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Long- and short-term effects of crop residues on aluminum toxicity, phosphorus availability and growth of pearl millet in an acid sandy soil*

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Key words: Al complexation, Al tolerance, crop residues, *Pennisetum glaucum*, P mobilization, soil solution

Abstract

In a long-term field experiment millet straw application (+CR) increased soil pH and base saturation and strongly improved pearl millet (*Pennisetum glaucum* L.) growth on acid sandy soils. Aluminum (Al) toxicity may be responsible for poor millet growth in plots without crop residues (–CR). Laboratory experiments were conducted to verify this assumption. The concentrations of labile Al (8-hydroxyquinoline, 15 sec) in equilibrium soil solutions of top soil samples from field plots were 14.0 and 0.6 μM in unfertilized samples of –CR and +CR soil, respectively. The corresponding values for labile Al in fertilized (NPK) samples were 51.8 and 11.0 μM , respectively. A short-term (14 days) incubation of –CR soil with ground millet straw (0.1% w/w) increased soil solution pH and decreased total and labile Al in the soil solution by more than 44%. In a water-culture experiment with increasing concentrations of Al (0–60 μM) pearl millet proved to be very Al-tolerant compared to cowpea, peanut and soybean. A short-term (12 days) pot experiment with the incubated soil showed that root growth of pearl millet is not restricted by Al toxicity in the acid soils from Niger, but that after millet straw incubation root growth is considerably enhanced. Phosphorus (P) concentration in the soil solution was about three times higher in +CR (1.75 μM) than in –CR (0.52 μM) top soil. Since P is the most growth-limiting nutrient in those soils, the beneficial effect of crop residues on pearl millet is likely due to improvement of P nutrition by both increase in P mobility in the soil and enhancement of root growth.

Introduction

Crop residues play a key role in increasing pearl millet (*Pennisetum glaucum* L.) yield and maintaining the fertility of the acid sandy soils (Psammentic Paleustalfs) of the Sahelian zone in West Africa. In long-term field experiments established in 1983 at the ICRISAT Sahelian Center (ISC, Niamey, Niger), annual removal of the crop residues (millet straw) resulted in further topsoil acidification, increase in exchangeable aluminum (Al) and a strong decrease in millet

yields on both plots with and without mineral (NPK) fertilizer (Bationo et al., 1987). It has been assumed that Al toxicity is the major responsible factor for the yield decrease. As the variability in millet growth over very short distances (microvariability) is high in this area and closely correlated with top soil acidity, Scott-Wendt et al. (1988) speculated that Al toxicity may also be the main factor causing this microvariability.

Aluminum toxicity in soil-grown plants depends on both soil solution composition and Al tolerance of the plants (Wright, 1989). According to Long et al. (1973) and Norman et al.

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(1984) pearl millet is a relatively Al-tolerant crop species. It was the objective of this study to contribute to a better understanding of the effect of crop residues on pearl millet growth in the acid sandy soils in West Africa. Therefore, (i) the Al tolerance of pearl millet was tested and compared with that of other crop species in water-culture experiments, (ii) equilibrium soil solutions were obtained and analyzed from topsoil samples of the long-term field experiment with and without crop residue application and (iii) the short-term effect of crop residues on soil solution composition and on millet growth was studied in a pot experiment.

Material and methods

Nutrient solution experiment

In nutrient solutions with increasing concentrations of Al the Al tolerance of pearl millet (*Pennisetum glaucum* L. cv. CIVT and ICMV-87902) was compared with that of soybean (*Glycine max* L. cv. Maple Arrow, Al-sensitive), peanut (*Arachis hypogaea* L. cv. 55-437) and cowpea (*Vigna unguiculata* L. cv. A18-1-1, Al-tolerant). Soybean, peanut and cowpea seeds were germinated in quartz sand and pearl millet seeds between filter paper, both moistened with 10 mM CaSO₄ solution. After germination the seedlings were transferred to a nutrient solution of the following composition (μM): 750 KNO₃, 325 Mg(NO₃)₂, 10 KH₂PO₄, 250 CaSO₄, 40 FeEDDHA, 8 H₃BO₄, 0.2 each CuSO₄, ZnSO₄, (NH₄)₆Mo₇O₂₄ and MnSO₄. Aluminum was added as AlCl₃ to give final Al concentrations of 0, 10, 30 and 60 μM . The nutrient solution was

permanently aerated and the pH kept constant at pH 4.2 (± 0.1) by automatic titration using HCl and NaOH.

