Plant and Soil **251:** 83–91, 2003.

Variation in phosphorus uptake efficiency by genotypes of cowpea (*Vigna unguiculata*) due to differences in root and root hair length and induced rhizosphere processes

Gitte Krasilnikoff[1], Tara Gahoonia & Niels Erik Nielsen
Plant Nutrition and Soil Fertility Laboratory, Department of Agricultural Science, The Royal Veterinary and Agricultural University, Thorvaldsensvej 40, DK-1871 Frederiksberg C, Copenhagen, Denmark. [1]*Corresponding author**

Received 29 May 2001. Accepted in revised form 5 September 2002

Key words: cowpea, genotypic differences, model calculation, P-acquisition, P uptake rates, rhizosphere, soil volume exploited

Abstract

The lengths of roots and root hairs and the extent of root-induced processes affect phosphorus (P) uptake efficiency by plants. To assess the influence of variation in the lengths of roots and root hairs and rhizosphere processes on the efficiency of soil phosphorus (P) uptake, a pot experiment with a low-P soil and eight selected genotypes of cowpea (*Vigna unguiculata* (L) WALP) was conducted. Root length, root diameter and root hair length were measured to estimate the soil volume exploited by roots and root hairs. The total soil P was considered as a pool of Olsen-P, extractable with 0.5 M $NaHCO_3$ at pH 8.5, and a pool of non-Olsen-P. Model calculations were made to estimate P uptake originated from Olsen-P in the root hair zone and the Olsen-P moving by diffusion into the root hair cylinder and non-Olsen-P uptake. The mean uptake rate of P and the mean rate of non-Olsen-P depletion were also estimated. The genotypes differed significantly in lengths of roots and root hairs, and in P uptake, P uptake rates and growth. From 6 to 85% of total P uptake in the soil volume exploited by roots and root hairs was absorbed from the pool of non-Olsen-P. This indicates a considerable activity of root-induced rhizosphere processes. Hence the large differences show that traits for more P uptake-efficient plants exist in the tested cowpea genotypes. This opens the possibility to breed for more P uptake-efficient varieties as a way to bring more sparingly soluble soil P into cycling in crop production and obtain capitalisation of soil P reserves.

Introduction

The generally poor food situation in Africa is related to the low soil fertility of nitrogen (N) and the low soil availability of phosphorus (P). Cropping and intercropping of nitrogen-fixing legume crops are for that reason an important choice to increase the supply of high-quality protein for human need and for the improvement of the soil N status, but the low availability of soil phosphorus may limit N_2 fixation.

Cowpea is an important food, fodder and cover crop in semi-arid Africa (Padulosi and Ng, 1990). In addition, cowpea is considered less prone to drought and has a high yield potential especially when P fertilizers are applied (Mortimore et al., 1997). However, P fertilizers remain the primary limitation to legume production in the tropics (Sanchez et al., 1997). Legumes differ in their P efficiency, defined as growth and yield in low-P soils (Yan et al., 1995). In contrast, moderate applications of P fertilizer often have only marginal effect on yields due to P fixation by Fe- and Al-oxides in the soils (Sample et al., 1980). Most of the soil-P is bound in sparingly soluble P pools not immediately available to support plant growth. Improving P uptake efficiency in cowpea may then be an alternative to achieve higher yields in cowpea. If such cowpea gen-

* E-mail: gkr@kvl.dk

otype can be identified or developed by breeding the capitalisation of the soil P reserves could be enhanced.

Earlier (Nielsen and Barber, 1978; Nielsen and Shjørring, 1983; Nye and Tinker, 1977) and recent studies (de Willigen et al., 2000; Nielsen, 1993) have revealed that net P uptake per unit weight of a plant is determined by root length, uptake kinetics and the root length per unit weight of the plant, and P movement by diffusion to the root cylinder (Barber, 1995; Tinker and Nye, 2000). Low P-soil is characterised by a very low mobility of P. For that reason P has to be very close to the root cylinder in order to be bio-available (Nielsen, 1993). Root hair exploitation of the soil increases the quantity of bio-available P, because plant-available P in the root hair cylinder is very close to P-absorbing root hair cell membranes. Furthermore, root-induced processes in the soil–root interface increase the transformation of non-available soil P to plant-available soil P. These processes, e.g., changes of pH, and excretion of organic acids and/or phosphatase are very important in low P soils. The colonization by mycorrhiza may increase P uptake later in the season in annual crops. All these factors may vary among genotypes.

Legumes such as common bean (*Phaselous vulgaris* L.) and pigeonpea (*Cajanus cajan* L.) have shown genotypic differences in their ability to obtain P (Bonser et al., 1996; Subbarao et al., 1997). It appears that P-acquisition efficiency traits in common bean have been acquired during or after domestication (Beebe et al., 1997).

