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The role of piscidic acid secreted by pigeonpea roots grown in an Alfisol with low-P fertility

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Abstract

In India, pigeonpea (*Cajanus cajan* (L.) Millsp.) has been traditionally grown as an intercrop, mainly with cereals such as sorghum (*Sorghum bicolor* (L.) Moench) and pearl millet (*Pennisetum americanum* (L.) Leeke) under low inputs of fertilizers. The response of pigeonpea to applied phosphorus (P) is generally low even in low-P Alfisols where a major fraction of inorganic P is in the iron-associated form (Fe-P). Pigeonpea has a special ability to take up P from low-P Alfisols on which other crops (sorghum, maize (*Zea mays* L.), soybean (*Glycine max* (L.) Merrill), and pearl millet) cannot survive. This characteristic is attributed to piscidic acid and its derivative, which is secreted from the roots of pigeonpea, but not by those of the other crop species. These substances can release P from Fe-P by chelating Fe^{3+}. From results of both the composition of mineral contents and the growth stimulated by the inoculation of VAM fungi we propose a mechanism of P acquisition by pigeonpea from an Alfisol.

Introduction

In the semi-arid tropics, the main soil types are Alfisols and Vertisols. Pigeonpea is widely intercropped with sorghum, pearl millet and other crops in these soil types in the Indian sub-continent (Aiyer, 1949). Many field experiments have shown that pigeonpea has little response to phosphorus (P) fertilizer even on Alfisols with low-P availability, compared to sorghum and pearl millet (Ae et al., 1991b; Johansen, 1990). To explain this, three possible reasons are usually given: 1) deeper root penetration, 2) association with VAM fungi, 3) special mechanisms of P uptake from insoluble P sources which are unavailable to other crop species.

As to the first reason, traditional pigeonpea genotypes have a large, deep tap root system (Sheldrake and Narayanan, 1979). It may be that pigeonpea can survive by taking up water and nutrients from deeper soil layers in the post-rainy season but cannot absorb P fertilizer nearer the surface in the dry season.

A second possible reason why pigeonpea responds less to P application than sorghum, is its dependence on vesicular-arbuscular mycorrhizal (VAM) associations that would permit better utilization of available soil P (Johansen, 1990). Most higher plant species examined have their nutrient uptake enhanced by mycorrhizal hyphae acting as an extension of the nutrient absorptive area (Mosse, 1981). But this explanation would depend on mycorrhizal fungi being more strongly associated with pigeonpea than with sorghum.

Thirdly, comparative studies by Itoh (1987) on kinetic parameters, such as maximum uptake rate (Imax) and Michaelis constant (Km), showed that they were of the same order among four crop species – soybean, chickpea (*Cicer arietinum* L.), maize and pigeonpea. He thus proposed further investigation on the development of root hairs, mycorrhizal associations and root activity to solubilize soil P. This paper further examines mechanisms of P uptake by pigeonpea from soils with low-P availability. Comparisons are made with other crop species normally grown on Alfisols and Vertisols in peninsular India.

Materials and methods

Deep-root and distribution

From ICRISAT Center (Patancheru, Andhra Pradesh, India), an Alfisol and a Vertisol with low P availability, on the basis of Olsen's bicarbonate extraction method (Olsen et al., 1954), were carefully chosen for field and pot experiments. The P status of these soils is shown in Table 1. Single superphosphate at rates of 0, 9, 18, 35, 70 kg P ha^{-1} was applied to determine the response of pigeonpea (ICPL87) and a sorghum hybrid (CSH5) to P fertilizer in the field, in both an Alfisol and a Vertisol. Nitrogen and potassium were applied as basal dressings at the rate of 100 kg N ha^{-1} as ammonium sulphate and 52 kg K ha^{-1} as potassium chloride, respectively. Only K, but not N, was applied to pigeonpea. A split plot design was used with crop species in main plots and P fertilizer treatment in sub-plots. There were three replications. Plot size was 8 × 5 m. The experiment was conducted during the 1987 rainy season.

The effect of restricted soil volume for root exploitation was examined in several crop species (pigeonpea, sorghum, maize, pearl millet, soybean, chickpea) in a pot experiment using 2.5 kg of each of the Alfisol and the Vertisol without addition of P fertilizer. Nitrogen was added at 100 mg kg^{-1} soil as ammonium sulphate and potassium at 52 mg kg^{-1} soil as potassium chloride. Plants were grown in a greenhouse and the above-ground portions harvested at the grain filling stage (for each crop). For the P analysis, dried tissues were digested with concentrated H_2SO_4 containing 0.5% selenium. Phosphorus concentrations in plant digests were then measured by the method of Murphy and Riley (1962).