The experiment was carried out with 4 replications. For each replication the seedlings of the different plant species grew together in 22-L pots (per pot 16 millet CIVT; 16 millet ICMV 87902; 3 peanut; 3 soybean; 3 cowpea). The plants were grown for 6 days under controlled climatic conditions at 30°/25°C day/night temperature, 16 h day length and 450 $\mu\text{E s}^{-1} \text{m}^{-2}$ light intensity.

After 1, 2, 3 and 6 days primary and lateral root elongation (length of longest lateral roots) was measured. After 6 days the plants were harvested, fresh and dry weight of roots and shoots was determined and roots and shoots were analyzed for Ca, Mg, K, P, Mn and Al (data not shown). Root elongation was the most sensitive parameter to demonstrate differences in Al tolerance.

Soil incubation and soil solution analysis

For the studies of long-term effects of crop residues on soil solution composition, topsoil samples (0–15 cm) were taken in 1988 from unfertilized plots of the long-term field experiment established in 1983 at the ISC in Niger (Bationo et al., 1987). In this field experiment with pearl millet as sole crop either all crop residues (excluding roots) had been removed every year (–CR) or left on the field (+CR, about 2 t ha⁻¹ year⁻¹). Some soil chemical properties are shown in Table 1.

The equilibrium soil solutions were obtained and analyzed as follows: 400 g air-dried soil were filled into plastic pots (8 × 8 × 6 cm) and adjusted to 8% (w/w) water content with distilled

Table 1. Chemical properties of top soil samples (Psammentic Paleustalf, sandy, siliceous, isohyperthermic) taken in 1988 from plots of a long-term field trial established in 1983 at the ICRISAT Sahelian Center, Niger

Soil sample	pH(H ₂ O)	pH(KCl)	P(H ₂ O) ^a (mg kg ⁻¹)	P(Bray-1) (mg kg ⁻¹)	Organic matter (%)	Exchangeable				EC _{EC} ^b
						Ca	Mg	K (meq kg ⁻¹)	Al	
–CR ^c	5.03	4.12	2.00	2.29	0.24	1.35	0.60	0.47	3.61	6.04
+CR	5.26	4.20	2.13	4.60	0.29	2.39	1.05	0.70	1.80	5.94

^a Water extraction method, soil/water ratio 1:50.

^b Effective cation exchange capacity, calculated by summation of exchangeable bases and exchangeable acidity.

^c –CR: crop residues removed annually.

+CR: crop residues left in the field.

water or fertilizer solution. The rate of fertilizer added was (in mg per kg soil) 8 mg N as NH_4NO_3 , 6 mg K as KCl and 6 mg P as superphosphate (equivalent to 24, 18 and 18 kg ha^{-1} N, P and K, respectively). The pots were sealed with a polyethylene foil (0.05 mm) and incubated for 14 days at 30°C. Subsequently the equilibrium soil solutions were obtained by centrifugation. About 70% of the total soil water could be obtained because of the coarse texture (S) of the soil samples. The soil solutions were immediately filtered through a 0.45- μm membrane (Sartorius, cellulose nitrate) and pH was measured with a glass electrode. Analyses of total and labile Al in the soil solutions were carried out using the 8-hydroxyquinoline method described by James et al. (1983). In addition, the soil solutions were analyzed for Ca, Mg, K, inorganic P (P_i), total P (P_{tot}), $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$. Calcium, Mg and K were measured with atomic absorption spectrophotometry (Hitachi 180-80) and P_i , P_{tot} , $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ colorimetrically using standard Technicon Auto-Analyzer II methods.

For the studies of short-term effects of crop residues on the soil solution composition, 400 g air-dried soil of the -CR field plots were incubated with 0.4 g (equivalent to 0.1% w/w) of ground millet straw either with or without mineral fertilizer (NPK, see above) for 14 days at 30°C and 8% (w/w) soil water content. Soil solution was collected and analyzed as described above.

