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Phosphorus efficiency and the forms of soil phosphorus utilized by upland rice cultivars

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Abstract

Experimental measurements of phosphorus (P) uptake and the forms of soil P depleted from an Ultisol by 6 upland rice cultivars are reported. In both P-fertilized and -unfertilized soil, the majority of P taken up was solubilized from a 0.1 *M* NaOH-soluble pool by root-induced changes. The soil pH within 4 mm of the roots was lowered by up to 0.5 units (from 4.6), but this by itself could not account for the P solubilized, and nor could increased phosphatase activity near the roots. The possible role of root-released low molecular weight organic acid anions in P solubilization is discussed. No significant differences in the extent of solubilization by a given root mass could be detected between cultivars. In P-unfertilized soil, but not in P-fertilized soil, there were significant differences between cultivars in 'internal' P efficiency as measured by shoot dry weight per unit total plant P. In unfertilized soil, root growth and P uptake were strongly correlated with the P content of the seeds from which the plants were grown.

Introduction

Upland rice is grown as a staple food by subsistence farmers on approximately 20 million hectares in the sub-humid and humid tropics, generally on poorly fertile, strongly weathered soils to which little lime and fertilizer are applied (IRRI, 1993). One of the key constraints to food production in these conditions is P deficiency, often associated with high P fixation and severe soil acidity. Although indigenous upland rice cultivars appear well suited to these conditions, being both low-P and high-acidity tolerant relative to other cereals, repeated cropping without fertilizer addition can only be sustained by shifting cultivation and long fallow periods. A key objective for upland rice research is therefore to improve cultivar yield potentials under the prevailing conditions.

This paper examines the ability of upland rice cultivars to utilize soil and fertilizer P with a view to assessing what plant properties may be best exploited by breeders in developing more 'P-efficient' cultivars. Limited information suggests there are differences between upland rice cultivars in this respect (Fageria et al., 1988), but the mechanisms involved are not well understood.

Two types of mechanism may confer P-efficiency: (a) 'internal' mechanisms, which allow high yield per unit P in the crop, and (b) 'external' mechanisms, which allow greater P

extraction from the soil. The main external mechanisms are (reviewed in greater detail by Kirk et al., 1993):

— ability to develop long, fine, hairy roots in soil zones containing plant-available P;
— ability to solubilize soil inorganic P (P_i) through pH changes or the release of chelating agents;
— ability to utilize soil organic P (P_o) through the release of phosphate enzymes;
— ability to associate with mycorrhizal fungi. Upland rice is mycorrhizal, but mycorrhizas are generally far less important for fine-rooted crops such as upland rice than for coarse-rooted ones.

The paper considers the first three of the above and the extent to which they can explain P depletion profiles around upland rice roots.

Table 1. Characteristics of Cavinti soil

Clay (%)	70
Silt (%)	26
Sand (%)	4
pH (1:1 H_2O)	4.6
Exchangeable Al (ceq kg^{-1})[a]	8.3
Effective CEC (ceq kg^{-1})[b]	10.5
Organic C (%)	2.9
Total N (%)	0.26
Active Fe (%)[c]	2.8
Active Mn (%)[c]	0.52
pH buffer power (mol H^+ kg^{-1} pH^{-1}) at pH 3.5–5.0[d]	0.10

[a] Extracted in 1 *M* KCl.
[b] (K + Na + Ca + Mg + Al) extracted in 1 *M* KCl.
[c] Extracted in 0.02 *M* EDTA.
[d] Determined by shaking 2.0 g samples in 10 cm^3 of 0.1 *M* NaCl containing graded amounts of HCl and NaOH.

Materials and Methods

Plants were grown in soil in split 66-mm i.d. PVC cylinders (SCs) separated into upper (5-cm deep) and lower (3-cm deep) cells by 24-μm pore-diameter polyester mesh so that the roots could not penetrate the lower cell. Thereby, the lower cell could be sectioned parallel to the inter-cell boundary to obtain profiles of P depletion and other root-induced changes close to root surfaces. Four improved lines and two traditional Philippine cultivars (Azucena and Dinorado) were used, obtained from the International Rice Germplasm Center, International Rice Research Institute. The soil was an isohyperthermic palehumult from Cavinti, Laguna, Philippines, air-dried and ground to pass a 2 mm sieve (properties in Table 1).

Half of the SCs were packed with fertilized soil (at 240 μg P as MCP g^{-1}) and half with unfertilized soil to a bulk density of 0.93 kg (dry soil) dm^{-3}. They were placed on the surfaces of 16-dm^3 porcelain pots filled with silica sand and connected to water reservoirs at a lower height so as to maintain a moderate suction on the soil. Six pre-germinated seeds were planted in each SC, then thinned to four plants per SC after a few days. Each treatment was made in triplicate. Initially, a surface application of 10 cm^3 of P-free nutrient solution (Yoshida et al., 1976) was made weekly to each SC, increased to bi-weekly after the third week.

