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Reprint Series
27 April 1990, Volume 248, pp. 477–480

SCIENCE

Phosphorus Uptake by Pigeon Pea and Its Role in Cropping Systems of the Indian Subcontinent

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Pigeon pea was shown to be more efficient at utilizing iron-bound phosphorus (Fe-P) than several other crop species. This ability is attributed to root exudates, in particular piscidic acid and its *p*-O-methyl derivative, which release phosphorus from Fe-P by chelating Fe^{3+}. Pigeon pea is normally intercropped with cereals under low-input conditions in the Indian subcontinent. Although pigeon pea can utilize the relatively insoluble Fe-P, intercropped cereals must rely on the more soluble calcium-bound phosphorus. This finding suggests that cultivation of pigeon pea increases total phosphorus availability in cropping systems with low available phosphorus.

PHOSPHORUS IS NORMALLY THE most limiting nutrient for growth of leguminous crops in tropical and subtropical regions. This particularly applies to soils of high iron or aluminum oxide content, where P is strongly bound and largely unavailable for crop uptake. Pulses have been cultivated as protein sources under low-input agriculture for thousands of years. Among these pulses, pigeon pea [*Cajanus*

Table 1. Electrical conductivity (EC), *p*H, and P contents (in milligrams per kilogram of soil) of low-available-P Alfisol and Vertisol at the ICRISAT Center at which pot and field experiments were conducted.

Soil	EC (mS cm^{-1})	*p*H	Total P	Ca-P	Al-P	Fe-P	Olsen P (NaHCO$_3$ extraction) (*18*)
Alfisol	0.04	6.0	122	3.8	8.1	51.3	4.1
Vertisol	0.11	8.1	153	52.8	18.1	77.4	0.7

cajan (L.) Millsp.], a legume crop widely cultivated as an intercrop with cereals and other crop species in semi-arid regions, is generally observed to yield better than other crops in low-P soils even without P fertilizer application (*1*). Possible reasons for this include (i) an extensive rooting habit, (ii) strong mycorrhizal development, and (iii) the ability of pigeon pea to extract soil P normally unavailable to other crop plants. In this study, mechanisms of more efficient P uptake by pigeon pea were explored and comparisons made with other crop species. These mechanisms are discussed in relation to improving the P fertility of soils in low-input cropping systems of the Indian subcontinent.

In the semi-arid tropics, Alfisols and Vertisols are major soil types, and a representative of each with low P availability was chosen for this study (Table 1). 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). The Vertisol is not as weathered as the Alfisol, and thus its large Ca-P fraction provides a source of soluble P (*2*). Phosphorus can be solubilized from this Ca-P fraction by acidification of the rhizosphere resulting from excretion of organic acids and H^+ from roots (*3–5*).

In a field experiment, in the absence of fertilizer P application, sorghum exhibited much greater dry matter production and P uptake on the Vertisol than on the Alfisol (Table 2). However, the reverse was true for pigeon pea (Table 2). These results were confirmed in a pot experiment with the same soils under controlled conditions in a greenhouse (Table 3). 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. By contrast, pigeon pea grew better on the Alfisol than on the Vertisol. The similar results from both field and pot trials suggest that root distribution is not the reason for the differences between pigeon pea and the other crops tested. They do suggest that the better growth of pigeon pea on the Alfisol is related to its ability to utilize Fe-P, the dominant form of P in the Alfisol (see Table 1).

To confirm the ability of pigeon pea to utilize Fe-P, we conducted a sand-culture experiment in which we compared the ability of different crop species to take up P from different sources. A complete nutrient solution was applied with P in the form of either CaHPO$_4$, AlPO$_4$, or FePO$_4$, instead of the three forms of inorganic P found in soils (Ca-P, Al-P, and Fe-P). Water solubilities of these chemicals were 44 ppm for CaHPO$_4$, 5.1 ppm for AlPO$_4$, and 2.9 ppm for FePO$_4$ at *p*H 7.0 in sand-vermiculite. Figure 1 shows P uptake from these sources by several crops that were harvested just before the flowering stage. Pigeon pea can take up 2.5 to 7.0 times as much P from FePO$_4$ as the other crops at a P application of 80 ppm. This confirms that pigeon pea can solubilize P from FePO$_4$ much better than can the other crops. Phosphorus uptake by pigeon pea from CaHPO$_4$ was similar to that from FePO$_4$, over the range of P levels used. Uptake of P by pigeon pea from AlPO$_4$ was inferior to that from FePO$_4$ or CaHPO$_4$. On the other hand, the other crops absorbed much more P from CaHPO$_4$ than from AlPO$_4$ or FePO$_4$ sources. These results indicate a unique ability of pigeon pea to solubilize FePO$_4$ when compared with the other crops tested. Such a special ability to solubilize P from Al-P or Fe-P forms has also been claimed for other plant species, such as *Eucalyptus* spp. (*6*). Explanations of the mechanisms involved have not been reported.