Pot experiment with pearl millet

For the studies of short-term effects of crop residue amendments on growth and mineral element uptake of pearl millet a pot experiment was carried out with +CR and -CR soil from the long-term field experiment. The pots (PVC tubes, 10.5 × 30 cm) were filled with 3.5 kg air-dried soil (+CR; -CR). In addition, either 0.1 or 0.2% (w/w) of ground millet straw (containing in mg g^{-1} dry matter: 8.0 N, 0.88 P, 5.68 K, 2.90 Mg and 2.58 Ca) was mixed into the upper half of pots filled with -CR soil (-CR + STR I; -CR + STR II). All pots were watered with 280 ml fertilizer solution (per kg soil 8 mg N as NH_4NO_3 , 6 mg K as KCl and 6 mg P as superphosphate). Next, the pots were sealed with a

polyethylene foil (0.05 mm) and incubated for 14 days at 30°C.

After incubation in each pot 6 seeds of pearl millet (cv. ICMV) were planted and after 3 days the number of seedlings reduced to 3 per pot. The plants were grown for 12 days under controlled climatic conditions at 30°/25°C day/night temperature, 14 h day length and 450 $\mu\text{E s}^{-1}\text{m}^{-2}$ light intensity. At harvest shoot fresh and dry weights were determined and the root separated from the soil by careful washing. Total root length was estimated using a line intersect method (Tennant, 1975). Afterwards root dry weight was determined. For mineral element analysis shoot dry matter was ashed at 450°C overnight and ash dissolved in 1:30 (v/v) HNO_3 . Magnesium was determined by atomic absorption spectrophotometry (Hitachi 180-80), Ca and K by flame photometry (Eppendorf 700), Mn and Al by plasma emission spectrometry (SMI-Spectraspan IV) and P colorimetrically using a Vanado-Molybdate method (Gericke and Kurmies, 1952). The average nutrient uptake rates per unit root length were calculated using the method described by Brewster and Tinker (1972).

Results

Nutrient solution experiment

The effects of increasing Al concentrations in the nutrient solution on primary and lateral root elongation are shown in Fig. 1. In the three legume species lateral root elongation was a more sensitive parameter to Al toxicity than primary root elongation. Both pearl millet cultivars proved to be very Al-tolerant, especially when lateral root elongation was used as parameter. The Al tolerance decreased in the order pearl millet > cowpea > peanut > soybean.

Soil solution composition

The effects of long-term field treatments with (+CR) and without (-CR) crop residues on pH and composition of the soil solution after a 14-day incubation period is shown in Table 2. The soil solution of the +CR soil was higher in pH

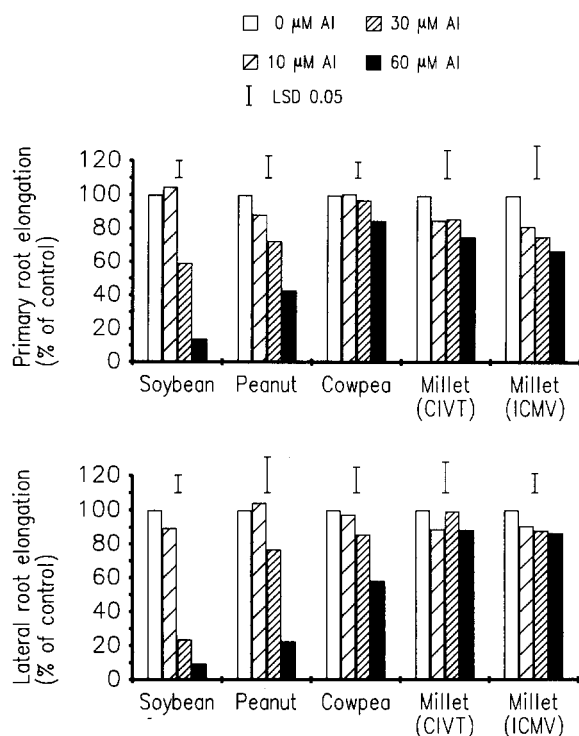


Fig. 1. Primary and lateral root elongation of soybean, peanut, cowpea and pearl millet grown for 6 days in nutrient solution with increasing Al concentrations (pH 4.2; 0.25 mM Ca). Relative values, control (0 μ M Al) = 100. LSD 0.05 calculated by Student-Newman-Keuls Test.

and the concentrations of Ca, Mg, K, $\text{NO}_3\text{-N}$ and inorganic P (P_i), and much lower in labile Al (Al_{lab}) compared to the $-\text{CR}$ soil solution. These differences are to be expected for the cations (Ca^{2+} , Mg^{2+} , K^+ , Al^{3+} , H^+) from the

effects of long-term crop residue application on soil chemical properties (Table 1). Addition of mineral fertilizer prior to soil incubation decreased soil solution pH (Table 2) and increased concentrations of Ca, Mg, K, N and particularly P_i (factor 16–17) and labile Al (factor 4–18).