At harvest, plant shoots were cut 0.5 cm above the soil surface. The lower cell was sliced into 0.5-mm thick sections with a microtome, starting at the inter-cell boundary, and the sections stored in sealed vials at 4 °C. The soil in the upper cell was sectioned 1 cm above the inter-cell boundary and the roots gently washed from each section. Root length was measured by the grid intersection method. Shoot and root dry wt were taken and 0.1 g samples digested in H_2SO_4/H_2O_2 as described below, for P analyses.

In a preliminary experiment, made in a greenhouse (av. max/min temperatures 40/23 °C), the time courses of plant growth and soil P depletion were followed with weekly harvests. In the main experiment, made in a Phytotron (day/night temperatures 27/21 °C), cultivar differences in growth and soil P depletion were followed with a single harvest at a date determined by the results of the preliminary experiment.

Soil P fractionation

We modified an established soil P fractionation scheme (Hedley et al., 1982) to make it suitable for highly weathered Ultisols and Oxisols. The following P fractions were determined sequentially on 0.5 g samples. (1) *Resin-P*, by shaking end-over-end for 16 h at 25 °C in 30 cm^3 of

deionised water containing a strip each of anion (AER) and cation (CER) exchange resin membrane (ca 0.5 meq of exchange capacity per strip), then removing the strips and recovering P from them (Saggar et al., 1990). (2) *NaOH-P_i*, by adding 3.3 cm^3 of 1 *M* NaOH to the suspensions from step (1) (i.e. final concentration 0.1 *M* NaOH) and re-shaking as above. (3) *NaOH-P_o*, by digesting 5 cm^3 of the NaOH extract in conc. H_2SO_4 and H_2O_2 as in step (5), and subtracting *NaOH-P_i* from the digested P. (4) *H_2SO_4-P*, by adding 30 cm^3 of 0.5 *M* H_2SO_4 to the soil residue from step (2) and re-shaking as above. (5) *Residual-P*, by refluxing the soil residue from step (4) in 8 cm^3 conc. H_2SO_4 for 2 h, cooling, adding 0.5 cm^3 of H_2SO_2 and re-heating, and repeating this step until the residue remained white on further re-heating. The digests were finally diluted to 50 cm^3 with deionised water. P concentrations in all the extracts and digests were determined colorimetrically.

The fractions delineated by this procedure roughly correspond to the following soil P pools:

- Resin-P, inorganic P that is freely plant-available;
- NaOH-P_i, inorganic P associated with positively-charged oxide surfaces;
- NaOH-P_o, labile organic P;
- H_2SO_4-P, P associated with negatively-charged oxide surfaces through exchangeable cations, and P held within oxide crystals;
- Residual-P, the remainder of the occluded P and the more recalcitrant organic forms.

The modified procedure was tested on soil that had been mixed with four rates (50, 100 and 200 μg P g^{-1} soil) of MCP, moistened to 60% by wt and incubated for 4 d at 40 °C, then dried at 60 °C and sieved to <1 mm.

Soil pH and phosphatase activity

0.5 g samples of the moist soil sections were shaken end-over-end in 2.5 cm^3 of water for 1 h at 25 °C, and the suspension pHs measured. The suspensions were then stored overnight at 4 °C, after which a further 7.5 cm^3 of water was added and the temperatures allowed to re-equilibrate at 25 °C. 0.5 cm^3 of 0.05 *M* 4-nitrophenyl phosphate was then added to each tube and the tubes shaken for 30 min before quenching with 2 cm^3 of 0.5 *M* NaOH plus 1 cm^3 of 0.5 *M* $CaCl_2$ and centrifuging. The absorbances of the supernatants were measured at 420 nm. Reagent and soil colour controls were created by adding the 4-nitrophenyl phosphate after shaking the soil-water suspensions and immediately quenching. Phosphatase activities were calculated from mmol of 4-nitrophenyl released h^{-1} kg^{-1} dry soil.

Results

P fractionation of Cavinti soil

Less than 0.2 μg P g^{-1} soil was extracted from the unfertilized soil with AER in the HCO_3^- form and CER in the H^+ form (Table 2). Combinations of other AER and CER resin forms (AER with Cl^-, SO_4^{2-}, lactate or acetate; and CER with Na^+) failed to extract greater amounts of P. The major P fractions were NaOH-P_i, NaOH-P_o and residual-P.

In the MCP fertilized soils, only small percentages of the added P were recovered in the resin fraction (Table 2). At least 75% was recovered in the NaOH-P_i fraction, indicating that the added P was quickly immobilized by Fe and Al oxides. The small recovery of H_2SO_4-P (10-15%) also indicates that the fertilizer P and its acid-soluble reaction products were very short-lived in the soil.