In order to determine the extent to which vesicular arbuscular mycorrhizal (VAM) associations contribute to the different P response of pigeon pea and sorghum in these soils, we conducted a pot experiment with the same soils, which were first sterilized

Table 2. Dry matter production and P uptake of pigeon pea (cultivar ICPL 87) and sorghum (cultivar CSH 5) at the flowering stage in fields of Alfisol and Vertisol (ICRISAT Center, rain-fed but not limited by moisture stress, 1987).

Crop	Soil	P application (kg ha^{-1}) 0	17	SE*
		Dry matter production (kg ha^{-1})		
Sorghum†	Alfisol	1384	3862	588
	Vertisol	3976	6053	773
Pigeon pea‡	Alfisol	2284	4117	683
	Vertisol	2053	3268	356
		Phosphorus uptake (kg ha^{-1})		
Sorghum	Alfisol	2.00	7.38	1.19
	Vertisol	6.21	9.35	2.23
Pigeon pea	Alfisol	3.18	6.91	1.28
	Vertisol	2.46	4.04	0.69

*Standard error of difference for comparing P treatment means (n = 3) within a soil type. †Amount of N applied, 120 kg ha^{-1}. ‡No N was applied.

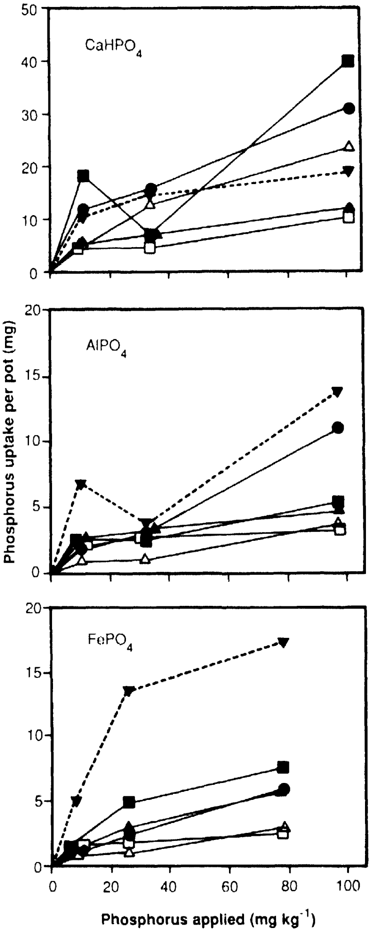

Fig. 1. Effect of P applied as different sources of phosphate (CaHPO$_4$, AlPO$_4$, and FePOP$_4$) on P uptake by various crops (▼, pigeon pea; ■, pearl millet; ▲, groundnut; ●, sorghum; △, maize; □, soybean) in a sand-culture experiment. Standard error of difference = 2.91, for comparing means (n = 3) for each crop at the same combination of source of P and P level.

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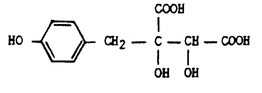
and then inoculated with VAM. VAM stimulated growth of pigeon pea in both soils, but it stimulated sorghum growth only in the Vertisol (Table 4). On the Alfisol, sorghum could not survive with or without VAM inoculation. This clearly shows that mycorrhizas act not by dissolving the relatively unavailable Fe-P but by allowing more efficient uptake of P that is already in a soluble form. This mode of action of mycorrhizas has been described (*7*).