In Table 2 also the effects on pH and composition of the soil solution of long-term crop residue application (+CR; $-\text{CR}$) can be compared with short-term effects of soil incubation with millet straw ($-\text{CR} + \text{STR}$). Without addition of mineral fertilizer ($-\text{NPK}$) the short-term effects of soil incubation with millet straw on soil solution pH, P_i and labile Al (Al_{lab}) were similar to the long-term effects of crop residue treatment. However, the soil solution concentrations of total Al (Al_{tot}) and of Ca, Mg, K and $\text{NO}_3\text{-N}$ were decreased by soil incubation with millet straw. The lower $\text{NO}_3\text{-N}$ concentrations likely reflect incorporation in microbial biomass, whereas the lower concentrations of Ca, Mg and K may result from an increase of the effective cation exchange capacity by straw amendment (additional cation exchange sites and pH increase).

Also in the fertilized treatments (+NPK) soil incubation with millet straw ($-\text{CR} + \text{STR}$) increased soil solution pH and decreased total Al by 44% and labile Al by 50%. Nevertheless, the Al concentrations remained at a much higher level compared to the +CR soil. The short-term effect of soil incubation with straw ($-\text{CR} + \text{STR}$) on soil solution P_i was negligible compared with the long-term effect of crop residue treatment (+CR).

Table 2. pH and soil solution composition of +CR and $-\text{CR}$ soils after 14 days of soil incubation with or without mineral fertilizer (NPK) and with or without 0.1% (w/w) ground millet straw ($-\text{CR} + \text{STR}$)

Treatment			pH	P_i	P_{tot}	Al_{lab}	Al_{tot}	Ca	Mg	K	NH_4	NO_3
Fertilizer	Soils	Straw		(μ M)				(mM)				
-NPK	+CR	-	5.69	1.75	2.28	0.6	35.1	1.98	0.75	0.92	-	6.54
	-CR	-	4.54	0.52	0.82	14.0	34.4	1.26	0.51	0.59	-	2.96
	-CR	+	6.15	1.30	4.06	0.2	10.1	0.20	0.09	0.27	-	0.52
	SE		0.18	0.21	0.58	3.1	7.2	0.14	0.07	0.16	-	0.69
+NPK	+CR	-	4.66	28.31	28.47	11.0	16.6	4.29	1.43	1.31	1.33	9.07
	-CR	-	4.10	8.96	9.42	51.8	70.7	2.83	0.56	0.85	1.31	6.25
	-CR	+	4.30	9.87	10.68	26.1	39.3	2.76	0.99	1.52	0.95	6.65
	SE		0.02	1.08	1.26	2.1	2.4	0.04	0.03	0.02	0.03	0.27

Pot experiment

The effects of long-term crop residue treatment (+CR; -CR) and of short-term soil incubation with millet straw (-CR + STR) on shoot dry weight and total root length of pearl millet are shown in Fig. 2. Millet growth during the 12-day period was not significantly different in the +CR and -CR soils, despite of the high concentration of labile Al in the -CR soil solution ($51.8 \mu\text{M}$, Table 2). Root elongation was not depressed and visual symptoms of Al toxicity (e.g. stunted roots) were absent.

Nevertheless, incubation of -CR soil with millet straw prior to planting strongly increased shoot dry weight and total root length (Fig. 2).

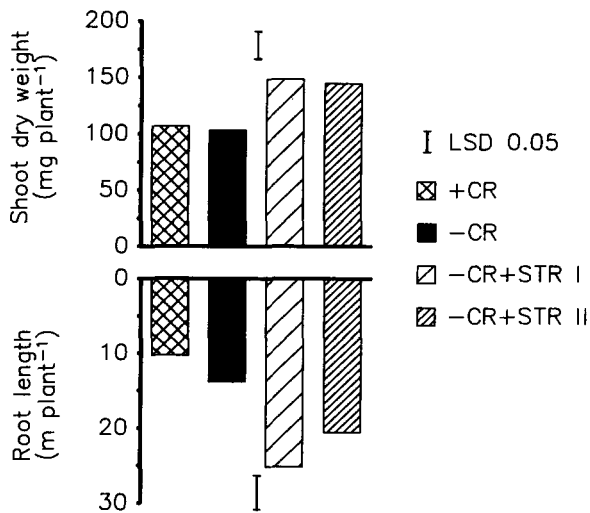


Fig. 2. Shoot dry weight and total root length of pearl millet grown for 12 days in +CR and -CR soils incubated with 0.1% or 0.2% (w/w) ground millet straw (-CR + STR I and -CR + STR II) for 14 days prior to planting. LSD 0.05 calculated by Student-Newman-Keuls Test.

