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Effect of crop residues on root growth and phosphorus acquisition of pearl millet in an acid sandy soil in Niger

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Abstract

The effect of long-term (1983–1988) applications of crop residues (millet straw, 2–4 t ha^{-1} yr^{-1}) and/or mineral fertilizer (30 kg N, 13 kg P and 25 kg K ha^{-1} yr^{-1}) on uptake of phosphorus (P) and other nutrients, root growth and mycorrhizal colonization of pearl millet (*Pennisetum glaucum* L.) was examined for two seasons (1987 and 1988) on an acid sandy soil in Niger. Treatments of the long-term field experiment were: control (−CR − F), mineral fertilizer only (−CR + F), crop residues only (+CR − F), and crop residues plus mineral fertilizer (+CR + F).

In both years, total P uptake was similar for +CR − F and −CR + F treatments (1.6–3.5 kg P ha^{-1}), although available soil P concentration (Bray I P) was considerably lower in +CR − F (3.2 mg P kg^{-1} soil) than in −CR + F (7.4) soil. In the treatments with mineral fertilizers (−CR + F; +CR + F), crop residues increased available soil P concentrations (Bray I P) from 7.4 to 8.9 mg kg^{-1} soil, while total P uptake increased from 3.6 to 10.6 kg P ha^{-1}. In 1987 (with 450 mm of rainfall), leaf P concentrations of 30-day-old millet plants were in the deficiency range, but highest in the +CR + F treatment. In 1988 (699 mm), leaf P concentrations were distinctly higher, and again highest in the +CR + F treatment. In the treatments without crop residues (−CR − F; −CR + F), potassium (K) concentrations in the leaves indicated K deficiency, while application of crop residues (+CR − F; +CR + F) substantially raised leaf K concentrations and total K uptake. Leaf concentrations of calcium (Ca) and magnesium (Mg) were hardly affected by the different treatments.

In the topsoil (0–30 cm), root length density of millet plants was greater for +CR + F (6.5 cm cm^{-3}) than for +CR − F (4.5 cm cm^{-3}) and −CR + F (4.2 cm cm^{-3}) treatments. Below 30 cm soil depth, root length density of all treatments declined rapidly from about 0.6 cm cm^{-3} (30–60 cm soil depth) to 0.2 cm cm^{-3} (120–180 cm soil depth). During the period of high uptake rates of P (42–80 DAP), root colonization with vesicular-arbuscular mycorrhizal (VAM) fungi was low in 1987 (15–20%), but distinctly higher in 1988 (55–60%). Higher P uptake of +CR + F plants was related to a greater total root length in 0–30 cm and also to a higher P uptake rate per unit root length (P influx). Beneficial effects of crop residues on P uptake were primarily attributed to higher P mobility in the soil due to decreased concentrations of exchangeable Al, and enhancement of root growth. In contrast, the beneficial effect of crop residues on K uptake was caused by direct K supply with the millet straw.

Introduction

Unreliable rainfall and low nutrient availability, in particular of P (Bationo et al., 1990), are the major constraints to pearl millet (*Pennisetum glaucum* L.) growth on acid sandy soils in the West African semi-arid tropics (Breman and De Wit, 1983; Van Keulen and Breman, 1990). Large yield increases can be achieved by the application of mineral fertilizer (Bationo and Mokwunye, 1991). However, under these environmental conditions, with mineral fertilizer application alone soil organic matter content declines and removal of nutrients by crops and leaching losses may cause lower base saturation and soil acidification, increase in exchangeable Al, and decline in crop yields (Bationo et al., 1987). Long-term yield decline following mineral fertilization has been related to Al toxicity and/or deficiency of other mineral nutrients not supplied with the fertilizer (Pichot et al., 1981; De Ridder and Van Keulen, 1990).

With application of crop residues (millet straw) in combination with mineral fertilizers, a relatively high production level can be maintained (Pichot et al., 1974; Vlek, 1990). The beneficial effect of crop residues on crop growth has been attributed largely to the prevention of Al toxicity, since crop residue application increased soil pH and base saturation (Bationo et al., 1987; Jones, 1976; Pichot et al., 1981). While this may explain the beneficial effect in Al sensitive leguminous crops such as cowpea or groundnut, for pearl millet, which is very Al tolerant (Long et al., 1973; Norman et al., 1984), growth in the acid soils of the Sahel is not restricted by Al toxicity (Kretzschmar et al., 1991). However, exchangeable Al strongly adsorbs P, and the decrease in Al saturation by crop residue application increases P mobility in these soils (Kretzschmar et al., 1991). This may directly affect plant growth, as P is the most limiting nutrient for millet growth in this area (Bationo et al., 1990).