Mycorrhizal association

The response of pigeonpea and sorghum to mycorrhizal inoculation was compared in a pot experiment using the same soils with low P fertility and at two levels of P application, 0 and 8.7 mg P kg^{-1} soil as single superphosphate. Nitrogen and potassium were applied as for the abovementioned experiment. Fifty gram of soil containing a mixed culture of VAM fungi (*Glomus constricum*, *G. fasciculatum*, *G. epigaerum*, *G. monosporum*, and *Acaulospora morroweae*) was used as an inoculation treatment into 2.5 kg of the sterilised potted soil. Sorghum (CSH5) and pigeonpea (ICPL87) were then sown and grown in a greenhouse until their harvest at the grain filling stage.

Better utilization of iron-associated P by pigeonpea

To compare the ability of different crop species to absorb P from different sources, a sand-vermiculite nutrient culture experiment was carried out in a greenhouse. Phosphorus was applied in the form of either $CaHPO_4$, $AlPO_4$, or $FePO_4$, to simulate the three forms of inorganic P found in soils. To 2.5 kg of the sand-vermiculite mix in pots, either $CaHPO_4$ was added at the rates of 11.3, 34, and 102 mg P kg^{-1}, $AlPO_4$ at the rates of 10.7, 32.96, mg P kg^{-1} or $FePO_4$ at the rates of 8.7, 26, and 76 mg P kg^{-1}. Nutrients other than P were applied as per Arnon (1938). Pigeonpea, maize, pearl millet, sorghum, and chickpea were grown in these pots under near-optimal environmental conditions in a greenhouse. At the flowering stage, the plants were harvested and P concentrations were measured. The solubility of these chemical forms of P in the absence of plants was measured after they were incorporated in the sand-vermiculite mix at levels of 117 mg P kg^{-1}.

Root exudates

To collect root exudates of several crop species, plants were grown in the same sand-vermiculite culture as described above, at a low P level (5 mg kg^{-1}). The roots of 2-month old plants were washed in water and then soaked in 2 m*M* $CaCl_2$ for collection of root exudates. The collected root exudates were passed through two ion-exchangers (Dowex 50 and 1) and the acid fractions were extracted from Dowex 1 resin with 6 *M* formic acid. After esterification with methyl alcohol, the acid fractions were analyzed by gas-chromatography (GC) and nuclear magnetic resonance (NMR) for identification of substances in the acid fraction of pigeonpea root exudates.

To test the ability of piscidic acid and related compounds to specifically release P from $FePO_4$, piscidic acid from *Narcissus poeticum* bulbs (Smeby et al., 1954) and derivatives of fukiic acid from *Petasites japonicus* (Yoshihara et al., 1974) were prepared. These chemical compounds were solubilized with ethylacetate to a concentration of 2.5 m*M*. One ml of this solution was mixed in a centrifuge tube with 1.0 ml suspension of 5 mg $FePO_4$ at pH 4.5 of acetate buffer. The solubilized P in the water layer was then measured colorimetrically after shaking for 30 min.

Results

Deep root distribution

In the Alfisol, most of the P is associated with iron (Fe-P), whereas in the Vertisol there is a large fraction of calcium-bound P (Ca-P) (Table 1). Responses of pigeonpea to P fertilizer were compared to those of other species in Alfisol and Vertisol fields with low P availability, as evaluated by Olsen's method. Despite the lower value of Olsen's P in the Vertisol (1.5 mg kg^{-1}) than in the Alfisol (3.5 mg kg^{-1}), grain yield of sorghum obtained in the Alfisol (87 kg ha^{-1}) was much lower than in the Vertisol (3043 kg ha^{-1}) without application of P fertilizer (Table 2). With increasing P applied, grain yield of sorghum increased in the Alfisol to a much greater extent than in the Vertisol. On the other hand, pigeonpea is comparatively less responsive to P application in the Alfisol and 929 kg ha^{-1} of grain yield was harvested in the Alfisol even where no P fertilizer was added. With this treatment, pigeonpea could take up 3.18 kg P ha^{-1}

Table 1. Some chemical characteristics of virgin soil taken from an Alfisol and a Vertisol field at ICRISAT Center, and of the type used for field and pot experiments

Soil	pH(H_2O)	Electrical conductivity (mS cm^{-1})	P fixation[a] (mg kg^{-1})	*Inorganic P* (*mg kg*$^{-1}$)			*Available P* (*mg kg*$^{-1}$)		
				Ca-P	Al-P	Fe-P	Olsen	Truog	Bray 2
Alfisol	6.9	0.05	1340	4	5	48	3.5	6.5	1.5
Vertisol	8.3	0.16	7380	58	20	55	1.5	49.2	18.1

[a] 20 mL of 2.5% ammonium phosphate was added to 10 g of soil. After 24 h, fixed P was measured from P content in the solution. (Source: Ae et al., 1991a).