This increase in root length was particularly the result of enhanced lateral root formation compared to the treatments without millet straw (Fig. 3).

The mineral element concentrations in the shoots of the 12-day-old pearl millet plants are shown in Table 3. The higher Ca and lower Al concentrations in the shoots of +CR plants compared with -CR plants were in accordance with the soil chemical properties (Table 1) and the soil solution composition (Table 2). The higher Mg and K concentrations in plants grown in soil with millet straw amendments are presumably caused by the additional Mg and K supplied with the millet straw (≈ 1.4 or 2.8 mg Mg and 2.8 or 5.6 mg K per kg soil).

Soil incubation with millet straw led to a much

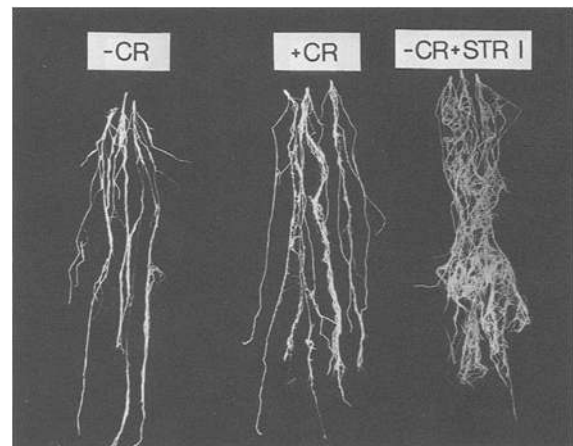


Fig. 3. Representative example of the effects of long-term soil treatment with crop residues (-CR; +CR) and of short-term soil incubation with millet straw (-CR + STR I; 0.1% w/w) on root morphology of pearl millet at harvest 12 days after planting.

Table 3. Mineral element concentrations in the shoots of 12-day-old pearl millet plants grown on +CR soil, -CR soil and -CR soil with two different amounts of millet straw amendments

Treatment		Ca	Mg	K	P	Mn	Al
Soils	Straw ^a	(mg g ⁻¹ d m)				(μg g ⁻¹ d m)	
+CR	-	8.66	2.54	37.0	3.48	640	84
-CR	-	6.54	3.09	37.9	3.57	983	183
-CR	+	5.25	3.39	45.0	3.52	889	193
-CR	++	5.29	3.75	47.9	3.34	1516	200
	SE	0.40	0.15	1.6	0.11	146	33

^a Straw amendment: - without straw amendment; + 0.1% (w/w) ground millet straw (+STR I); ++ 0.2% (w/w) ground millet straw (+STR II).

higher plant uptake of P, K, Mg and less distinctly also of Ca (Fig. 4). The higher P uptake was exclusively due to the increased root length (Fig. 2), since the average P uptake rates per unit root length were not affected by straw amendments (Fig. 5). This is in accordance with the minor effect of straw amendments on soil solution P in fertilized soil samples (Table 2).

The relationship between the average P uptake rate per unit root length of pearl millet and the P_i concentration in the soil solution is shown in Fig. 6. In the low concentration range (up to $2.5 \mu M$ P) P uptake rates per unit root length

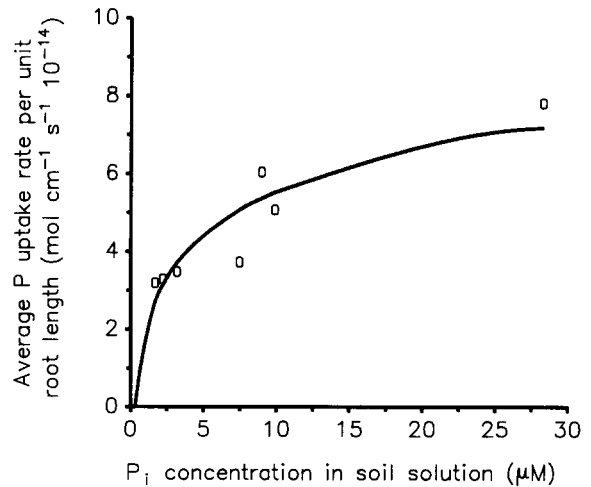


Fig. 6. Relationship between the average P uptake rate per unit root length of pearl millet and the P_i concentration in the soil solution (Psammentic Paleustalf).

increased steeply; maximum P uptake rates were achieved when the P_i concentration in the soil solution was at least $10 \mu M P_i$.