Phosphorus uptake by plants is determined not only by the solubility and mobility of P in soil, but also by plant properties, for instance the total root length, reflecting the capacity of a plant to acquire nutrients (Föhse et al., 1988; Jungk and Claassen, 1989). In addition, colonization of the roots with vesicular-arbuscular mycorrhizal (VAM) fungi may improve plant P uptake (Kothari et al., 1991; Tinker, 1984). In the present study, the effect of long-term applications of crop residue and mineral fertilizer on nutrient uptake of pearl millet was examined in two seasons (1987 and 1988) in a field experiment established in 1983 on an acid sandy soil in Niger, West Africa. Main emphasis has been placed on the influence of crop residues on root growth, mycorrhization and on the P acquisition of pearl millet.

Materials and methods

The studies were conducted during the rainy season 1987 and 1988 in a long-term field experiment established in 1983 at the research station of the ICRISAT Sahelian Center (13°15′ N; 2°18′ E), 40 km southeast of Niamey, Niger, West Africa. The soil of the experimental site is classified as a sandy, siliceous, isohyperthermic psammentic Paleustalf (West et al., 1984), and is representative of the soils used for pearl millet production in Niger. Some physical and chemical properties of the top soil (0–30 cm) are: 91% sand, 5.3% clay; a field capacity for water of approximately 14% (v/v); pH (H_2O; 1:1) of 4.9; effective cation exchange capacity of 0.64 meq 100 g^{-1} soil; base saturation of 42%; organic carbon concentration of 0.17%; total nitrogen (N) of 190 mg kg^{-1}; total P of 73 mg kg^{-1}; available P (Bray I) of 2.6 mg kg^{-1}.

The rainy season starts in June and lasts until September. The average rainfall in Niamey is 560 mm, and with a probability of 75% more than 441 mm are received (Sivakumar, 1986). Total rainfall for the experimental site was 450 mm in 1987 and 699 mm in 1988. Thus, in 1987 rainfall was by 20% below the long-term average with a conspicuous water deficit at the end of August, while in 1988 rainfall was 25% above average and distribution was very favorable for millet growth (Fig. 1).

The long-term field experiment consisted of four treatments with four replications laid out in randomized complete blocks. The individual plot size was 10 × 10 m. Treatments were: (i) millet straw (crop residues; CR) removed after harvest,

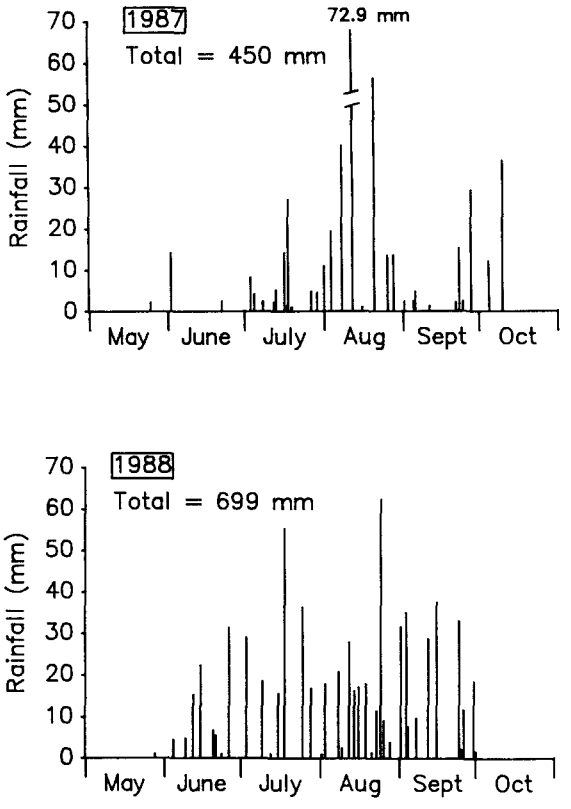

Fig. 1. Rainfall distribution at Sadoré, Niger, during the rainy season 1987 and 1988.

no mineral fertilizer applied (−CR − F); (ii) millet straw left in the field, no mineral fertilizer applied (+CR − F); (iii) millet straw removed after harvest, application of mineral fertilizer (−CR + F); (iv) millet straw left in the field, application of mineral fertilizer (+CR + F). At the onset of the experiment (1983), each crop residue plot received an additional 4 t ha^{-1} of millet straw two weeks prior to planting. In subsequent years, all straw produced in a +CR plot was returned to the plot by applying it as non-chopped surface mulch. Thus, for each plot and year individual rates of crop residues were applied, being on average (1983–1988) 2 t ha^{-1} yr^{-1} in +CR − F and 4 t ha^{-1} yr^{-1} in +CR + F plots. Mineral fertilizer application comprised of 13 kg P ha^{-1} yr^{-1} as single superphosphate, 30 kg N ha^{-1} yr^{-1} as urea, and 25 kg K ha^{-1} yr^{-1} as KCl. Phosphorus and K fertilizers were applied broadcast prior to planting, N fertilizer application was split into two doses of 15 kg N ha^{-1} each, 21 and 42 DAP. Some soil chemical properties in the topsoil (0–20 cm) after six year (1983–1988) application of crop residues and mineral fertilizer are given in Table 1. The soil samples were taken in 1988 from all plots of the trial after harvesting the millet crop.

