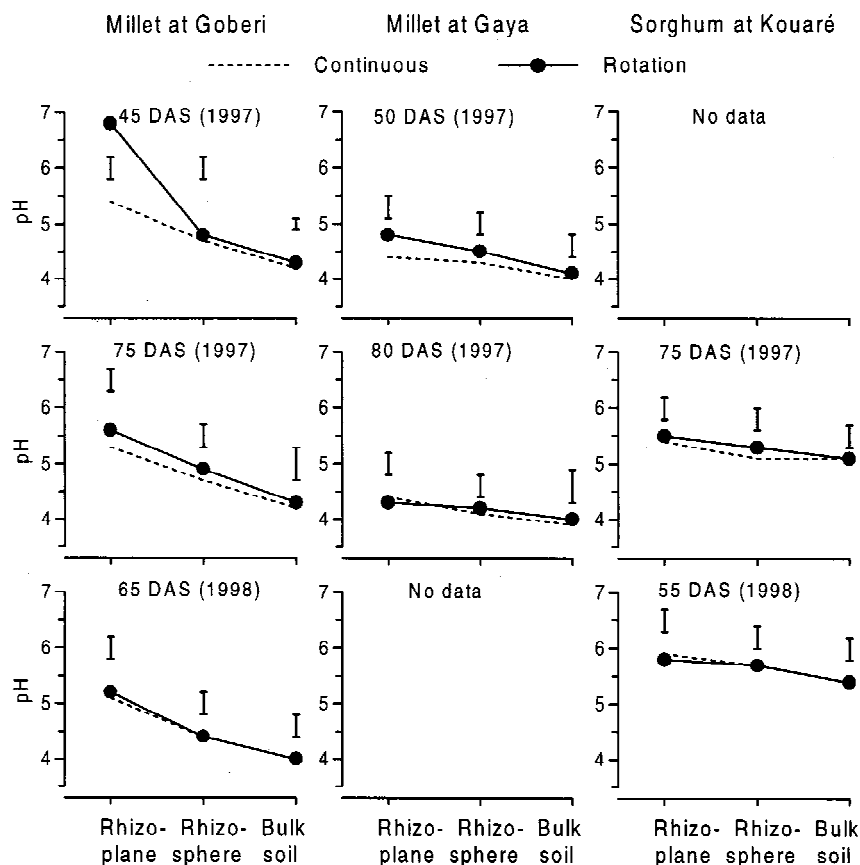


Figure 1. pH in the rhizoplane, rhizosphere and bulk soil of millet at Goberi and Gaya and of sorghum for different dates (DAS = days after sowing) at Kouaré in 1997 and 1998. Vertical lines represent  $\pm$  one standard error of the difference.

the rhizoplane pH at 75 DAS was nearly one unit lower than at compared with 45 DAS, demonstrating a narrowing of the difference between rhizoplane and bulk soil pH over time (Figure 3). In nutrient solution, cowpea roots were also found to increase the pH (Figure 2). In contrast to cowpea, there was no pH increase in the rhizoplane of groundnut compared with the bulk soil at Kouaré.

#### *Rhizosphere-induced changes in nutrient availability*

In 1997, the millet soil samples from Goberi showed that across both cropping systems P-Bray levels in the rhizoplane were 2.4-fold and P-water 3.6-fold higher than in the bulk soil. Also, in rotation millet but not in continuous millet effective cation exchange capacities (CEC) were larger in the rhizoplane than in the bulk soil (Table 2). In 1998, nutrient availability was also significantly affected by the rise in pH towards the millet root (Table 3). Averaged over both cropping systems, P-Bray levels were 2.1-fold higher

in the rhizoplane and 1.7-fold higher in the rhizosphere soil compared with the bulk soil. Respective increases in P-water were 3-fold and 2.5-fold. Soil mineral nitrogen levels were 3.5- and 2.5-fold higher in the rhizoplane and rhizosphere than in the bulk soil. Calcium and Mg levels followed a similar pattern. Available P, mineral N, Mg and Ca levels were more closely correlated with soil pH ( $r = 0.63$ – $0.87$ ) than K ( $r = 0.39$ ; Figure 4). Exchangeable aluminium was negatively correlated with pH (Figure 4) and was 2.3-fold lower in the rhizosphere and 3.6-fold lower in the rhizoplane than in the bulk soil (Table 3).