Due to the very low mobility of soil P in relation to plant demand, it appears reasonable to look for differences among cowpea genotypes in their volume of soil exploited by roots and root hairs. If root-induced processes differ among the genotypes, it is expected that the quantity of P absorbed by the soil volume exploited by roots and root hairs would differ. This paper reports results of such rhizosphere studies in pot experiments, where the ability of eight selected cowpea genotypes to acquire Olsen-P and non-Olsen-P was studied.

Materials and methods

Growth medium

The soil used for the experiment was a Danish sandy loam (clay 15%, silt 18%, sand 65%; Gahoonia et al., 1999), to which no P has been applied since 1966. To facilitate isolation of roots, the soil was mixed with an equal amount of purified riverbank sand. Main properties of the soil–sand mixture are given in Table 1. To facilitate nodule development and thereby fixation of nitrogen, the soil N content was reduced (<10 μg g^{-1} N in soil solution) by washing the soil. Subsequently the following fertilizers were added to the soil (kg^{-1}soil): 439 mg KH_2PO_4, 124.5 mg K_2SO_4, 124.5 mg $CaCl_2{\cdot}2H_2O$, 3.5 mg $CuSO_4{\cdot}5H_2O$, 8.8 mg $ZnSO_4{\cdot}H_2O$, 17.5 mg $MnSO_4{\cdot}H_2O$, 0.61 mg $CoSO_4{\cdot}7H_2O$, 0.32 mg $Na_2MoO_4{\cdot}H_2O$, 75 mg $MgSO_4{\cdot}7H_2O$.

Table 1. Main properties of the soil–sand mixture

Parameter	Value
Bulk density	1.4 μg mm^{-3}
Soil pH (0.01 M $CaCl_2$)	5.4
Soil CEC (pH 7)	0.53 molc kg^{-1}
Total soil C	0.5%
Total soil N	0.05%
Soil Olsen-P ($NaHCO_3$)*	10 ppm P (0.014 μg P mm^{-3})
Soil P (NaOH)*	57 ppm P (0.078 μg P mm^{-3})
Total soil P*	260 ppm P (0.357 μg P mm^{-3})

*Determined 14 days after the application of P, 10^{-3} μg mm^{-3} = ppm (μg g^{-1}) × bulk density (μg mm^{-3}).

Genotypes

Eight varieties were selected from a screening experiment performed by Sanginga et al. (2000) based on different responses to P fertilization. The seeds were provided from the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria. Some properties of the genotypes are shown in Table 5. The eight varieties can be divided into three groups of duration. IT82D-889 and IT82D-849 are 'short duration'; IT90K-59, IT82D-716 and IT86D-715 are 'intermediate duration'; and IT89KD-391, IT89KD-349 and Danila 'long duration' varieties. As IT89KD-349 and Danila are photosensitive they were transported daily to a dark chamber for 12 h. This made them flower and set pods earlier than expected.

Pot experiment

The pot experiment was conducted at The Royal Veterinary and Agriculture University, Copenhagen, in the spring (April to June) of 1999 in a green house with temperatures of (day/night) 25/18 °C, relative humidity of about 70% and 16 hours of natural daylight.

The plants were grown in 5.5 kg of air-dried soil–sand mixture filled in 4.5-L pots (bulk density of the soil of 1.4 μg mm^{-3}).

Seeds were sterilized with 10% NaClO for 1 min, washed with distilled water and pre-germinated (see Lynch et al., 1990). Pre-germinated seeds were planted (on 1 April 1999) and *Rhizobium* inoculum (commercial product Nitragen for cowpea with 100 mio viable *Rhizobium* spp. g^{-1}, LibhaTech Inc) was added at the time of planting. Five seeds were planted in each pot and after 2 weeks the seedlings were thinned to three plants per pot. Nine replicates of each of the eight varieties were randomized on a table in the greenhouse. The plants were watered every second to the third day to ensure some drying out of the soil between water applications. Four replicates of each variety were harvested after 34 days (1st harvest) and after 61 days (2nd harvest) after planting.

Sampling

Dry weight of the shoot biomass was determined after drying at 60–65 °C for minimum 48 h. Roots were washed manually just after harvest. All removable nodules were collected and weighed fresh, and after drying at 60–65 °C dry weight was determined. Roots were conserved in 15% alcohol stored at 5 °C. The nodules removed from the roots were weighed separately.