Table 2. P fractionation of unfertilized and fertilized Cavinti soil

P fraction	P extracted from unfertilized soil (μg g^{-1})	% of added P extracted from fertilized soil		
		P added (μg g^{-1})		
		50	100	200
Resin-P	0.2 (0.1)[a]	5	5	6
NaOH-P_i	78 (3)	75	82	80
NaOH-P_o	240 (16)	6	−8	−12
H_2SO_4-P	37 (2)	15	10	11
Residual-P	373 (14)	0	5	13
Total	728 (22)	101	94	98

[a] Standard error of mean.

Plant growth and P uptake

Plant growth in the unfertilized soil was poor and plants quickly became P deficient with shoot and root P concentrations decreasing below 0.1% P (considered the deficiency threshold for rice during the tillering stage) after 2 wk (data not shown). In the P-fertilized soil, plant growth was vigorous. Shoot and root P concentrations decreased with time but mostly stayed above 0.1% P. In preliminary experiments in pots containing 1 kg of Cavinti soil, growth of all the cultivars ceased to respond to P addition at levels greater than 100 μg P g^{-1} soil (data not shown). We deduce that P did not limit growth in the P-fertilized SCs.

After 6 wk in the unfertilized soil, all the cultivars produced higher root dry wt and root %P than shoot dry wt and shoot %P (Table 3). There were no significant differences ($p = 0.05$) between cultivars in the ratios of shoot:root %P (from data in Table 3), and no significant differences in root morphology as measured by the percentages of root length in fine (< 0.015 mm radius), medium (0.015–0.35 mm) and coarse (> 0.35 mm) categories (data not shown). These percentages were 63, 28 and 9, respectively.

Plant P uptake up per SC was calculated by subtracting the quantity of seed P added to each SC from the total plant P per SC. The differences between cultivars in plant P uptake were not statistically significant. However, considering all replicates independently, there were significant differences in plant P uptake which were correlated with root dry wt (Fig. 1a). Also, seed P content (Table 4) was correlated with root dry wt (Fig. 1b) and shoot dry wt (Fig. 1c).

Addition of P to the soil produced up to a 9-fold increase in shoot dry wt and up to a 3-fold increase in root dry wt (Table 3). Shoot:root dry wt ratios averaged across all cultivars increased 2-fold and shoot:root P content ratios increased 3.5-fold. As in the unfertilized soil, differences between cultivars in plant P uptake were not statistically significant. But contrary to the results with unfertilized soil, differences in plant P uptake considering all replicates independently were not correlated with differences between seed P content and root dry wt (Fig. 1e) or shoot dry wt (Fig. 1f).

An index of plant internal P efficiency was obtained from shoot dry wt per unit total plant P. (This index is preferable to the more commonly used shoot dry wt per unit shoot P because it

Table 3. Plant growth characteristics

Cultivar	Shoot		Root		Total plant P (mg SC^{-1})	Plant P uptake (mg SC^{-1})	Internal P efficiency index[y]
	Dry wt (g SC^{-1})	% P	Dry wt (g SC^{-1})	% P			
Unfertilized soil							
CNA 5164	0.28 d	0.049 a	0.48 c	0.057 ab	0.42 b	0.19 a	0.67 bc
CNA 4097	0.39 cd	0.048 a	0.55 bc	0.055 ab	0.53 ab	0.24 a	0.77 ab
IRAT 216	0.43 bc	0.048 a	0.78 ab	0.065 ab	0.71 a	0.37 a	0.62 c
AZUCENA	0.48 bc	0.052 a	0.72 abc	0.064 ab	0.71 a	0.34 a	0.67 bc
DINORADO	0.54 ab	0.049 a	0.67 abc	0.066 a	0.71 a	0.38 a	0.75 ab
IR47686-9-2-B	0.65 a	0.041 b	0.90 a	0.054 b	0.75 a	0.31 a	0.86 a
Fertilized soil (240 μg g^{-1})							
CNA 5164	2.43 ef	0.142 d	1.51 d	0.124 c	5.32 c	5.09 b	0.46 d
CNA 4097	2.53 e	0.152 cd	1.60 d	0.106 d	5.54 c	5.25 b	0.46 d
IRAT 216	1.94 h	0.173 c	1.79 d	1.118 c	5.48 c	5.13 b	0.36 d
AZUCENA	2.14 gh	0.154 cd	1.65 d	0.118 c	5.27 c	4.90 b	0.41 d
DINORADO	2.23 fg	0.174 c	1.60 d	0.122 c	5.94 c	5.61 b	0.39 d
IR47686-9-2-B	2.15 gh	0.135 d	1.72 d	0.105 d	4.71 c	4.26 b	0.46 d

Common letters in a column indicate means are not significantly different at $p = 0.05$ by Duncan's Multiple Range Test.
[z] Total plant P–seed P.
[y] Shoot dry wt/total plant P.