At planting, 20 to 30 seeds of pearl millet (*Pennisetum glaucum* L. cv. CIVT) were placed in a 4–5 cm deep hole, with a spacing between planting sites of 1 × 1 m to achieve a density of 10,000 planting sites per hectare as recommended in Niger. After seedling emergence, the number of plants per planting site was reduced to three, giving a 'pocket' of millet plants. The millet crop was planted on first of July in 1987 and on 11th June in 1988.

To determine the time course of dry matter accumulation, eight pockets (one row) were harvested in each plot at 30, 42, 65 and 80 DAP. At crop maturity (100 DAP), the remaining area (36 m^2) was used for determination of final grain yield and shoot dry weight. Above-ground plant parts were separated into leaves, stems and heads, and dry weight data recorded after drying at 60°C. To assess the nutritional status of pearl millet throughout the growing season a subsample of mature leaf blades was taken at each

Table 1. Some soil chemical properties of the topsoil (0–20 cm) of an acid sandy soil of Niger (Psammentic Paleustalf, sandy, siliceous, isohyperthermic) as affected by long-term (1983–1988) applications of crop residue (CR) and mineral fertilizer (F). Soil samples were taken in 1988 after harvesting of the millet crop[a]

Treatments	P (Bray I) (mg kg^{-1})	pH (KCl)	Organic carbon (%)	Al saturation (%)	Base saturation (%)	Exchangeable (meq kg^{-1})				
						Ca	Mg	K	Na	Al
−CR − F	2.21	3.84	0.21	36	47	1.9	0.6	0.8	0.30	2.8
+CR − F	3.20	4.37	0.25	12	79	3.1	1.3	1.3	0.25	0.9
−CR + F	7.43	3.86	0.23	37	45	2.1	0.8	0.9	0.30	3.0
+CR + F	8.93	4.58	0.31	4	92	5.5	1.7	1.7	0.27	0.4

[a]The data are means of four replications

sampling date and analyzed for mineral elements.

Ground plant samples of leaves, stems and heads were dry-ashed at 450°C and ash disolved in 1:30 (v/v) diluted HNO_3. Potassium and Ca were determined by flame photometry (Eppendorf 700), Mg by atomic absorption spectrometry (Hitachi 180-80), and P photometrically using the vanado-molybdate assay according to Gericke and Kurmies (1952). Total N concentrations of ground plant dry matter subsamples were determined using an automatic N analyzer (ANA 1300 Erba Science).

After harvesting the above-ground plant parts, four of the harvested pockets per plot were sampled for root growth in close proximity to the pockets and in a distance of 50 cm (between pockets). Soil cores (10 cm diameter) were taken in 0–15, 15–30, 30–60, 60–90, 90–120, 120–150 and 150–180 cm intervals using an auger. At the first sampling date (42 DAP), the maximum soil depth sampled was 90 cm, at the second (65 DAP), 150 cm, and at the third (80 DAP), 180 cm. Since pearl millet growth in −CR − F plots was very poor, roots were not sampled in this treatment. Roots were separated from soil by careful washing over a 0.75 mm sieve. Root length of the sample was determined using the modified line intersect method according to Tennant (1975). Average P uptake rates per unit of root length (P influx) were calculated for the time period from 42 to 65 DAP by the formula of Williams (1948):

$$I_p = \frac{(U_2 - U_1)}{(L_2 - L_1)} \quad \frac{(\ln L_2 - \ln L_1)}{(t_2 - t_1)}$$

where I_p = P uptake rate per unit of root length (P influx); U = P uptake, mol pocket^{-1}; L = total root length in 0–30 cm, cm pocket^{-1}; t = time, s; and subscripts 1 and 2 refer to the sampling date i.e. t_1 = 42 DAP, t_2 = 65 DAP. Total root length in 0–30 cm was calculated from the respective root length densities in 0–15 cm and in 15–30 cm, and the soil area designated to each pocket (i.e., 1 m × 1 m).

Percentage mycorrhizal colonization was determined in two subsamples (2–5 g fresh weight) of each root sample using the modified gridline-intersection method (Giovannetti and Mosse, 1980). After clearing in 10% KOH for 2 h at 80°C, the roots were rinsed thoroughly with water and acidified for 10 min in 1% HCl. Acidified roots were stained with 0.1% acid fuchsin in lactic acid for two hours at room temperature and thereafter destained for several days in lactic acid. VAM colonized root length was calculated from total root length and per cent mycorrhizal colonization.