Table 2. Response of grain yield (kg ha^{-1}) of pigeonpea and sorghum to phosphorus fertilizer application in an Alfisol and a Vertisol field. ICRISAT Center, rainy season, 1987

Crop	Soil	P fertilizer application (kg ha^{-1})					
		0	9	18	35	70	SE
Sorghum	Alfisol	87	673	2101	2621	3640	(727)
	Vertisol	3043	3364	3853	3697	3972	(570)
Pigeonpea	Alfisol	929	727	1113	629	678	(393)
	Vertisol	248	457	674	744	301	(128)

and sorghum 2.00 kg P ha^{-1} from the Alfisol. Phosphorus uptake by several crop species in potted Alfisol and Vertisol without P fertilizer added, under the restricted rooting volume that occurs in pots, is shown in Table 3. All of the crops, except pigeonpea, produced more dry matter and could extract more P up to the grain filling stage in the Vertisol than in the Alfisol. Without P addition, growth and P uptake of sorghum, soybean, pearl millet, and maize were severely limited on the Alfisol and these crops died as a result of P deficiency within 1 month after sowing. Phosphorus uptake by pigeonpea was the highest for all crop species tested in the Alfisol.

Mycorrhizal association

In order to determine whether VAM associations contribute to the different P response of pigeonpea compared to sorghum, in these soils, a pot experiment was conducted. Inoculation with VAM enhanced growth of pigeonpea in both soils whether P was applied or not, but it stimulated sorghum growth only on the Vertisol. On the Alfisol without P fertilizer, sorghum could not survive either with or without VAM inoculation (Table 4). VAM could enhance growth of sorghum on Alfisol when 8.7 mg kg^{-1} P fertilizer was added. Sorghum roots which had died on the Alfisol without P were colonised with VAM (infection rate: 18%) to the extent of half as much as on sorghum roots in the Vertisol (35%).

Better utilization of iron-associated P by pigeonpea

To confirm the ability of pigeonpea to solubilize Fe-P in the Alfisol with low-P fertility, a sand-vermiculite culture experiment in which P was

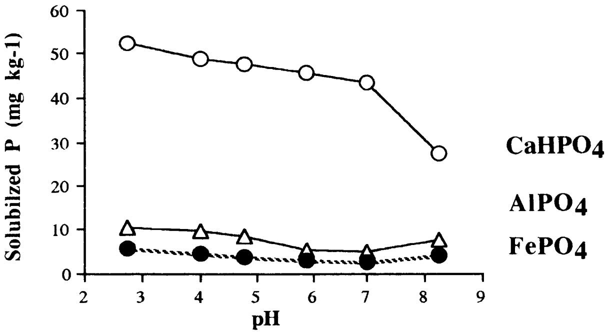


Fig. 1. Effect of pH on P released from $CaHPO_4$, $AlPO_4$ and $FePO_4$ applied in sand-vermiculite culture.

Table 3. Shoot phosphorus contents (mg per pot) of several crop species at the grain-filling stage after growth in potted Alfisol and Vertisol without phosphorus fertilizer in a greenhouse

Soil	Chickpea	Pigeonpea	Sorghum	Soybean	Pearl millet	Maize
Alfisol	4.73	5.72	0.59[a]	1.4[a]	0.64[a]	0.51[a]
Vertisol	7.79	2.34	3.91	6.53	5.38	6.13
(SE)	(0.77)	(0.82)	(0.39)	(0.20)	(0.34)	(0.25)

[a] Plants died one month after sowing.
(Source: Ae et al., 1991a).

Table 4. Effect of VAM fungi on phosphorus uptake (mg per pot) by sorghum and pigeonpea in sterilized Vertisol and Alfisol in pots. (Values are means ±SE. Three replications)

Crop	VAM inoculation	Vertisol		Alfisol	
		−P	+P[a]	−P	+P[a]
Sorghum	−	0.24 ± 0.04	14.08 ± 1.77	0.07 ± 0.03[b]	11.72 ± 4.59
	+	20.68 ± 4.52	44.84 ± 4.48	0.08 ± 0.02[b]	17.62 ± 6.39
Pigeonpea	−	0.32 ± 0.06	1.07 ± 0.08	0.26 ± 0.05	1.61 ± 0.44
	+	11.39 ± 0.54	17.50 ± 0.65	10.04 ± 1.43	15.23 ± 1.35

[a] P was applied at 8.7 mg P kg^{-1}.
[b] Plants died one month after sowing.