Although exudation of H^+ and organic acids into the rhizosphere can result in dissolution of acid-soluble forms of inorganic P (*8–10*), this mainly affects Ca-P rather than the less soluble Fe-P or Al-P. Nevertheless, Gardner *et al.* (*11, 12*) proposed that citric acid exudates from the roots of lupin could complex such compounds as $FePO_4$ and then release P with reduction of Fe^{3+} to Fe^{2+} on the root surface. However, this does not explain the differential effects between pigeon pea and the other species examined here, as citric acid is a major root exudate from all species tested. For example, in root exudates collected from 2-month-old plants, pigeon pea had 0.10 mg of citrate per gram of dry root as compared to 0.48 mg g^{-1} for soybean. Similarly, pigeon pea root exudates had less malonate, malate, and succinate than those of soybean. Therefore, we searched for components distinctly different from the commonly secreted organic acids, such as citric acid.

Root exudates collected from pigeon pea were separated into three fractions by ion-exchange resin column chromatography. We tested the capacity of these fractions to solubilize $FePO_4$ by adding 20 ml of the fraction to a test tube containing 10 mg of $FePO_4$, shaking for 30 min, and then measuring P in the supernatant. The activity of the anionic fraction (solubilizing 40.8 μg of P from $FePO_4$ per pot) was much more than that of the cationic fraction (15.5 μg of P), and the neutral fraction was inactive. In gas chromatograms of the acid fraction of root exudates from soybean, sorghum, and pigeon pea (Fig. 2), there were peaks peculiar to pigeon pea at a retention time of 23 to 24 min. Subsequent gas chromatographic, mass spectrometric, and nuclear magnetic resonance analysis allowed identification of these components as (*p*-hydroxybenzyl) tartaric acid and its *p*-O-methyl derivative, (*p*-methoxybenzyl) tartaric acid. The former compound is named piscidic acid and has the following formula:



Piscidic acid has long been known as one of the constituents of hypnotic and narcotic drugs extracted from the root bark of the Jamaica dogwood tree (*Piscidia erythrina* L.) (*13, 14*). However, these substances have not been considered in relation to the P absorption ability of roots.

To test the ability of piscidic acid and related compounds to specifically release P from $FePO_4$, we prepared piscidic acid from *Narcissus poeticus* bulbs (*15*) and three derivatives of fukiic acid from *Petasites japonicus* (*16*). The absolute configuration of fukiic acid is the same as that of piscidic acid (*17*). It was also of interest to determine the relation between the ability of these compounds to chelate Fe^{3+} from $FePO_4$ and such reactive groups as phenolic-OH, alco-

Table 3. Shoot P contents (milligrams of P per pot) of crop plants at the grain-filling stage after growth in potted Alfisol or Vertisol in the greenhouse, without P addition.

Soil	Sorghum (cultivar CSH 5)	Pigeon pea (cultivar ICPL 87)	Soybean (cultivar JS 7244)	Pearl millet (cultivar WCC 75)	Maize (cultivar Deccan 103)
Alfisol	0.59*	5.72	1.40*	0.64*	0.51*
Vertisol	3.91	2.34	6.53	5.38	6.13
SE†	0.39	0.82	0.20	0.34	0.25

*Plants died 1 month after sowing. †Standard error of difference for comparing means (*n* = 3) within a crop across soil types.

Table 4. Effect of VAM inoculation on the growth of pigeon pea and sorghum. Before inoculation of VAM, soils were sterilized. Values are means ± SE, *n* = 5. Values in parentheses indicate the percentage of VAM-infested roots.

Crop	Soil	Dry matter production (g per pot)	
		−VAM	+VAM
Sorghum	Alfisol	0.10 ± 0.04 (0)	0.09 ± 0.03 (17.8 ± 4.9)
Sorghum	Vertisol	0.30 ± 0.05 (0)	16.61 ± 3.28 (34.9 ± 6.9)
Pigeon pea	Alfisol	0.36 ± 0.08 (0)	11.18 ± 1.61 (20.2 ± 2.9)
Pigeon pea	Vertisol	0.36 ± 0.08 (0)	13.46 ± 0.23 (38.4 ± 5.1)

Table 5. Effect of piscidic acid and its derivatives on P released from $FePO_4$. Piscidic acid and its derivatives were dissolved in 0.2 m*M* acetate buffer (*p*H 4.5) with 5.0 mg of $FePO_4$ per 1.0 ml of solution. The concentration of these chemicals was adjusted to 2.5 m*M*. After shaking for 30 min, the P content in the supernatant was measured.