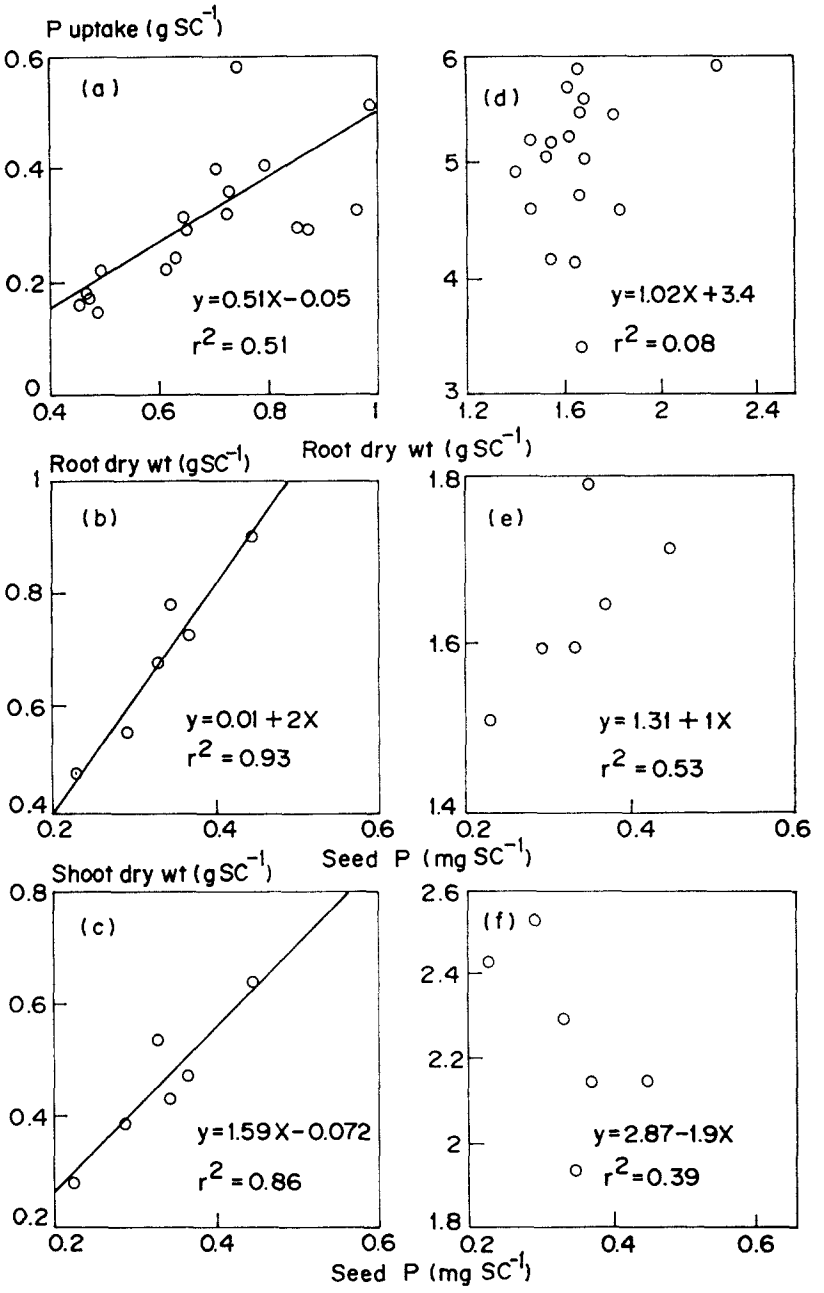

Fig. 1. Relationships between root dry wt and soil P taken up (**a** and **b** in unfertilized and fertilized soil, respectively); seed P and root dry wt (**b** and **e**); and seed P and shoot dry wt (**c** and **f**). (a) and (d) contain points for all cultivars and replicates; points in other plots are means of three replicates. Lines are included where the correlations are significant at $p = 0.05$.

allows for cultivar differences in P translocation from root to shoot). There were significant differences between cultivars in this index in unfertilized soil, IR47686-9-2-B being the most efficient and IRAT 216 the least. But there were no significant differences in the index in fertilized soil, in spite of the large differences in shoot dry wt. In all cultivars, fertilization decreased the

Table 4. Cultivar seed P contents

Cultivar	Seed P content (mg per 4 seeds or mg SC^{-1})
CNA 5164	0.230 d
CNA 4097	0.292 c
IRAT 216	0.347 bc
AZUCENA	0.368 b
DINORADO	0.331 bc
IR47686-9-2-B	0.447 a

Common letters indicate means are not significantly different at $p = 0.05$ by Duncan's Multiple Range Test.

index. In both fertilized and unfertilized soil, there were no correlations between the index and root dry wt, P uptake or seed P content.