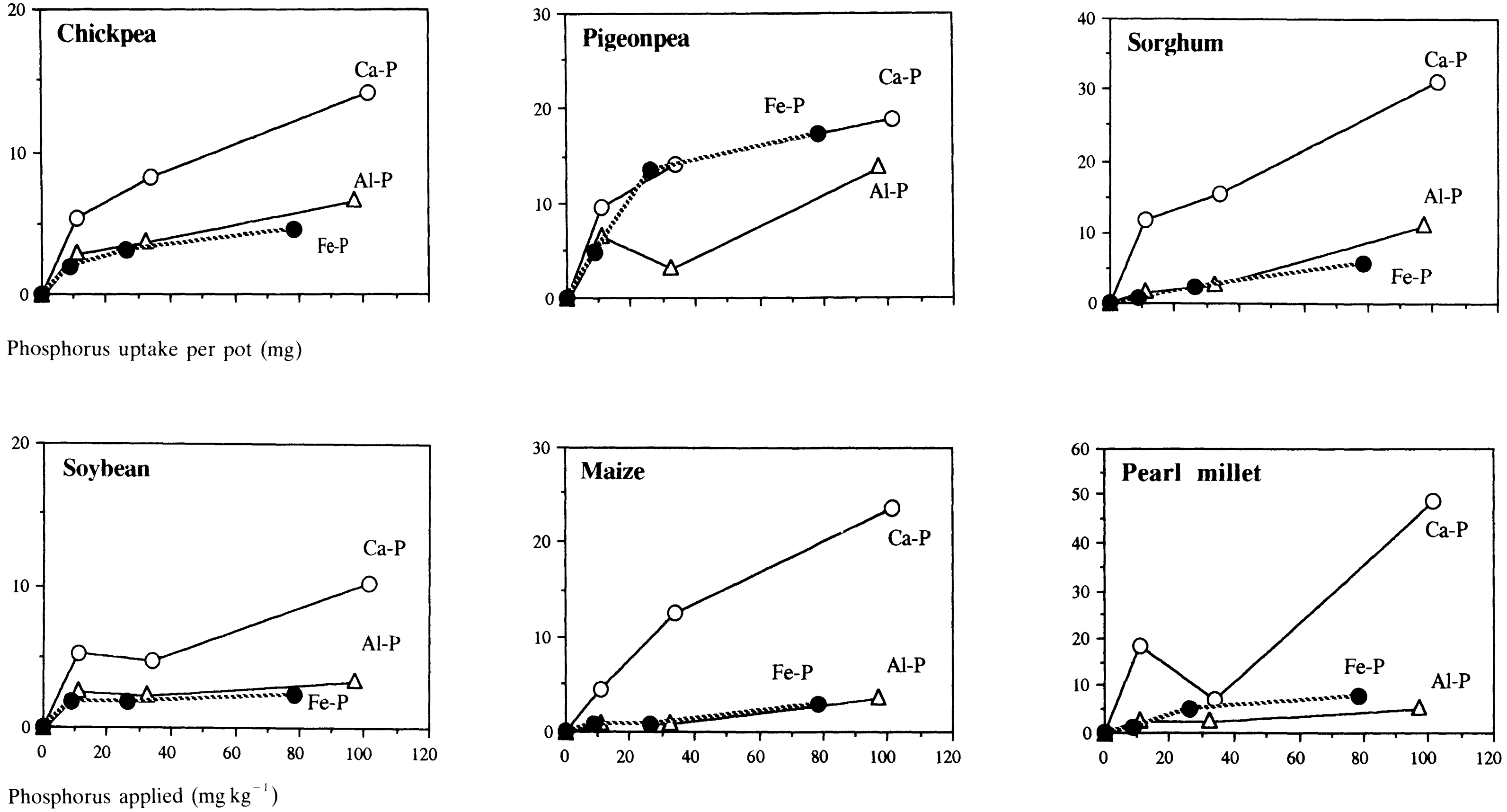


Fig. 2. Effect of P applied as different sources of phosphate (CaHPO$_4$, AlPO$_4$, and FePO$_4$) on P uptake by shoots of several crops (pigeonpea, sorghum, chickpea, maize, pearl millet, and soybean). SE = ±2.91, for comparing means (n = 3) for each crop at the same combination of P source and P level.

applied as different P sources of either $CaHPO_4$, $AlPO_4$ or $FePO_4$ was conducted. The solubility of these chemicals added to the sand-vermiculite mixture was tested at various pH levels before the pot experiment was carried out (Fig. 1). $CaHPO_4$ was the most soluble form over the pH range 3–8. For example at pH 7.0, values were 44 mg P kg^{-1} for $CaHPO_4$, 5.1 mg kg^{-1} for $AlPO_4$ and 2.9 mg kg^{-1} for $FePO_4$. All crops except pigeonpea absorbed much more P from $CaHPO_4$ than from $AlPO_4$ and P uptake from $FePO_4$ was less than from $AlPO_4$ (Fig. 2). On the other hand, pigeonpea could take up P from $FePO_4$ as well as it could from $CaHPO_4$ over the range of P levels used. Phosphorus uptake by pigeonpea from $AlPO_4$ was less than that from $FePO_4$ or $CaHPO_4$.