Replicate and representative root system samples (1 g fresh root) were collected from each pot. The samples were spread out in a film of water on a shallow plastic tray and scanned, using ScanJet IIcx and Dt-Scan software (Delta-T Devices, Cambridge, England) for measurement of root sample length and root diameter (Gahoonia et al., 1999). After scanning the root samples were collected in coffee filters and the dry weights were determined by drying at 60–65 °C. For calculation of the total root length (L, m) per pot, the following formula was used:

$$L = L_s(DW_r/DW_s)+L_s, \quad (1)$$

where DW_r is root dry weight of the whole pot excluding dry weight of the sample, DW_s is root dry weight of the sample and L_s is root length of the sample.

For measurement of root hair lengths, soil cores with roots of each genotype were collected at the first harvest. The soil cores were immersed in water overnight and the soil attached to roots was removed by ultrasound treatment (120 W, 47 kHz) in an ultrasound bath (Branson 5200) for a few minutes (Gahoonia and Nielsen, 1997). For each genotype the images of six roots bearing root hairs were taken, using a video camera fitted to a microscope interfaced with a computer image grabber board. Root hairs were measured using the Quantimet 500$_+$ Image Processing and Analysis System (Leica). The lengths of 30 root hairs were measured on each picture. In total, 180 root hairs in each variety were measured. The measured root hair length was assumed to represent the root hair zone providing the plants with nutrients.

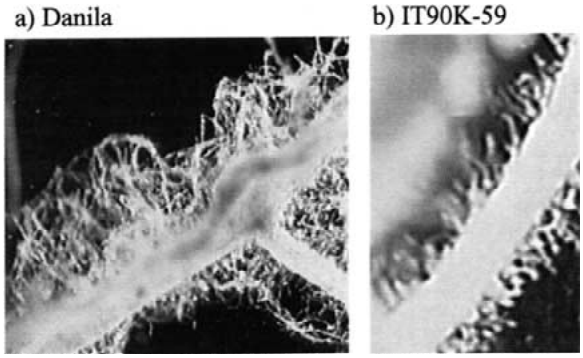

Figure 1. Root hairs after 31 days of planting: (a) Danila and (b) IT90K-59.

It appeared that the density of root hairs was high enough to exploit the entire soil volume inside the perimeter of the root hairs (Figure 1).

Analytical procedures

Soil C and N was determined by a combined elemental analyser (Carlo Erba NA1500) and mass spectrophotometer (ANA-MS method). Soil P was determined by sequential extraction, first with 0.5 *M* $NaHCO_3$ (pH 8.5) and then with 0.1 *M* NaOH (described in Gahoonia and Nielsen, 1995) a method earlier used to quantify the P available fractions in tropical soils (Manske et al., 2001; Oberson et al., 1999). Total P was released by dry ashing at 700 °C and extraction with 6 *M* HCl. The P in the extracts was determined by the colorimetric method suggested by Murphy and Riley (1960) pH was measured in 0.01 *M* $CaCl_2$.

Shoots were finely ground. Carbon and nitrogen contents were determined by mass spectrometry. One gram of the dry shoots was ashed at 500 °C for 3 h, extracted with 3 *M* HCl as mentioned above.

Model

The quantity of Olsen-P (Q_1) in the root hair zone (V) and the Olsen-P (Q_2) moving by diffusion into the root

hair zone can be considered as readily bioavailable soil-P. The quantity of non-Olsen-P ($Q_{\text{non-Olsen-P}}$) absorbed by the plants may then be estimated by:

$$Q_{\text{non-Olsen-P}} = Q_{\text{P}} - Q_1 - Q_2 \quad (2)$$

in which Q_{P} is the quantity of P absorbed by the plant (mg P per pot).

It is assumed that the whole root length (L_{61}) is active in the experimental period 6 days after planting, and that the density of root hairs is high enough to deplete the Olsen-P in the entire soil volume inside the outer perimeter of the root hairs. The volume explored is then estimated from:

$$V_{61} = \pi L_{61}(\varsigma + r_{\text{o}})^2, \quad (3)$$

$$Q_1 = 14 V_{61} \quad (4)$$

in which ς is the root hair length, r_{o} is the root radius, and L_{61} is the root length in cm per pot 61 days after planting. The 0.014 μg P mm^{-3} is the concentration of Olsen-P in the soil (Table 1). It is assumed that P depletion zones do not overlap.