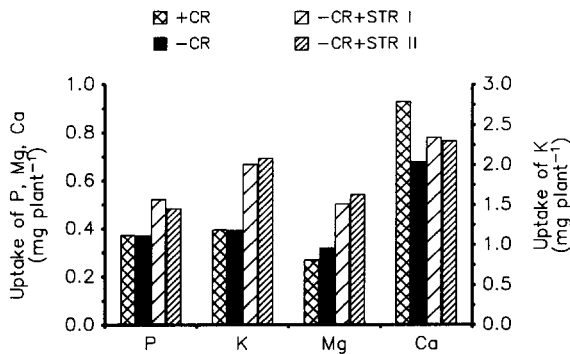


Fig. 4. Amounts of mineral nutrients in the shoots of pearl millet grown for 12 days in +CR soil, -CR soil, and -CR soil with two different amounts of millet straw amendment. All pots were incubated for 14 days at $30^\circ C$ prior to planting. -CR + STR I and -CR + STR II: 0.1% and 0.2% w/w ground millet straw mixed into the upper half of the pots.

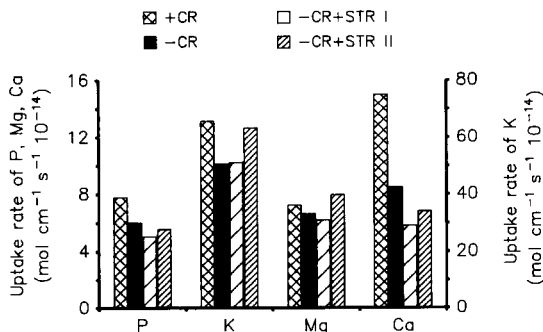


Fig. 5. Average uptake rates per unit root length of P, K, Mg and Ca in pearl millet grown for 12 days in +CR soil, -CR soil, and -CR soil with two different amounts of millet straw amendment. All pots were incubated for 14 days at $30^\circ C$ prior to planting. -CR + STR I and -CR + STR II: 0.1% and 0.2% (w/w) ground millet straw mixed into the upper half of the pots.

Discussion

The overall objective of this study was to evaluate whether Al toxicity limits pearl millet growth in an acid sandy soil (Psammentic Paleustalf) from Niger (West Africa) and whether the beneficial effect of crop residue application on growth of pearl millet (Bationo et al., 1987) is due to detoxification of Al. The increase in soil pH and percent base saturation and the decrease in exchangeable Al by long-term application of crop residues (Table 1) would support this assumption. However, Al toxicity in soils can not be reliably predicted by soil pH, exchangeable Al and percent Al saturation (Rechigl et al., 1988; Wright et al., 1989). The evaluation of potential Al toxicity by soil solution analysis is also difficult, since in soil solutions Al exists in a variety of species differing in phytotoxicity (Cameron et al., 1986; Hue et al., 1986) and analytical methods that properly distinguish between toxic and nontoxic species of Al in soil solutions are still missing (Wright, 1989). Therefore, a short-term bioassay (pot experiment) currently represents the most reliable method to

evaluate the potential Al toxicity in acid soils (Wright et al., 1989). In a short-term bioassay, both soil solution chemistry and Al tolerance of a plant species or cultivar can be taken into account simultaneously.

In water culture both pearl millet cultivars from West Africa proved to be very Al-tolerant (Fig. 1) compared with cowpea, which is known as an Al-tolerant crop species (Sanchez and Salinas, 1981). High Al tolerance of pearl millet has already been shown by Long et al. (1973) in a nutrient solution experiment and can also be assumed from its high tolerance of acid soil conditions (Norman et al., 1984). Compared to pearl millet and cowpea, the Al tolerance of peanut and particularly of soybean was much lower (Fig. 1).

Six years of crop residue application resulted in much lower concentrations of total and labile Al in the soil solution compared to the -CR soil (Table 2). Similarly, a short-term incubation of the -CR soil with 0.1% (w/w) of ground millet straw strongly decreased both total and labile Al in the soil solution (Table 2). This short-term effect of organic matter can be explained by a strong complexation of Al to the solid state organic matter, a pH increase with a subsequent precipitation of Al hydroxides, and by a complexation of Al by soluble organic ligands (Hue and Amien, 1989).