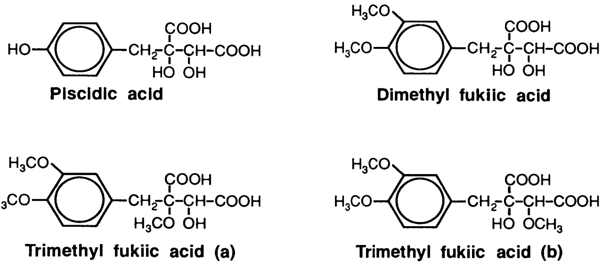
Root exudates

Root exudates were collected from pigeonpea grown on sand culture and separated into three fractions by ion-exchange resins. The acid fraction had twice as much ability to solubilize $FePO_4$ than the cationic fraction while the neutral fraction was inactive. The acid fraction from 2 month-old plants was collected and the major organic acids in each of the crops tested were analyzed (Table 5). Citric acid was the major organic acid found. Most was found in chickpea, followed by soybean, pigeonpea and sorghum in that order.

Ae et al. (1990) studied the acid fraction from the root exudates of four crop species, pigeonpea, sorghum, maize and soybean and found that (p-hydroxybenzyl) tartaric acid, named piscidic acid, and its p-methyl derivative, (p-methoxybenzyl) tartaric acid, were peculiar to pigeonpea. To test the ability of piscidic acid and related compounds (Fig. 3) to specifically release P from $FePO_4$, we prepared piscidic acid from *Narcissus poeticus* bulb (Smeby et al., 1954). Some derivatives of fukiic acid from *Petasites japonicus* (Sakamura et al., 1973) were also synthesized to investigate the chelating ability between Fe^{3+} and reactive groups, such as phenolic, alcoholic, and carboxylic groups in piscidic acid. Phosphorus released by these compounds was measured (Table 6). The P releasing ability of dimethyl fukiic acid was similar to that of piscidic acid. Trimethylfukiic acids, where an alcoholic group is replaced by a methoxyl group, are less able than piscidic acid to release P.

Table 5. Major organic acids of root exudates from sorghum, pigeonpea, soybean, and chickpea

Crop	Organic acids (mg/g-dry root)			
	Malonate	Succinate	Citrate	Malate
Sorghum	Trace	Trace	0.045	0.008
Pigeonpea	Trace	0.025	0.101	0.047
Soybean	0.324	0.046	0.481	0.078
Chickpea	Trace	0.054	1.292	0.025



Piscidic acid

Dimethyl fukiic acid

Trimethyl fukiic acid (a)

Trimethyl fukiic acid (b)

Fig. 3. Chemical structure of piscidic acid and derivatives.

Table 6. The effects of piscidic acid and its derivatives on phosphorus release from $FePO_4$

Chemical	Released P ($\mu g\, mL^{-1}$)
Control (water)	1.48
Piscidic acid	4.37
Dimethyl fukiic acid	4.44
Trimethyl fukiic acid[a]	3.27
Trimethyl fukiic acid[b]	3.23
SE[c]	±0.395

[a,b] Refer to structural formulae (a) and (b) respectively in Figure 3.

[c] 3 replicates.

Discussion

Olsen's sodium bicarbonate extraction (Olsen et al., 1954) is generally recommended for evaluating P availability of soils, especially calcareous and/or alkaline soils (Banger et al., 1979). According to Olsen's method, P availability of the Alfisol (3.5 mg P kg^{-1}) is better than that of the Vertisol (1.5 mg P kg^{-1}). When we compared P fertility on both soils with low-P fertility, better growth and P uptake of sorghum was obtained on Vertisol than on Alfisol in both field and pot experiments (Tables 2 and 3). In the Alfisol most of the inorganic P is associated with iron (Fe-P), whereas in the Vertisol there is a large fraction of calcium bound P (Ca-P). The large Ca-P fraction in Vertisols can release soluble P as a result of acidification of the rhizosphere by secretion of organic acids and H^+ from roots (Ae et al., 1991a; Moghimi and Tate, 1978) but the Fe-P fraction cannot. Therefore, Olsen's method is not appropriate to compare the soil P fertility of Alfisols and Vertisols, and an acid extraction method, such as that of Truog (1930) or Bray No. 2 (Bray and Kurts, 1945), gives a better prediction of P fertility of soils (Ae et al., 1991a). Although P availability of the Alfisol is less than that of the Vertisol according to acid extraction methods, P uptake by pigeonpea on the Alfisol was much better than that of sorghum.