Analyses of variance were carried out on the data, excluding the −CR − F treatment when appropriate. Standard errors of means were calculated and means separated by the Student-Newman-Keuls test using the COSTAT program. For correlations, values of the individual plots were used.

Results

Maximum dry matter yields in 1987 were 244 (−CR − F treatment), 1650 (+CR − F), 1350 (−CR + F) and 3950 (+CR + F) kg ha^{-1}, and in 1988 were 608 (−CR − F), 2980 (+CR − F), 2750 (−CR + F) and 6020 (+CR + F) kg ha^{-1}. Leaf P concentrations declined during the season in all treatments, particularly in the low rainfall year 1987 (Fig. 2). In both years, throughout the season the leaf P concentrations were distinctly higher when both crop residues and P fertilizer were supplied, and lowest in the −CR − F treatment. Total P uptake remained at a very low level in the −CR − F treatment, was similar in the +CR − F and −CR + F treatment, but approximately three to four times higher in the +CR + F treatment. In both seasons the time course of total P uptake in the various treatments (Fig. 2) was similar to the time course of dry matter accumulation (data not shown).

As a representative example of treatment effects on the mineral element concentrations in the leaves, the data of 30-day-old plants are shown in Table 2. In 1987, the P concentrations were clearly in the deficiency range, perhaps with the exception of the +CR + F treatment. In 1988 (high rainfall), the P concentrations were distinctly higher and at least in the +CR + F treatment in the sufficiency range. In both seasons, returning of crop residues (+CR − F; +CR + F) substantially raised the leaf K concen-

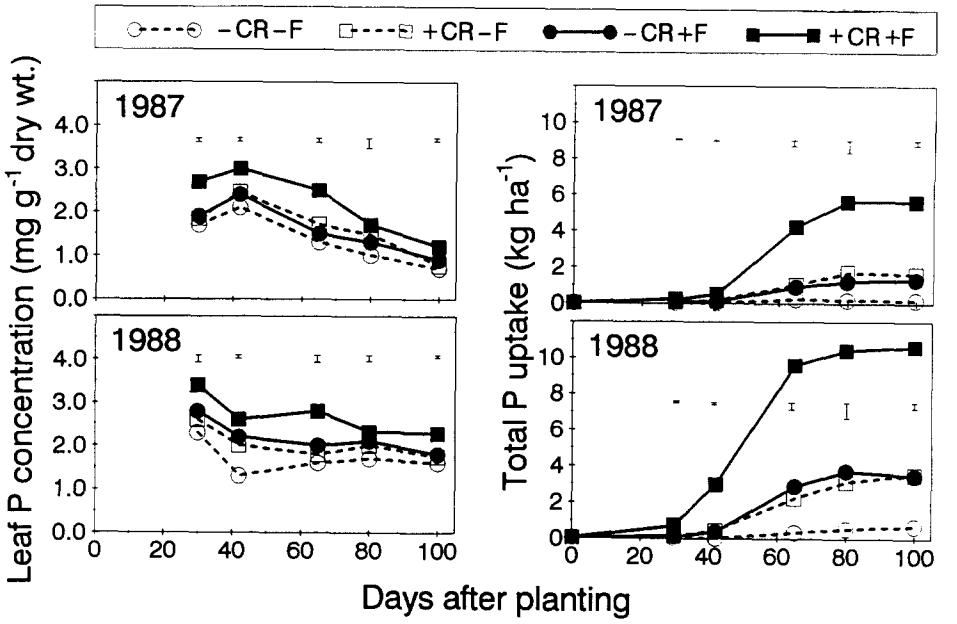

Fig. 2. Effect of crop residue (CR) and mineral fertilizer (F) application on P concentration in fully expanded millet leaves and on total P uptake (excluding roots) of pearl millet. Crop residues and mineral fertilizer were applied for six consecutive years (1983–1988). Vertical bars are standard errors of means.

Table 2. Mineral element concentrations in fully expanded leaves of 30-day-old pearl millet plants and total uptake of N, P, K, Ca and Mg (excluding roots) at maturity as affected by long-term applications of crop residue (CR) and mineral fertilizer (F)