#### *Root-induced pH changes of millet and cowpea in solution culture*

Pearl millet induced a net alkalinisation of the nutrient medium which was much more pronounced with P than without P application. In contrast to many other leguminous crops such as lupin (*Lupinus albus* L.) and chickpea (*Cicer arietinum* L.; Neumann and Römheld,

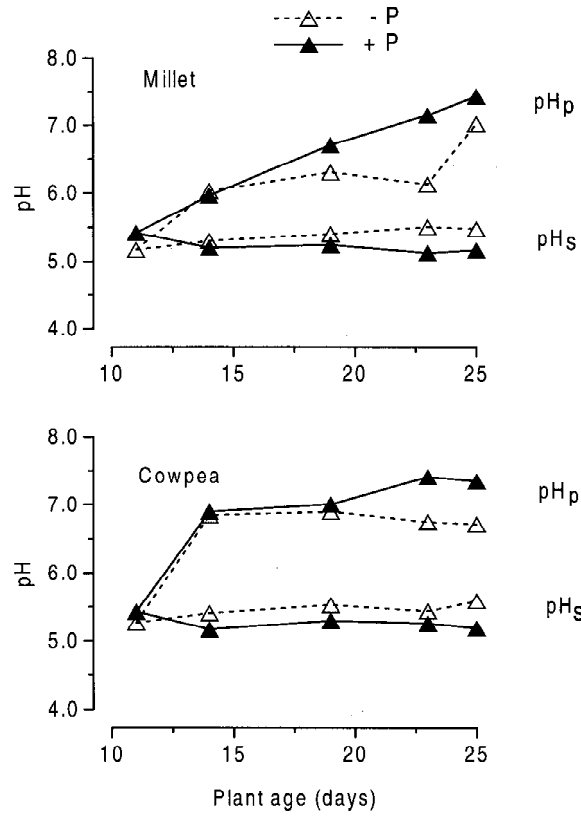


Figure 2. Root-induced changes in pH for millet and cowpea grown in nutrient solution; pH<sub>p</sub> = solution pH after 3–5 days of plant growth, pH<sub>s</sub> = pH of nutrient solution without plants immediately after preparation. Data points represent one single measurement.

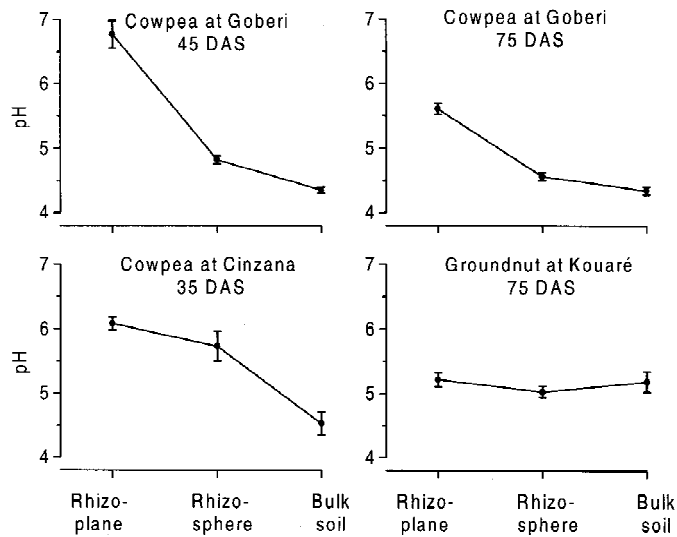


Figure 3. pH in the rhizoplane, rhizosphere and bulk soil of cowpea at Goberi and Cinzana and of groundnut at Kouaré for different dates (DAS = days after sowing) in 1997. Vertical lines represent  $\pm$  one standard error of the difference.