The better growth of pigeonpea than sorghum on the Alfisol (Table 2) may possibly be attributed to the deep-rooting characteristic of this crop. To eliminate the effect of rooting habit of pigeonpea, a pot experiment with the same soils, in which rooting volume was restricted compared to the field experiment, was conducted using several crop species (Table 3). In pots also, the growth and P uptake of chickpea, sorghum, soybean, pearl millet, and maize is higher on the Vertisol than on the Alfisol. Without P applied, sorghum, soybean, pearl millet and maize died on the Alfisol within 1 month after sowing. However, pigeonpea could not only survive and grow on the Alfisol but could also obtain more P from that soil than from the Vertisol. This shows that pigeonpea has an ability to take up P from the Alfisol irrespective of its deep rooting habit.

As it has been reported that pigeonpea has strong mycorrhizal associations (Manjunath and Bagyaraj, 1984), it is necessary to ascertain whether VAM associations contribute to the different P responses of pigeonpea and sorghum on these soils. Growth of pigeonpea and sorghum were markedly stimulated by VAM on the Vertisol. This means that inoculated VAM fungi on sterilized soils was effective for both crops. On the Alfisol, however, only the growth of pigeonpea could be stimulated, and sorghum failed to survive with or without VAM inoculation when no P fertilizer was added. However, when 8.7 mg kg^{-1} was added on the Alfisol, sorghum could grow well on the plot without inoculation and VAM fungi enhanced the growth of sorghum to a similar level as that of pigeonpea (Table 4). These results demonstrate that VAM acts not by dissolving relatively insoluble forms of P, but by allowing more efficient uptake of P that is already in a soluble form. This mode of action has been previously described (Mosse, 1981). Therefore, the ability to solubilize Fe-P in Alfisols appears to be an inherent characteristic of pigeonpea.

The fact that pigeonpea performed better on the Alfisol than on the Vertisol, and also better than the other crops (chickpea, maize, sorghum, and pearl millet) on the Alfisol (Table 3), suggests that it is better able to access the large Fe-P fraction in the Alfisol. Generally, Fe-P is more insoluble than Ca-P or Al-P. These results presented in Figure 2 demonstrate a unique ability of pigeonpea to solubilize Fe-P. Ability to solubilize P from Al-P or Fe-P has also been claimed for other plant species, such as *Eucalyptus* spp. (Mullette et al., 1974).

Gardner et al. (1983) proposed that citric acid exuded from the roots of lupin formed high molecular-weight complexes with Fe-P, causing P to be released on reduction of Fe^{3+} to Fe^{2+} on the root surface. Mullette et al. (1974) also proposed the hypothesis that citric acid and oxalic acid from *Eucalyptus gummifera* chelated with Al^{3+} and/or Fe^{3+} to release P in infertile soils. Of the 3 fractions (cationic, anionic and neutral fraction) collected from pigeonpea roots, the anionic fraction showed the highest activity to solubilize $FePO_4$. Citric acid was the major component of root exudates of all crop species tested (Table 5). Pigeonpea exuded much less citric acid than soybean or chickpea but more than sorghum. Pigeonpea also exuded less malonate, succinate and malate than soybean. Thus the citric acid mechanism proposed by Gardner and co-workers would not explain the particular advantage shown by pigeonpea in being able to solubilize Fe-P because soybean, which exuded more citric acid than pigeonpea, could not survive on the Alfisol (Table 3).

To identify the other organic acids which are unique to pigeonpea, comparisons of gas chromatographs (GC) of the acid fraction from soybean, sorghum, maize and pigeonpea were made. The 2 peaks at 23–24 min retention time that were peculiar to pigeonpea were identified as piscidic acid ((p-hydroxybenzyl) tartaric acid) and its methyl derivative ((p-methoxybenzyl) tartaric acid) (Ae et al., 1990). Piscidic acid is one of the chemical constituents of hypnotic and narcotic drugs that have been extracted from the bark of Jamaica dogwood tree (*Piscidia erythrina* L.) (Freer and Clover, 1901; Bridge et al., 1948). However these substances have not been previously considered in relation to P acquisition ability from soils.

To test the relationship between ability to chelate with Fe^{3+} and chemical structure, piscidic acid and derivatives of fukiic acid (Yoshihara et al., 1974) were prepared (Table 6). The absolute configuration of fukiic acid is the same as that of piscidic acid (Yoshihara et al., 1974). Piscidic acid and dimethylfukiic acid have similar P releasing ability. Trimethylfukiic acids have less ability than the original piscidic acid. From the results obtained, alcoholic OH and carboxyl groups in the tartaric part of piscidic acid appear to be involved in chelation with Fe^{3+} (Ae et al., 1990).