Year	Treatment	Concentration (mg g^{-1} dry wt)					Uptake (kg ha^{-1})				
		N	P	K	Mg	Ca	N	P	K	Mg	Ca
1987	−CR − F	42.6	1.69	27.5	3.00	4.76	3.1	0.18	2.5	0.81	0.43
	+CR − F	41.4	1.84	36.6	3.30	4.90	20.1	1.69	17.3	4.57	3.57
	−CR + F	39.5	1.93	25.0	3.52	5.90	17.1	1.59	10.7	3.53	3.09
	+CR + F	46.8	2.69	45.8	3.79	6.21	50.2	5.64	43.9	12.90	8.79
	SE	0.68	0.08	1.5	0.20	0.27	2.94	0.71	2.6	0.65	0.88
1988	−CR − F	35.0	2.26	22.0	2.58	3.88	9.4	0.68	7.3	1.29	1.73
	+CR − F	37.1	2.57	37.1	3.21	4.39	40.3	3.48	35.5	6.40	8.68
	−CR + F	35.3	2.79	25.5	3.29	5.10	36.0	3.69	32.9	5.91	8.63
	+CR + F	40.6	3.43	50.5	3.65	4.73	76.6	10.60	84.3	15.00	19.36
	SE	0.95	0.16	1.6	0.16	0.20	3.8	0.83	4.2	0.93	1.01
Sufficiency range[a]		35–51	3.0–6.0	30–45	3.5–5.0	9.0–13.0					

[a]Jones et al., 1991. Sufficiency range was derived from 23 to 39-day-old sorghum plants (*Sorghum vulgare* and *S. bicolor*).

trations while for −CR treatments (−CR − F; −CR + F) the low leaf K concentrations suggested K deficiency. Leaf concentrations of Ca were relatively low. However, since with increasing plant age the leaf concentrations of Ca increased, Ca supply was likely not a limiting factor for millet growth. The leaf Mg concentrations did not vary distinctly between the seasons and were in the sufficiency range for all treatments.

As for P, total uptake of N, K, Mg and Ca was similar in the +CR − F and −CR + F treatments, but distinctly higher in the +CR + F treatment. Although pearl millet was cultivated continuously since 1983, and only 30 kg N ha^{-1} were applied annually, in both 1987 and 1988 the

total N uptake of +CR + F treatment was higher than the amount supplied by mineral fertilizer. Despite the marked differences in total N uptake, leaf N concentrations were in the adequate range (35–47 mg N g^{-1} dry weight) for all treatments. Nutrient uptake and plant growth were poor in the −CR − F treatment, which was therefore excluded from further analysis.

Root length density between millet pockets was highest in the topsoil (0–15 cm) and declined rapidly below 15 cm (Fig. 3). In both years, root length density in the top 30 cm was considerably greater for +CR + F than for +CR − F and −CR + F treatments. This difference was particularly distinct at the earlier growing stages. Below 30 cm soil depth, the differences in root growth became smaller and were negligible at approximately 120 cm. With increasing soil depth also the variability of the root samples increased, so that significant differences in root growth were found only in the 0–30 cm soil layer. Sixty-five days after planting, in all treatments a few roots penetrated the soil almost uniformly to a depth of 150 cm and at 80 days to a depth of 180 cm. No soil cores were taken in deeper soil layers.

Differences in root growth were also found between years (Fig. 3). In 1987, when rainfall was unfavourable in terms of distribution and amount (Fig. 1), root growth between millet pockets was greater than in 1988, particularly in the topsoil (0–15 cm). Root growth in close proximity to the pockets (not shown) was in both years three to four times higher than between the pockets, but this high rooting density was confined to the planting site and to the top 15–20 cm.

Colonization rates with VA mycorrhizal fungi were not influenced by the various treatments (Fig. 4). However, the level of colonization was different in both years. In 1987, the root coloni-

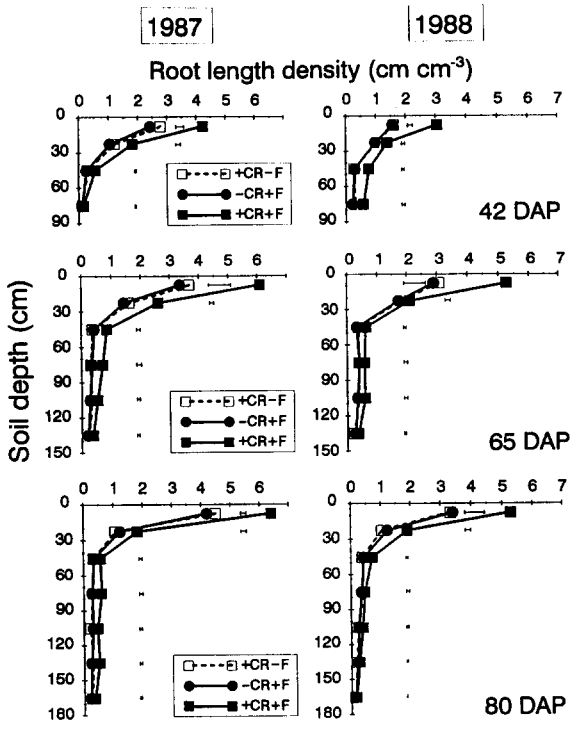

Fig. 3. Root length density of pearl millet in different soil depths at 42, 65 and 80 days after planting (DAP). Root samples were taken in a distance of 50 cm from the planting site (pocket). Horizontal bars are standard errors of means.