The concentration of labile Al in the -CR soil solution ($51.8 \mu\text{M}$) was similar to the highest Al concentration used in the nutrient solution experiment ($60 \mu\text{M}$). However, when comparing solution culture with soil culture it has to be considered that rhizosphere effects (e.g. root exudates, pH changes) can increase the Al tolerance of roots severalfold against a given Al concentration (Horst et al., 1990). Furthermore, in the soil solutions the Ca concentrations were much higher ($2.76\text{--}4.29 \text{ mM}$) than in the nutrient solution (0.25 mM). Since Ca has a strongly ameliorating effect on Al toxicity (Kinraide and Parker, 1987) growth inhibition of pearl millet roots by Al toxicity seems to be rather unlikely in these soils. This assumption was strongly supported by the results of the pot experiment (bioassay). Despite of the high concentrations of labile Al in the -CR soil solution (Table 2) root elongation was not depressed

(Fig. 2) and visual symptoms of Al toxicity (e.g. stunted roots) were absent (Fig. 3). Thus, the beneficial effect of crop residues on pearl millet growth under field conditions (Bationo et al., 1987) can not be explained by prevention of Al toxicity.

It seems more likely that the beneficial effect of crop residues is related to improvement of the P nutrition of pearl millet. Phosphorus is the most growth-limiting mineral nutrient for pearl millet in the acid sandy soils of the Sahelian zone. In the long-term field experiments P uptake and growth of pearl millet are much higher on +CR than on -CR field plots (Bationo et al., 1987). This is in accordance with the higher concentrations of extractable P (Table 1) and particularly the much higher P concentration in the soil solution of the +CR than in that of the -CR soil (Table 2). This indicates that long-term application of crop residues (+CR) increases solubility and thus mobility of P in these soils.

The long-term effects of crop residue application on P availability are summarized schematically in Fig. 7. Annual removal of crop residues results in further topsoil acidification, and hence an increase in percent Al saturation (Bationo et al., 1987). Since exchangeable Al strongly adsorbs P (Robarge and Corey, 1979) soil solution P is decreased considerably (Table 2). In contrast, with crop residue application topsoil acidification can be prevented and the P concentration in the soil solution kept at a higher level (Table 2). According to Fox and Kamprath (1970) the minimum P concentration required for optimal pearl millet growth (C_{opt}) is $6.45 \mu\text{M}$. In sandy soils, however, C_{opt} is much higher than in fine-textured soils due to much lower diffusion coefficients (Sanchez, 1976). In the sandy soil from Niger the P concentrations in the soil solutions were increased by long-term crop residue application from 0.52 to $1.75 \mu\text{M}$ in the unfertilized soil and from 8.96 to $28.31 \mu\text{M}$ in the fertilized soil (Table 2). In view of the steep increase in P uptake rate by pearl millet in the low-P concentration range (Fig. 6) even small variations in soil solution P concentration may cause large variations in P uptake rates and growth of pearl millet as observed in the long-term field experiment (Bationo et al., 1987).

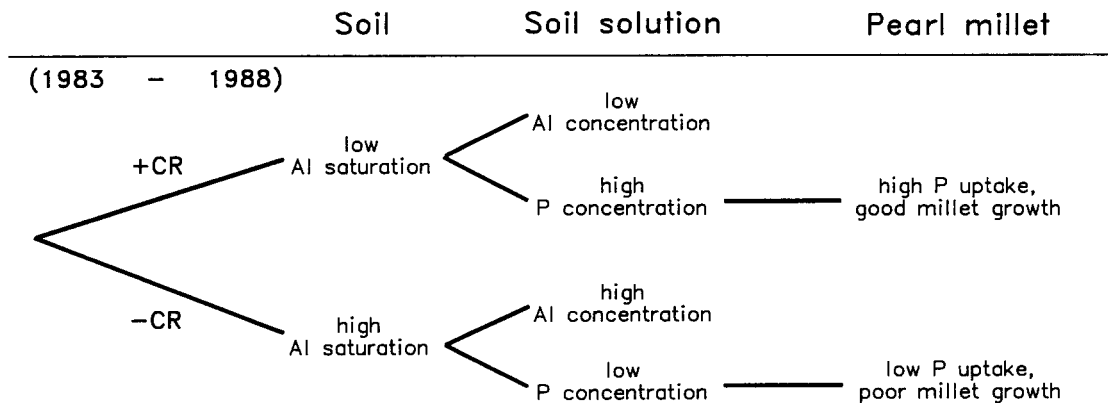


Fig. 7. Schematic presentation of the long-term effects of crop residue application on Al saturation, soil solution composition, and pearl millet growth in an acid sandy soil.