In order to take up P from Fe-P in iron-rich soils like Alfisols, it is proposed that pigeonpea exudes piscidic acid. Therefore, it is necessary that piscidic acid-Fe^{3+} complexes be excluded from the rhizosphere because of the possibility of excess Fe uptake into roots which could result in precipitation of P in plant cells. Table 7 shows mineral element concentrations of several crop species which were grown on the Alfisol at various P levels (Ae et al., 1991a). Pigeonpea has the lowest concentration of Fe among the three legumes (chickpea, pigeonpea, and soybean) and it is also lower than in maize. The Fe/P ratio, which indicates the degree of exclusion of Fe in relation to P uptake, is also lowest for pigeonpea. As Mn is also expected to be chelated by piscidic acid, the Mn/P ratio may also be a good indicator of the exclusion ability of the piscidic acid-Mn complex. The Mn/P ratio of pigeonpea is also the lowest among the crop species tested (Table 7). Piscidic acid is a phenolic acid like p-hydroxybenzoic acid, ferulic acid, and p-coumaric acid, and these phenolic acids are considered to be toxic and contribute to 'soil sickness' (Börner 1955, 1956, 1958). It would be potentially detrimental for the piscidic acid-Fe complex to remain in the rhizosphere. The postulated mechanism involved is shown in Figure 4

Table 7. Concentrations of various elements, and Fe/P and Mn/P ratios, in shoots at the grain-filling stage of crop species grown on an Alfisol of low P status. Values are means for the P application rates of 0, 9, 22, 44, 87, mg P kg^{-1}. Standard errors are in parentheses. Date from an experiment described by Ae et al. (1991a); their Table 3

Crop	P	Ca	Mg	Zn	Fe	Cu	Mn	Ratios	
	(%)			(mg kg^{-1})				Fe/P	Mn/P
Sorghum	0.14 (0.02)	0.38 (0.07)	0.29 (0.02)	75 (13)	168 (17)	9 (1)	206 (37)	0.12	0.15
Pigeonpea	0.27 (0.03)	0.72 (0.06)	0.23 (0.01)	50 (1)	259 (15)	8 (1)	93 (6)	0.10	0.03
Chickpea	0.28 (0.04)	2.27 (0.22)	0.44 (0.02)	200 (135)	453 (35)	25 (1)	279 (28)	0.16	0.10
Soybean	0.19 (0.03)	1.09 (0.14)	0.44 (0.01)	82 (9)	410 (123)	43 (16)	269 (9)	0.22	0.14
Pearl millet	0.12 (0.03)	0.85 (0.10)	0.62 (0.05)	138 (27)	167 (23)	31 (1)	302 (31)	0.14	0.25
Maize	0.13 (0.02)	1.33 (0.25)	0.70 (0.07)	88 (16)	274 (65)	33 (7)	316 (40)	0.21	0.24

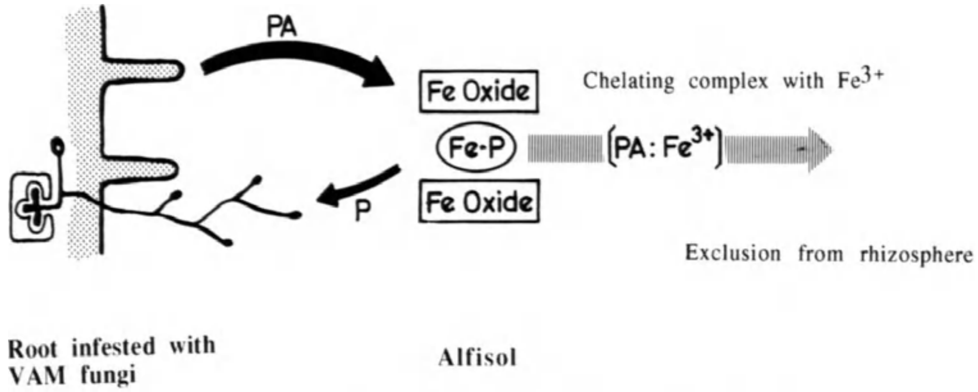


Fig. 4. Postulated P uptake mechanism in pigeonpea involving piscidic acid (PA).

and is similar to Mechanism III of Marschner (1986). It is suggested that piscidic acid, exuded from the roots of pigeonpea, releases phosphate from Fe-P compounds. This phosphate can then be taken up into the root surface or through VAM hyphae. The low Fe/P ratios in pigeonpea suggest that Fe^{3+} is excluded from the rhizosphere, we suggest as a complex with piscidic acid. However, further studies are needed to confirm this hypothesis.

References

Ae N, Arihara J and Okada K 1991a Phosphorus response of chickpea and evaluation of phosphorus availability in Indian Alfisols and Vertisols. *In* Phosphorus Nutrition of Grain Legumes in the Semi-arid Tropics. Eds. C Johansen, K K Lee and K L Sahrawat. pp 33–41. ICRISAT, Patancheru A P India.