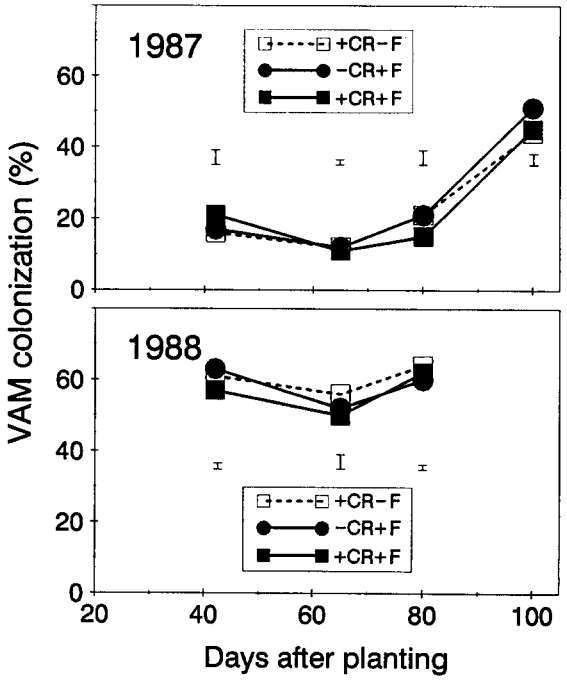

Fig. 4. VAM colonization rates of millet roots at 42, 65, 80 and 100 (harvest) days after planting as influenced by long-term application (1983–1988) of crop residues (CR) and mineral fertilizer (F). In 1988, colonization rates were not determined for final harvest. Vertical bars are standard errors of means.

zation rates ranged between 10% and 20% until 80 DAP and increased to 40–50% towards crop maturity (100 DAP). In contrast, root colonization rates for 1988 ranged from 40% to 60% between 42 and 80 DAP. In 1988, root colonization rates at crop maturity (100 DAP) were not determined because the root cortex of more than 50% of the roots examined was decomposed so that the determination of colonization rates became unreliable.

Average P uptake rates (P influx) per unit root length for the time period of highest P demand (i.e. 42 to 65 DAP; Fig. 2) is shown in Figure 5. Notwithstanding the differences in available P by a factor of more than two (Table 1), P influx was similar for +CR − F and −CR + F treatment in 1987, but was significantly higher for −CR + F treatment in 1988. Combined application of crop residues and P fertilizer (+CR + F) substantially increased P influx in comparison to crop residue and P fertilizer application alone. For all treatments, P influx was higher in the wetter year 1988.

In both years, total P uptake at 65 DAP was linearly correlated with the total root length in 0–30 cm soil depth at the same time (Fig. 6). Inclusion of the VAM-colonized root length in the regression did not improve the correlation (data not shown).

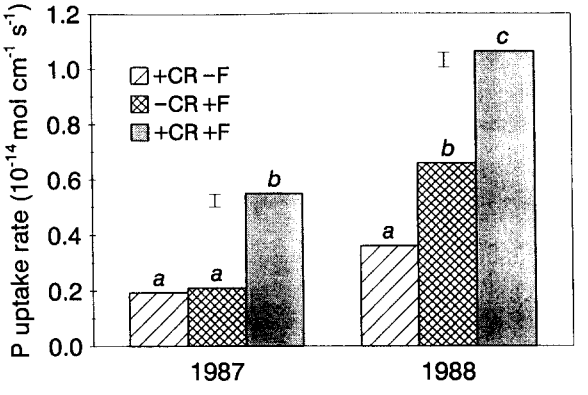

Fig. 5. Effect of crop residue (CR) and mineral fertilizer (F) application on P uptake rates per unit root length (P influx). Uptake rates of pearl millet were calculated for the time period from 42 to 65 days after planting. Vertical bars are standard errors of means. Columns within one year are not statistically different by the Student-Newman-Keuls test when marked by the same letter.

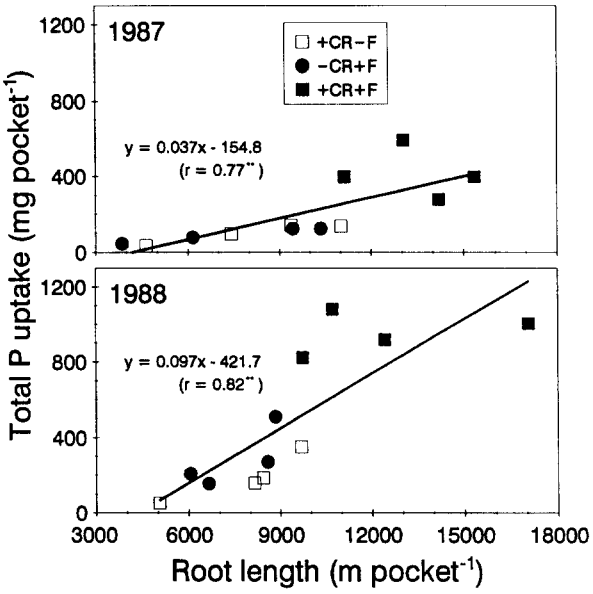

Fig. 6. Linear correlation between total P uptake and total root length in 0–30 cm soil depth of pearl millet at 65 days after planting as influenced by the application of crop residues (CR) and mineral fertilizer (F).