Plant-induced changes in the soil

After 6 wk, the main P fraction depleted by all the cultivars in both unfertilized and fertilized soil was NaOH-P_i (Fig. 2). Some H_2SO_4-P was also removed from the fertilized soil. Resin-P remained negligible in both soils (data not shown). There were no statistically-significant changes in NaOH-P_o. There were no significant differences between cultivars in the forms of P taken up.

The zone of P depletion extended 3–4 mm from the root plane in the unfertilized soil, and 5–6 mm in the fertilized soil. In the unfertilized soil, the total depletion of NaOH-P_i – which contained approximately 80 μg P g^{-1} soil – was on average <6 μg P g^{-1} soil in 6 wk (soil P taken up divided by soil wt in upper cell). Fertilization raised NaOH-P_i to 270–280 μg P g^{-1} soil and the plants removed 30–60 μg P g^{-1} soil in 6 wk, i.e., 12.5–25% of the P added.

Figure 3 shows the time course of depletion of the combined Resin-P and NaOH-P_i fractions for IR47686-9-2-B in the preliminary experiment. Figures 4 and 5 show the corresponding profiles of phosphatase activity and pH. Phosphatase activities near the root plane were considerably greater than those in the bulk from 2 wk. But there were no corresponding depletions of NaOH-P_o or accumulations of P_i. There were some significant differences between cultivars in phosphatase profiles (data not shown), but they were not associated with any differences in P profiles.

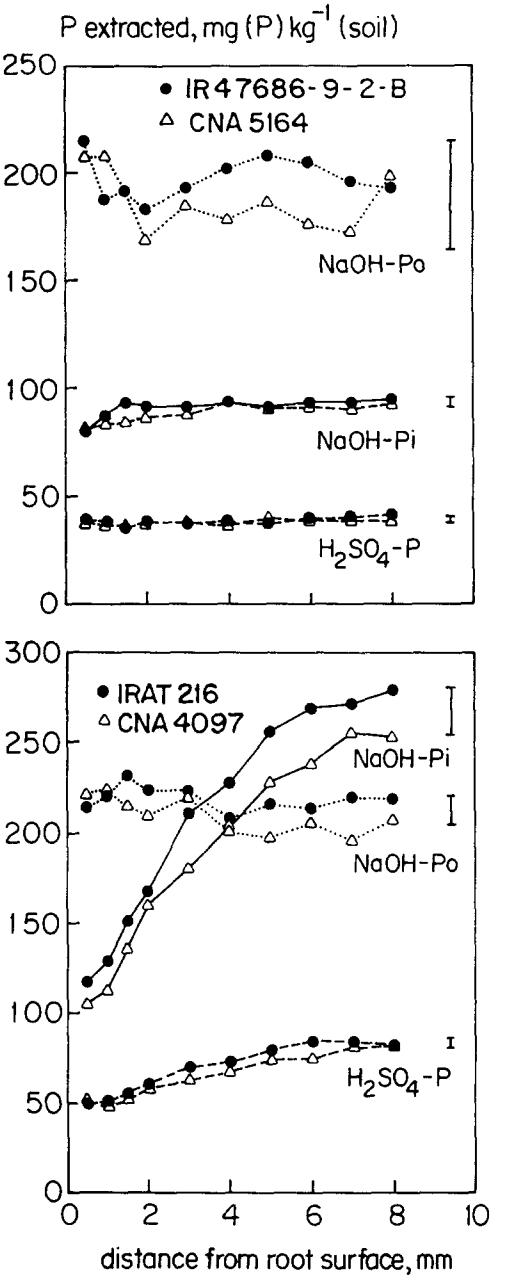

Fig. 2. Profiles of soil P fractions for different cultivars after 6 wk of growth in (**a**) unfertilized soil, IR47686-9-2-B and CNA 5164 having highest and lowest shoot dry wt, respectively; and (**b**) fertilized soil, CNA 4097 and IRAT 216 having highest and lowest shoot dry wt, respectively. Vertical bars are $LSD_{0.05}$.