Ae N, Arihara J and Okada K 1991b Phosphorus uptake mechanisms of pigeonpea grown in Alfisols and Vertisols. *In* Phosphorus Nutrition of Grain Legumes in the Semi-arid Tropics. Eds C Johansen, K K Lee and K L Sahrawat. pp 91–98. ICRISAT, Patanchera A P, India.

Ae N, Arihara J, Okada K, Yoshihara T and Johansen C 1990 Phosphorus uptake by pigeonpea and its role in cropping systems of Indian subcontinent. Science 248, 477–480.

Aiyer A K Y N 1949 Mixed cropping in India. Indian J. Agric. Sci. 19, 439–543.

Arnon D I 1938 Microelements in culture-solution experiments with higher plants. Am. J. Bot. 25, 322–325.

Banger A R, Mane V B and Zende G K 1979 Evaluation of soil tests at different depths and fertility levels of Vertisols. Indian J. Agric. Sci. 49, 542–549.

Börner H 1955 Untersuchungen über phenolische Verbindungen aus Getreidestroh und Getreiderückständen. Naturwissenschaften 42, 583–584.

Börner H 1956 Der papierchromatographische Nachweis von Ferulasäure in wässrigen Extrakten von Getreidestroh und Getreiderückständen. Naturwissenschaften 43, 129–130.

Börner H 1958 Untersuchungen über den Abbau von Phlorizin im Boden. Ein Beitrag zum Problem der Bodenmüdigkeit bei Obstgehölzen. Naturwissenschaften 45, 138–139.

Bray R H and Kurtz T 1945 Determination of total, organic and available forms of phosphorus in soils. Soil Sci. 59, 39–45.

Bridge W, Coleman F and Robertson A 1948 Constituents of 'Cortex pisciae erythrina'. Part 1. The structure of piscidic acid. J. Chem. Soc. 1948, 257–260.

Freer P C and Clover A M 1901 On the constituents of Jamaica dogwood. Am. Chem. J. 25, 390–413.

Gardner W K, Barber D A and Parbery D G 1983 The acquisition of phosphorus by *Lupinus albus* L. III. The probable mechanism by which phosphorus movement in the soil/root interface is enhanced. Plant and Soil 70, 107–124.

Itoh S 1987 Characteristics of phosphorus uptake of chickpea in comparison with pigeonpea, soybean, and maize. Soil Sci. Plant Nutr. 33, 417–422.

Johansen C 1990 Pigeonpea: mineral nutrition. *In* The Pigeonpea. Eds Y L Nene, Susan D Hall and V K Sheila. pp 209–231. C A B International, Wallingford, UK.

Manjunath A and Bagyaraj D J 1984 Response of pigeonpea and cowpea to phosphate and dual inoculation with vesicular-arbuscular mycorrhiza and *Rhizobium*. Trop. Agric. (Trinidad) 61, 48–52.

Marschner H 1986 Mineral Nutrition of Higher Plants. Academic Press, London, UK. 456 p.

Moghimi A and Tate M E 1978 Does 2-ketogluconate chelate calcium in the pH range 2.4 to 6.4? Soil Biol. Biochem. 10, 289–292.

Mosse B 1981 Vesicular-arbuscular mycorrhiza research for tropical agriculture. Research Bulletin, Hawaii Institute of Tropical Agriculture and Human Resources. University of Hawaii, Honolulu, HI. 82 p.

Mullette K J, Hannon N J and Elliott A G L 1974 Insoluble phosphorus usage by Eucalyptus. Plant and Soil 41, 199–205.

Murphy J and Riley J P 1962 A modified single solution method for determination of phosphate in natural waters. Anal. Chem. Acta 27, 31–36.

Olsen S R, Cole C V, Watanabe F S and Dean L A 1954 Estimation of available phosphorus in soils by extraction with sodium bicarbonate. USDA Circ. US Gov. Printing Office, Washington, DC.

Sakamura S, Yoshihara T and Toyoda K 1973 The constituents of *Petasites japonicus*: Structure of Fukiic acid and Fukinolic acid. Agric. Biol. Chem. 37, 1915–1921.

Sheldrake A R and Narayanan 1979 Growth, development and nutrient uptake in pigeonpeas (*Cajanus cajan*). J. Agric. Sci., Cambridge 92, 513–526.

Smeby R R, Zbinovsky V and Burris R H 1954 The organic acids of *Narcissius poeticua*. Am. Chem. Soc. 76, 6127–6130.

Truog E 1930 Determination of the readily available phosphorus of soils. J. Am. Soc. Agron. 22, 874–882.

Yoshihara T, Ichihara A, Nuibe H and Sakamura S 1974 The stereochemistry of fukiic acid and its correlation with piscidic acid. Agr. Biol. Chem. 38, 121–126.