## Millet at Goberi

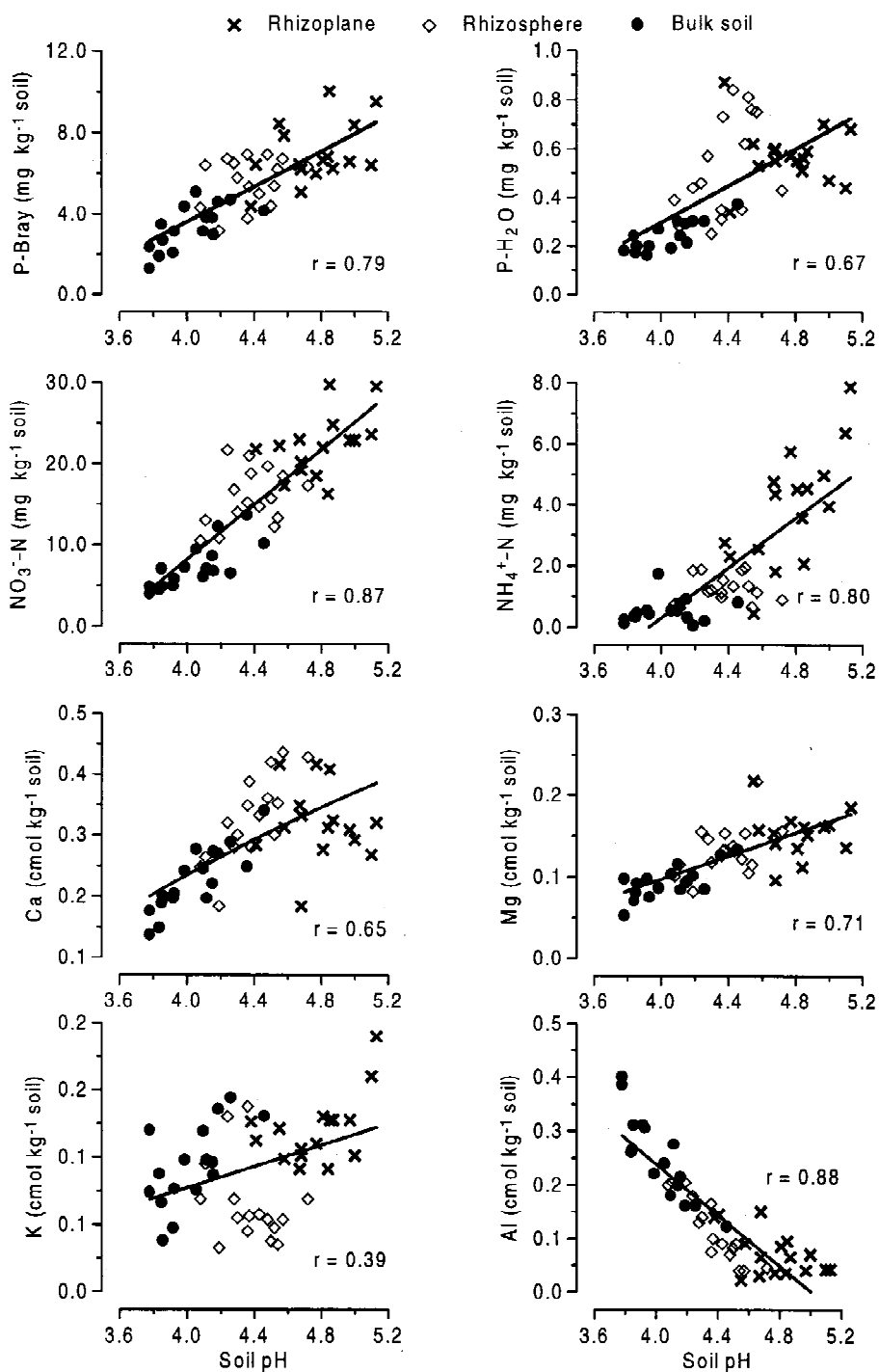


Figure 4. Correlation between soil pH and nutrient availability to pearl millet in the rhizoplane, rhizosphere and bulk soil in millet/cowpea rotations at Goberi in 1998.

Table 5. Soil P-Bray and P-water concentration in the bulk soil after 3 weeks of incubation at various pH levels. The data did not reveal any interaction between cropping systems and adjusted pH levels.