Discussion

For assessing available soil P in the sandy soils of the Sahel, the Bray I P method is the most appropriate soil testing procedure, and 7.9 mg P kg^{-1} soil is considered as sufficient to achieve 90% of the maximum yield (Bationo and Mokwunye, 1991). However, plant-available soil P as determined by chemical extraction methods and actual P uptake by plants are often poorly correlated because chemical soil analysis does not consider factors like P mobility in the soil or properties of the root system which can largely modify the P supply to plants (Jungk and Claassen, 1989). In both years of the study, total P uptake was similar for +CR − F and −CR + F treatments (Fig. 2), although extractable soil P concentration was distinctly lower in the CR − F soil (Table 1). In the mineral fertilizer treatments (−CR + F; +CR + F), crop residue application increased extractable soil P concentration from 7.4 to 8.9 mg kg^{-1} soil (Table 1), while total P uptake increased by a factor of three to four (Fig. 2).

The additional P supply by annual crop res-

idue application cannot account for the higher P uptake as with 2 t (+CR − F) and 4 t (+CR + F) of millet straw only 1 and 3 kg P ha^{-1} yr^{-1}, respectively, were returned, compared to 13 kg P supplied with the fertilizer. In a soil incubation experiment using soil samples of this field experiment (−CR − F and +CR − F soils), Kretzschmar et al. (1991) showed that long-term application of crop residues influences the P mobility in these soils, as indicated by a higher P concentration in the soil solution of +CR − F (1.75 μM) compared to −CR − F (0.52 μM) soil. In that study, addition of mineral fertilizer (equivalent to 24 kg N, 18 kg P and 18 kg K per hectare) increased the P concentrations in the soil solutions to 8.98 μM for the incubated −CR − F and to 28.31 μM for the incubated +CR − F soil. Crop residue application increased soil pH and base saturation, and it decreased exchangeable Al and Al saturation (Table 1). Since exchangeable Al strongly adsorbs P, a decrease of this fraction will improve the solubility of P, thus supplying more P in soil solution (Kretzschmar et al., 1991). In soils low in P, a small increase in P mobility may strongly increase P uptake (Jungk and Claassen, 1986). Therefore, the improvement of P nutrition following crop residue application can be attributed to increase in mobility of soil and fertilizer P.

In both years, root length density between pearl millet pockets was higher in +CR + F than in −CR + F treatment (Fig. 3), especially in the topsoil at the earlier growing stages (i.e. 42 and 65 DAP). As growth rate and surface area of the root system are important factors for P acquisition by plants (Jungk and Claassen, 1989), the promotion of root growth in the topsoil may have contributed, in addition to the increase in P mobility, to the beneficial effect of crop residues on P nutrition of pearl millet. This enhancement effect of crop residues on early root growth of pearl millet could also be demonstrated in a short-term pot experiment (12 days) where incubation of −CR − F soil with millet straw (equivalent to 2 t ha^{-1}) led to a distinct increase especially of lateral root growth, before an increase in shoot growth could be observed (Kretzschmar et al., 1991).

Beside root size, P uptake by plants is determined by P influx per unit root length (Föhse et al., 1988). When crop residues were applied in combination with P fertilizer, P influx was considerably enhanced (Fig. 5). Thus, the better P supply of +CR + F plants can be explained by both a larger root system and a higher P influx per unit root length. Accordingly, the overall utilization (1983–1988) of fertilizer P as determined by the difference in P uptake of plants from fertilized and unfertilized treatments was approximately 20% without (−CR + F) and 44% with (+CR + F) crop residues.

There is strong evidence that the promotion of root growth by crop residues is related to a stimulation of microbial activity in the rhizosphere of pearl millet. Like other tropical grasses (C_4 species), pearl millet forms rhizosphere associations with N_2-fixing bacteria (Wani et al., 1988) which may affect plant growth not only by the supply of N from fixation (Chalk, 1991), but also by the production of phytohormones promoting root growth and especially root hair formation (Joshi and Rao, 1989; Martin et al., 1989). Since energy supply by root exudates is often a limiting factor for microbial activity (Neyra and Döbereiner, 1977), addition of energy rich compounds with a high C/N ratio (for instance, millet straw, C/N > 100/1) may enhance the activity of N_2-fixing bacteria in the rhizosphere (Martin et al., 1989). In the present experiment application of crop residues led to a large increase in numbers of N_2-fixing bacteria and total bacteria in the rhizosphere soil (Hafner et al., 1993). Therefore, the promotion of root growth by crop residues is most likely related to a proliferation of diazotrophic bacteria in the rhizosphere of pearl millet. As another factor, the increase in P mobility by crop residue application improved P nutrition of +CR plants leading to an increased shoot and root growth. Since root hairs strongly affect P influx per unit root length (Föhse et al., 1991), a stimulation of root hair growth by bacterial production of phytohormones may be an additional factor responsible for the higher efficiency of P uptake in +CR plants.