Chemical	Formula	Released P (μg ml^{-1})
Control (water)		1.48
Piscidic acid	$HOC_6H_4CH_2C(OH)(COOH)CH(OH)COOH$	4.37
Dimethyl fukiic acid	$(H_3CO)_2C_6H_3CH_2C(OH)(COOH)CH(OH)COOH$	4.44
Trimethyl fukiic acid(a)	$(H_3CO)_2C_6H_3CH_2C(OCH_3)(COOH)CH(OH)COOH$	3.27
Trimethyl fukiic acid(b)	$(H_3CO)_2C_6H_3CH_2C(OH)(COOH)CH(OCH_3)COOH$	3.23
SE		0.40

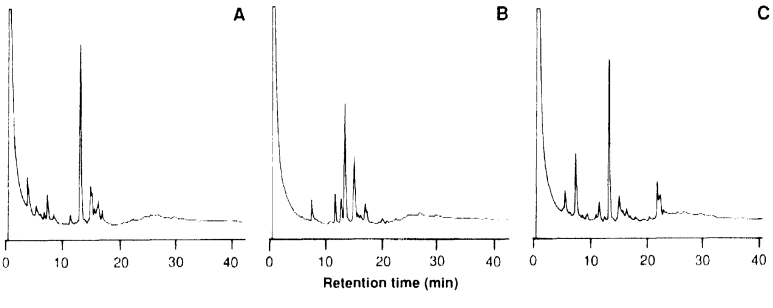


Fig. 2. Gas chromatogram of acid fraction of root exudates from (**A**) soybean, (**B**) sorghum, and (**C**) pigeon pea. Plants were grown in sand culture with 5 ppm of P as single superphosphate. Roots of 2-month-old plants were washed in water and then soaked in 2 m*M* $CaCl_2$ for collection of root exudates. Collected root exudates were eluted through an ion-exchange resin, and acid fractions obtained with 6*N* formic acid were analyzed by gas chromatography after esterification with methyl alcohol.

holic-OH, and carboxyl groups in piscidic acid and its derivatives We compared the ability of these compounds to release P from $FePO_4$ at pH 4 5, a pH to be expected in the rhizosphere The P releasing ability of dimethyl fukiic acid was similar to that of piscidic acid (Table 5) This result shows that the phenolic OH group is not related to chelation with Fe^{3} Trimethyl fukiic acids, where alcoholic OH groups are replaced by methoxyl groups, have a lesser ability than piscidic acid to release P (Table 5) Thus the interrelations between the –OH and –COOH groups of the tartaric portion are the active components, perhaps acting by chelating Fe^{3+} Further studies are required to determine the actual method of P release from an Alfisol Also the question of how much piscidic acid and its derivatives are secreted and at which stage of pigeon pea growth must be investigated

These findings imply that there are several advantages to introducing pigeon pea into low input agriculture in the tropics First pigeon pea can grow and yield well in soils of low available P level and without P fertilizer applications because of its ability to tap Fe P Second the available P pool in Alfisols and other related soils may be increased by the introduction of pigeon pea Pigeon pea can utilize occluded Fe P, which cannot be easily utilized by the other crops, as well as more soluble forms of soil P Consequently the successive crop may have access to such P from the residues or former rhizosphere soil of pigeon pea Third, pigeon pea is usually cultivated as an intercrop with companion crops such as sorghum There are indications that pigeon pea, because of its ability to utilize P from Fe P, does not unduly compete with companion crops for fertilizer P or other sources of available P such as Ca P For example, we conducted a pot experiment with a similar Alfisol (1 kg per pot) of low P availability as a model system of intercropping pigeon pea and sorghum Pigeon pea grown alone and sorghum grown alone could take up 5 18 and 4 10 mg of P per pot, respectively, from the Alfisol without P application However, 8 32 mg of P per pot (5 27 mg from pigeon pea and 3 05 mg from sorghum) was recovered from a pot in which pigeon pea and sorghum were grown together This observation indicates that there is little competition between sorghum and pigeon pea for P uptake from soil

In view of the likely increasing cost and scarcity of soluble P fertilizers, especially for resource-poor farmers in marginal environments, a search for pigeon pea genotypes or other crop species with high efficiency in the use of relatively insoluble P sources would seem a worthwhile endeavor

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19 This report has been designated as ICRISAT journal article 962 We thank T Takahashi for encouragement and help concerning this work and are grateful to the Government of Japan for funding this collaborative project at ICRISAT We also thank J M J de Wet for help in preparing this manuscript

10 October 1989 accepted 13 February 1990