Cropping system (CS)	P-Bray	P-water
	mg kg <sup>-1</sup> soil	
Continuous millet	3.54	0.05
Rotation millet	5.50	0.05
Continuous cowpea	3.22	0.07
sed <sup>a</sup>	0.30	0.02
Adjusted pH		
4	4.40	0.06
5	3.94	0.01
6	4.34	0.08
7	3.31	0.06
8	4.44	0.09
	P>F <sup>b</sup>	
CS	0.031	0.120
pH	0.130	0.378
CS × pH	0.355	0.509

<sup>a</sup>Standard error of the difference.

<sup>b</sup>Probability of a treatment effect (significance level).

1999), there was no net acidification of the growth medium in response to P deficiency in cowpea, only less alkalisation than in the +P treatment was observed (Figure 2).

#### *Cowpea root exudation in solution culture*

Under hydroponic conditions, organic acid exudation was mainly limited to the 5 mm apical root zones of P deficient plants which released less than 30 pmol s<sup>-1</sup> m<sup>-1</sup> root length of malate, malonate, citrate, fumarate and cis- and trans-aconitate with malate and malonate being the main components. Phosphorus application decreased the exudation of organic acids to even lower levels except for malate at 20 mm subapical (Table 4).

#### *Soil incubation at various pH levels*

The adjustment of soil pH showed no significant influence on P-water or P-Bray levels in the bulk soil from Goberi (Table 5). Water soluble P levels were extremely low and did not show significant differences between cropping system treatments. The P-Bray levels over the entire pH range were much lower

compared with the values observed in rhizoplane and rhizosphere soils from the field study, but were similar to those observed in the bulk soil. There was, however, a significant cropping system effect on P-Bray. When averaged over all pH levels, rotation millet plots had 64% more P. Bray than continuous millet plots.

## Discussion

While root-induced changes in the physical and chemical conditions of the rhizosphere have been frequently associated with P depletion (Gahoonia and Nielsen, 1992; Joner et al., 1995), the results of this study indicated an increase in easily soil extractable P, mineral N and soluble Ca and Mg for millet. Similar results were found by Youssef and Chino (1987) who reported higher pH and accumulation of Ca and Mg in the rhizosphere of barley (*Hordeum vulgare* L.). Accumulation of Ca and Mg near the root surface has been mainly attributed to their supply by mass flow (Barber et al., 1962) in a rate exceeding that of plant uptake (Marschner, 1998). Similar effects have been reported also for inorganic P (Häussling and Marschner, 1989) and have been related to intense mineralisation of organic P (Porg) at a rate which may sometimes exceed the rate of nutrient uptake capacity in distinct root zones. Since the incubation of bulk soils with raised pH did not demonstrate a direct relationship between increased pH and P-water or P-Bray, it is more likely that increased P availability near the root zone was related to biochemical mineralisation of the soil Porg pool rather than to a dissolution of Fe/Al-P at elevated pH levels. Hydrolytic cleavage of Porg by extracellular phosphatases of microbial or root origin is one mechanism of P mineralisation (Eivazi and Tabatabai, 1977). Phosphatases of plant and microbial origin have been detected on the root surface (Dracup et al., 1984), in the rhizosphere (Hedley et al., 1982) and in the bulk soil (Eivazi and Tabatabai, 1977). Higher phosphatase activities have been frequently observed in rhizoplane soil versus bulk soil (Joner et al., 1995; Tarafdar and Marschner, 1994).

In acid soils, the effects of H<sup>+</sup> and Al are additive with respect to replacement of Ca<sup>2+</sup> and Mg<sup>2+</sup> which have lower exchange power (Marschner, 1989). Therefore, high Al concentrations in the soil solution generally cause a decrease in the uptake of Ca and Mg by root and consequently induce a deficiency of these elements (Marschner, 1989). In the present study, an increase in the rhizosphere and rhizoplane pH was



negatively correlated with Al concentration (Figure 4) and probably improved the uptake of Ca and Mg by millet.