In the Sahelian zone of West Africa, drought stress periods are frequent (Lawson and Sivakumar, 1991). Under such conditions, a deep root system may be advantageous to utilize water and nutrients from the subsoil. During a drought period in September 1987 (Fig. 1), soil water potential in the +CR + F treatment in-

creased in the 150–180 cm depth from 6.5 (62 DAP) to 35.3 (93 DAP) kPa, equivalent to a contribution of 24 mm from this horizon (Bley, 1990). The deep root system enabled pearl millet to meet its water requirement during this drought period largely from the subsoil. This can explain in part the drought tolerance of this plant species.

Although deep roots cannot contribute much to plant P uptake because P is concentrated in the topsoil, they may take up significant amounts of nutrients with high mobility in these soils, i.e. cations such as K, Ca and Mg and especially nitrate, the dominant form of N in these soils (Piéri, 1985). In 1988, approximately 50% of the N taken up between 34 and 69 DAP was derived from the 45–120 cm soil layer (Bley, 1990).

While in transient drought periods water supply and uptake of certain nutrients can be ensured from the subsoil, low water availability in the top soil may affect the nutrient uptake from this horizon, especially P uptake (Payne et al., 1991). In 1987, when 82 mm of rainfall were received during the first month after planting, P concentrations in leaves of 30-day-old millet plants were distinctly lower than in 1988, when 129 mm were received during this time (Table 2). For the rest of the season, leaf P concentrations and total P uptake remained lower in 1987 when rainfall was more erratic than in 1988 (Fig. 2). The lower P uptake was exclusively due to a decreased P influx per unit root length (Fig. 5), because root growth was not reduced in comparison to 1988 (Fig. 3). Since in a dry soil P transport to the root by diffusion can be reduced drastically (Bhadoria et al., 1991), soil P supply will be decreased in years with low and irregularly distributed rainfall. After a rainfall, due to the low water holding capacity of the sandy soils (14%; v/v) and the high evapotranspiration, the surface soil layers dry out within two or three days with a corresponding decrease in P mobility. Thus, in the acid sandy soils of the Sahel, the decrease in millet yields in years with low and irregular rainfall is presumably more related to P deficiency than to limited water supply, although pearl millet yield is also sensitive to low moisture availability, in particular during midseason (stem elongation, anthesis; Bationo and Mokwunye, 1991). At this growing stage, pearl millet has also its highest P demand (Fig. 2) so that low soil moisture will strongly increase P deficiency and, thus, additionally reduce growth.

In soils low in P, root colonization with vesicular arbuscular mycorrhizal (VAM) fungi can increase P uptake per unit root length by enhancement of the surface area resulting from hyphae growth (Li et al., 1991). Rapid root colonization is considered as an important prerequisite for an effective contribution of VAM fungi to P nutrition of the host plant (Menge, 1983). Comparisons between the development of root colonization (Fig. 4) and the time-course of P uptake (Fig. 2) show that in 1987 root colonization was still low (15–20%) when P demand of pearl millet plants was highest (i.e. 40 to 80 DAP). Towards crop maturity the colonization levels increased, but at this time P uptake of pearl millet already ceased. This pattern and the high rooting density in the top soil suggest a minor benefit of the host plants from an enlarged surface area by mycorrhizal hyphae in this dry year. This assumption is supported by the fact that total P uptake at 65 DAP was significantly correlated with total root length in 0–30 cm (Fig. 6), while inclusion of VAM-infected root length did not improve the correlation. In 1988, the colonization levels were distinctly higher already at earlier growing stages (Fig. 4) and also plant P uptake was much higher than in the preceding season (Fig. 2) despite lower root length densities (Fig. 3). Differences in moisture availability affecting for example the germination of VAM fungal spores (Daniels Hetrick, 1984) are not likely accounting for the higher colonization rates in the wetter year. In another field experiment conducted during the rainy season 1986, rainfall was similar as in 1988, but colonization rates as well as development of root colonization throughout the growing season was very similar to the dry year 1987. Since root colonization by VAM fungi can be influenced by a wide range of factors (Daniels Hetrick, 1984), the causes for the higher colonization rates in 1988 remain obscure.

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