pHs near the root plane were as much as 0.5

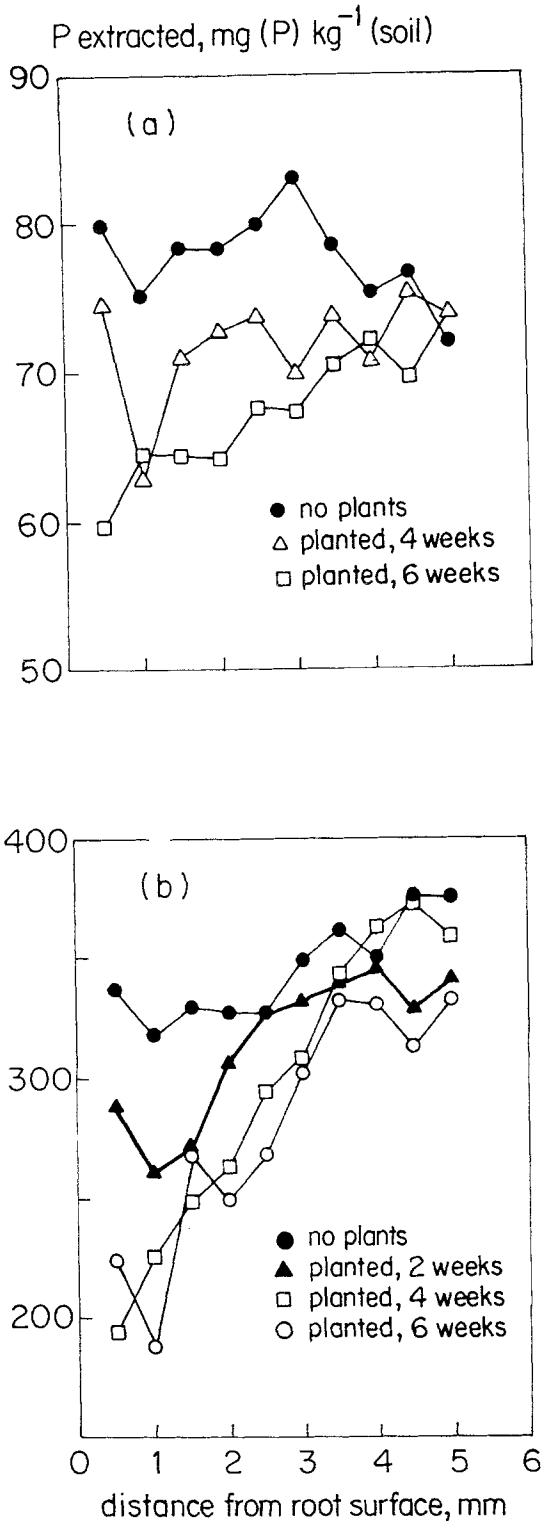

Fig. 3. Profiles of Resin-P + NaOH-P_i after different periods of IR47686-9-2-B growth in (**a**) unfertilized and (**b**) fertilized soil.

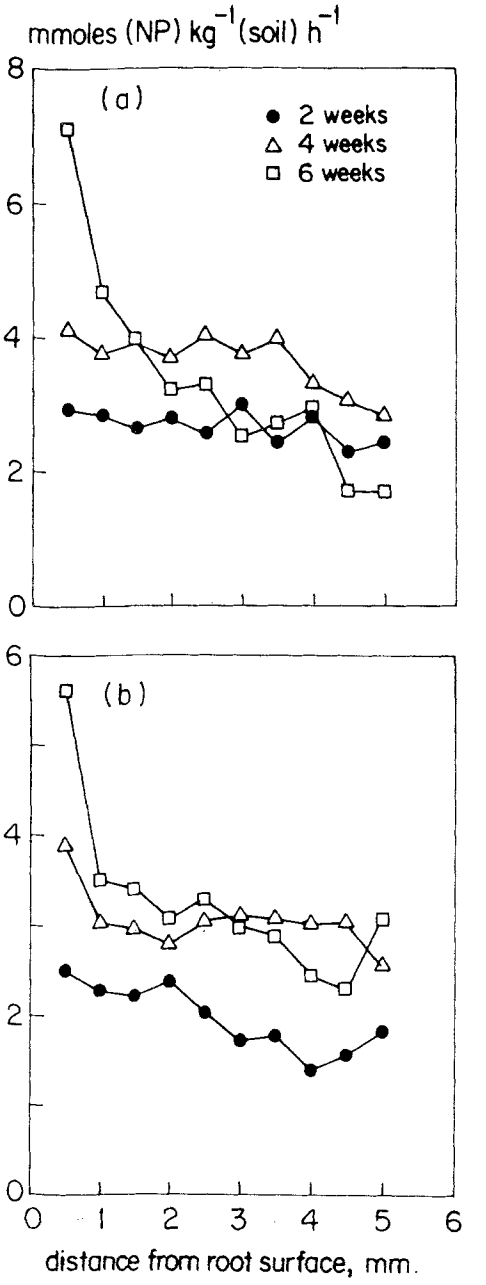

Fig. 4. Profiles of soil phosphatase activity after different periods of IR47686-9-2-B growth in (**a**) unfertilized and (**b**) fertilized soil.

units less than those in the bulk soil, and the zones of acidification extended at least as far into the soil as the zones of P depletion. The extent and spread of the acidification increased with time. There were no significant differences between cultivars in pH profiles (data not shown).