The observed pH increases in the rhizosphere of pearl millet were likely related to a much larger uptake of nitrate over ammonium and other cations and the subsequent release of OH<sup>-</sup> ions originating from NO<sub>3</sub><sup>-</sup> reduction in the root tissue (Gahoonia et al., 1992; Gijssman, 1990; Nye, 1981). This pH increase is in contrast to pH shifts reported by Ae et al. (1991) who noted that compared with the bulk soil, the pH values in the rhizosphere and rhizoplane of millet decreased by 0.41 and 1.29 units, respectively, in a Vertisol and by 1.16 and 1.91 units in an Alfisol. In contrast to the Sahelian soils of the present study, those soils were alkaline, with pH values of 9.1 for the Vertisol and 8.7 for the Alfisol. The different results of our study may be the result of a physiological response of millet in order to regulate the pH in the rooting environment.

Plant age seemed to have large effects on root-induced changes in soil pH. At Goberi and Gaya, the pH gradients were much steeper at 45 DAS than at 75 DAS (Figure 1). Possible explanations are a reduction in plant available nitrate over time due to leaching and crop uptake decreasing the anion/cation uptake ratio. Also, one may argue that the presence of a larger proportion of old roots, less effective in NO<sub>3</sub><sup>-</sup> uptake may have led to a decrease in the alkalisation effect. It seems unlikely that rhizosphere alkalisation was an artefact of sample collection because care was taken during the sampling procedure to avoid root damage and both rhizosphere and rhizoplane samples were free from roots fragments.

The relatively lighter soil with lower buffering capacity at Goberi in comparison with Kouaré may have led to the higher observed pH increases in the rhizosphere of millet and cowpea *versus* sorghum which was grown solely at the Kouaré site. Genetic differences between crop species might also affect the manner and intensity by which roots alter the rhizosphere chemistry. The increase in rhizosphere and rhizoplane pH of cowpea was unexpected as legumes are commonly reported to decrease the soil pH as a consequence of N<sub>2</sub>-fixation (Aguilars and Van Diest, 1981; Mengel and Steffens, 1982; Mengel, 1994).

Root exudation measured in the growth chamber experiments revealed only a small amount of organic acids released from cowpea roots (Table 4), and did not contribute to a net acidification of the growth medium (Figure 2), which has been previously reported for other leguminous plant species, such as

white lupin and chickpea under P-deficient conditions (Neumann and Römheld, 1999). Only small quantities of organic acids released by cowpea roots (malonate, malate, citrate) have been similarly reported by Ohwaki and Hirata (1992) in a comparative study with different leguminous plant species. Thus, the observed pH increase in the rhizosphere and rhizoplane of cowpea may indicate low symbiotic N<sub>2</sub>-fixation as a consequence of the very low pH of the bulk soil and probably the low molybdenum availability of the Sahelian soils (Hafner, 1992). This was also indicated by low nodulation levels apparently unaffected by N application. On the soils of our study, cowpea may have covered a major proportion of its N needs through nitrate uptake from the soil solution which would have led to the observed rise in pH. The much lower pH increases in the rhizosphere of groundnut may also indicate that growth of this legume was less dependent on soil nitrate. The hypothesis that cowpea may fix less nitrogen on these West African soils than groundnut is also supported by recent measurements of soil mineral N (Bagayoko et al., 1999) which showed larger increases in N<sub>min</sub> levels of rotation plots with groundnut than with cowpea *versus* the continuous cereal plots at the respective sites.

The observed pH rise in the rhizosphere of young millet (Figure 1) was associated with an increased availability of nutrients (Table 2) and likely helped to overcome P deficiency, one of the most limiting constraints to plant growth in many West African soils.

This increase in nutrient availability near the root, which appears to be crop species dependent, indicates that the nutrient distribution at the soil root interface is more important for the assessment evaluation of plant available nutrients than their solubility in the bulk soil (Tables 2, 3 and 5). The observed phenomenon may also be related to the low organic C content in the soils of our study. The accumulation of nutrients by the plant, increased microbial activity and rhizodeposition may contribute extensively to nutrient availability and the accumulation of nutrients in the rhizosphere, particularly N and P. The mechanisms and processes involved in the increased availability of specific plant nutrients in the rhizosphere observed in this study should be the focus of further research.

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