A short-term incubation of -CR soil with millet straw, however, increased the soil solution concentration of P only in non-fertilized soil samples (-NPK), whereas in fertilized soil samples (+NPK) this increase was only marginal (Table 2). Extending the duration of soil incubation from two weeks (Table 2) to six weeks gave similar results (data not shown). Millet straw incubation increased the pH and decreased the concentrations of total and labile Al in the soil solution (Table 2). A pH increase can result in a partial neutralization of exchangeable Al to hydroxy-Al species and a precipitation of amorphous Al hydroxides, and thus in the formation of highly active P adsorbing surfaces (Haynes, 1982; Robarge and Corey, 1979). Also Al complexed to soil organic matter can strongly adsorb P (Bloom, 1981). Thus, liming acid mineral soils or increasing pH by addition of organic matter not necessarily leads to a short-term mobilization of soil P (Haynes, 1982; Mokwunye, 1975).

Irrespective of the small effects of millet straw incubation on soil solution composition in the fertilized soil (Table 2), millet growth was considerably stimulated, particularly lateral root growth (Figs. 3 and 4). Tropical grasses (C₄ species), such as pearl millet, are known for their rhizosphere associations with N₂-fixing bacteria (diazotrophs), Azospirillum in particular (Martin et al., 1989). Some diazotrophs such as Azospirillum produce phytohormones (e.g. auxin) and promote lateral root development and root hair formation in a range of plant species (Martin et al., 1989) including pearl millet (Tien et al., 1979; Wani et al., 1988). Since energy supply by root exudates is often a limiting factor, additional carbon sources with a high C/N ratio (such as millet straw, C/N > 100/1) can increase the activity of diazotrophs in the rhizosphere (Alexander and Zuberer, 1988; Martin et al., 1989). This assumption is supported by data obtained in the long-term field experiment where crop-residues

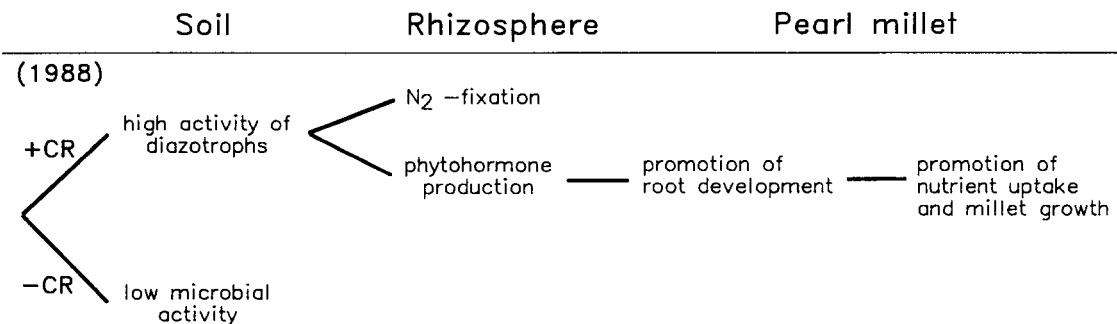


Fig. 8. Schematic presentation of the short-term effects of crop residues on lateral root formation and growth of pearl millet in an acid sandy soil.

application (4 t ha^{-1}) increased the numbers of N_2 -fixing and total bacteria in the rhizosphere soil (Hafner et al., in prep.). Therefore, it seems likely that the stimulation of root growth following soil incubation with millet straw is related to a proliferation of diazotrophic bacteria in the rhizosphere.

Such a phytohormone-induced increase in root surface area (Fig. 3) may be of crucial importance for P acquisition by pearl millet in P-deficient soils. The possible short-term effects of millet straw application on microbial activity and root growth of pearl millet are summarized in Fig. 8. A stimulating effect of crop residues on diazotrophs could also enhance N_2 -fixation (Fig. 8) and affect the long-term nitrogen balance in pearl millet-based cropping systems (Hafner et al., in prep.).

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