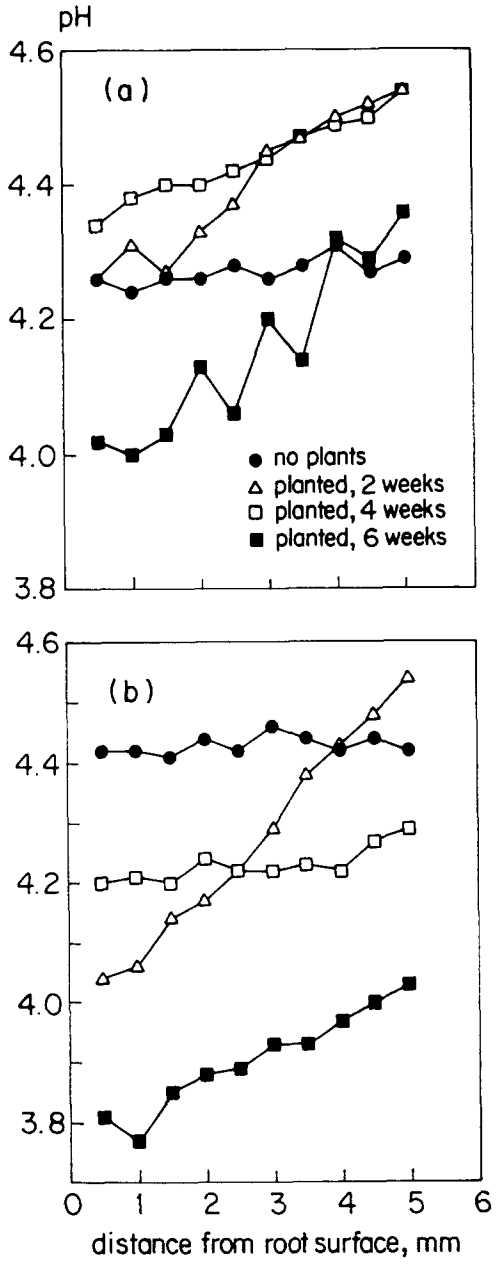

Fig. 5. Profiles of soil pH after different periods of IR47686-9-2-B growth in (**a**) unfertilized and (**b**) fertilized soil.

Discussion

The unfertilized Cavinti soil contained negligible amounts of easily exchangeable P but large amounts of insoluble NaOH-P_i, and the bulk of added P was retained in the NaOH-P_i fraction. Thus, it was necessary for the plants to induce changes in the soil so as to solubilize P from the NaOH-P_i fraction, and the ability to do this must be central to the plants' external P efficiency. This P distribution is typical of tropical Ultisols and Oxisols (Sanchez, 1976), and various authors have also reported the value of alkaline extractants as predictors of plant available P in such soils (Chang and Juo, 1963; Rubens, 1953; Saunder, 1956; Williams, 1950).

Cultivar differences in P efficiency

We could not detect differences between cultivars in their abilities to recover soil and fertilizer P, nor in the forms of soil P taken up. In the fertilized soil, the P addition was sufficient that P no longer limited growth, and under these conditions, all the cultivars apparently had similar P requirements. But all the cultivars suffered severe P deficiency in the unfertilized soil and no one cultivar proved more efficient at extracting P from the soil. Detection of cultivar differences in external efficiency was also hampered by the differences in the amounts of P taken up by cultivars being comparable to the errors of determination. Further studies are needed with modest P additions to resolve this question. The errors inherent in the measurement of soil P fractions are such that, to be statistically significant, the differences between cultivars in the forms of P extracted would have to be at least c. 6, 15 and 8% of the fraction for NaOH-P_i, NaOH-P_o and H_2SO_4-P, respectively in unfertilized soil, and 9, 7 and 9% in fertilized soil (from LSD in Fig. 2).

Although we could not detect differences between cultivars in P uptake, there were significant differences between individual replicates, 50% of which could be explained by differences in root dry wt in the unfertilized soil. The unexplained variability would include the effects of differences in the release of solubilizing agents and mycorrhizal infection. Relative differences in root dry wt were far smaller in fertilized soil, possibly because the SC volume limited further root growth, and there was no correlation between root dry wt and P uptake. All the cultivars were evidently highly efficient at extracting P associated with oxide surfaces, and they were able to recover nearly all the fertilizer P from the soil within 1-2 mm of the root plane (compare

$NaOH\text{-}P_i$ and H_2SO_4-P curves between Figs. 2a and 2b).

We found significant differences between cultivars in internal P efficiency in unfertilized soil, as measured by shoot dry wt per unit total plant P. The differences in shoot dry wt per unit shoot P (i.e. 1/shoot P conc.) were smaller suggesting that the differences in internal efficiency were in part due to differences in P translocation from root to shoot. Since there were no significant differences in the index when P was non-limiting, the differences under limiting conditions are due to differences in response to the P limitation and not to differences in response to some other factor affecting growth. Therefore they may be due to real P efficiency traits that would be manipulable through breeding. We are unable to draw any conclusions about the relation between internal and external efficiency at low P because the question of cultivar differences in external efficiency is unresolved.

In unfertilized soil, the amounts of shoot dry wt and root dry wt produced in 6 wk were strongly correlated with seed P content. Enhanced early growth from seeds of higher P content has also been found in other plant species (Bolland and Paynter, 1990, and references cited therein). High rice seed P content would therefore be advantageous in P deficient soils, allowing early root development independent of soil P supply. Seed P contents were significantly different between cultivars, but these differences may have been due to differences in agronomic husbandry during seed preparation rather than genetic differences per se. The effect of seed P content on early root growth and P uptake in moderately P-fertilized soil, and the relative roles of agronomic husbandry and genetics in determining seed P content, merit further investigation.

The mechanism of P solubilization

None of the P solubilized from the $NaOH\text{-}P_i$ fraction reappeared in other fractions within 8 mm of the root plane. Therefore, all of the P solubilized must have diffused across this zone, either towards the root plane where it was absorbed by roots, or away from it into the soil beyond 8 mm. The latter movement must be smaller because the gradient of soil solution P concentration towards the soil bulk is necessarily smaller. The spread of the solubilizing agent away for the roots, indicated by the width of the $NaOH\text{-}P_i$ depletion zones, greatly exceeds the mean inter-root distance in the upper cell ($= 1/\sqrt{\pi L_V} = 0.08 - 0.04$ cm, where L_V = root length density = 45 – 165 cm cm^{-3}, excluding those roots in the mat at the inter-cell boundary), and thus all the P solubilized would have been taken up.

We now discuss root-induced changes that may account for the observed P depletion.

(*1*) *pH changes*. The soil within 4 mm of the root plane was acidified by up to 0.5 pH units. These seemingly modest pH reductions in fact require quite large additions of acid. Using the pH buffer power of Cavinti soil (Table 1) and the degree and spread of the pH disturbance, we calculate that roughly 0.13 mmol of H^+ were produced in the unfertilized soil and 0.55 mmol in the fertilized soil.

Generally, the most important cause of rhizosphere acidification is the export of H^+ from roots to balance excess intake of cations over anions, and this balance is usually dominated by the form of N uptake up (Nye, 1986). The flux of acidity across the root plane required to produce 0.55 mmol of H^+ in 6 wk is 0.4 nmol dm^{-2} s^{-1}, which is comparable to values estimated for this process for plants taking up their N as NH_4^+ (Nye, 1986). But since the plants were fed an equal mixture of NO_3^- and NH_4^+, this is unlikely to have been the cause. Nitrification of NH_4^+ by rhizosphere microbes does not appear to be the cause either, because, although 2 mol of H^+ would be released per mol of NH_4^+ nitrified, the roots would export 2 mol of H^+ less for each mol of NO_3^- being taken up in place of NH_4^+.

An additional component of the charge balance across the root-soil interface may be the release of low molecular wt organic acid anions such as citrate and malate, so as to mobilize P (see below). These must leave the root cell cytoplasm largely in the dissociated salt form because the cytoplasmic pH (6–7) is well above the pKs of the acids in question. But they may be released in such quantity that they dominate the charge balance and consequently there is a

net release of H^+. Substantial release of citrate from upland rice roots has been reported (Liu et al., 1990), and, in the absence of other explanations, this seems a likely cause of the observed acidification.

The zone of strong acidification coincided with the zone of P depletion. However, the acidification cannot explain the observed mobilization of alkali-soluble P. In experiments in which the P-fertilized soil was shaken with graded amounts of H^+ in the presence of an anion exchange resin as a sink for solubilized P (data not shown), additions of H^+ of the magnitude calculated above produced only a negligible release of P to the exchange resin (< 0.2 μg P g^{-1} soil). Thus, an alternative or additional P-solubilizing agent must be involved.

(*2*) *Hydrolytic agents*. The P-solubilizing agent does not appear to have been phosphatase. Although phosphatase activities were increased near the root plane, and to a greater extent in the unfertilized soil, there was no corresponding depletion of organic P forms. Other authors have also found that increased phosphatase activity near root surfaces was not matched by increased organic P depletion (Kirk et al., 1993). It is possible that organic P hydrolysed by phosphatase is resynthesised into organic forms so rapidly that there is no net increase in inorganic P availability. Alternatively, since phosphatase activity is end-product inhibited (i.e., it decreases as the P concentrations increases, P being the end-product of the reaction it catalyzes (Burns, 1978)), increased phosphatase activity near a root may simply reflect a decreased P concentration in the soil solution.

(*3*) *Chelating agents*. High rates of release of P-solubilizing organic acid anions from roots in response to P deficiency have been reported for many plant species (references given in Kirk et al., 1993), including upland rice (Liu et al., 1990). Their action involves the chelation of Al and Fe in solution, resulting in dissolution of Al and Fe solid phases on which P is held. Thus they would tend to deplete the NaOH-P_i fraction. In experiments not reported here, we found that repeated extraction with citrate (90 μmol g^{-1}) was an extremely effective means of solubilizing NaOH-P_i in Cavinti soil. This mechanism will be assessed more thoroughly in a further paper.

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