The low concentration of P in the soil solution implies that P movement by mass-flow can be neglected. The P (Q_2) that diffuse through the outer perimeter of the root hair zone can then be calculated from:

$$Q_2 = \sum_{1}^{t=61} q = \pi(\text{Olsen} - \text{P}) \sum_{1}^{t=61} (\Delta L_t(\sqrt{2D_{\text{e}}(61-t)} + \varsigma + r_{\text{o}})^2 - (\varsigma + r_{\text{o}})^2) \quad (5)$$

in which q is the quantity per day and t is time varying from 1 to 61 and ΔL_t is the root length growth at day t, assuming exponential growth, e.g., $\Delta L_t = L_{t-1}e^k$ and $k = \ln(L_{61}/L_{34})/(61–34)$. The mean distance, $\sqrt{2D_{\text{e}}(61-t)}$ of diffusion to each ΔL_t was estimated from:

$$\sqrt{2D_{\text{e}}(61-t)} = \sqrt{2(61-t)D_l f\theta/b} \quad (6)$$

in which D_{e} is the diffusion coefficient of Olsen-P in the soil, $D_{\text{l}} = 0.89\ 10^{-3}$ mm^2 s^{-1} is the diffusion coefficient of $H_2PO_4^-$ in water at 25 °C, θ is the relative weight content of water in the soil, f is the impedance factor and $b = \Delta C/\Delta c$ is the differential buffer power. Equation (6) is in accordance with the theory of diffusion in soils by Tinker and Nye (2000).

The value of $\theta = 0.3$ was estimated from the average content of soil water in the pot experiment. The f = 0.304 was calculated from f = 1.58θ − 0.17 (Barraclough and Tinker, 1981). The value of $b = \Delta C/\Delta c$ = 300 was calculated from:

$$c_{\text{P in soil solution}} = 0.00334\, C_{\text{Olsen-P}} - 0.03 \text{ for } C_{\text{Olsen-P}} > 0.058\ \mu\text{g P mm}^{-3} \quad (7)$$

which was determined by Gahoonia et al. (1994) for the same soil.

The D_{e} value is then equal to $0.89\times0.3\times0.304\times10^{-2}/300$ mm^2 s^{-1} = 2.7×10^{-7} mm^2 s^{-1} which is in accordance with values given by Jungk (1996) and Gahoonia et al. (1994).

It is assumed that the root length development is exponential. The soil volume exploited will then be exponential, too. The mean volume of soil exploited ($\bar{V}$, mm^3)can then be estimated as:

$$\bar{V} = (V_{61} - V_0)/\ln(V_{61}/V_0), \quad (8)$$

where V_{61} is soil volume exploited by roots at the end of the experiment and V_0 is the estimated soil volume exploited by roots at the beginning of the experiment. The V values were obtained from Equation (3).

Calculation of uptake rates

In accordance with Williams (1948) and Engels et al. (2000) the mean uptake rate (U, 10^{-3} μg P mm^{-3} day^{-1}) per volume of soil exploited by roots was calculated from:

$$U_{\text{soil volume=}}(Q_{61}/61)/\bar{V}, \quad (9)$$

where Q_{61} is nutrient content (biomass * concentration) of P in the shoots, 61 = 61 days is the length of the experimental period, $\bar{V}$ is mean soil volume exploited by root (Equation (8)).

The calculation of root density (RD, 10^{-2} mm mm^{-3}) followed standard methods. The percentage of the soil volume within the root + root hair zone was calculated from

$$\%\text{RZ} = 100(\pi(\varsigma + r_{\text{o}})^2 * \text{RD}). \quad (10)$$

Results

Biomass production, root length, root density, root hair length, soil volume explored by roots + root hairs

and P uptake are shown in Table 2. Biomass production was significantly higher in the non-photosensitive genotypes compared to the photosensitive genotypes, IT89KD-349 and Danila.

From calculations based on Equation (2) we estimated the part of the P uptake that originated from Olsen-P and from non-Olsen P. As seen in Table 2, a widely varying part of the P uptake originated from non-Olsen-P. The uptake of this P source from the soil volume exploited by roots and root hairs varied from 1 to 35 mg pot^{-1} among the cowpea genotypes. The non-Olsen-P uptake may be considered as P mainly mobilized from more strongly bound P due to root-induced processes, e.g., acidification of the rhizosphere, exudation of organic acids, phosphatase and may be some effect of mycorrhiza colonisation.

Differences were observed among the eight genotypes in total P uptake and in the mean uptake rate per mm^3 of soil exploited by the root + root hairs (Table 2). The two photosensitive genotypes had the lowest total P uptake and biomass production, whereas the six other genotypes had a considerably higher P uptake.

To asses the variability in P uptake efficiency of the eight genotypes, soil volume exploited by roots and root hairs, mean uptake rate per mm^3 soil exploited by roots and root hairs, and mean uptake rate of P from the pool of non-Olsen-P were calculated. The values were expressed as fractions of their mean (Figure 2). Values larger than 1.0 indicate that the genotypes are above average in this character. Four genotypes (IT82D-849, IT90K-59, IT82D-716 and IT86D-715) had a relatively high total P uptake, whereas the two photosensitive genotypes had a very low relative total P uptake. Three genotypes (IT82D-716, IT86D-715 and Danila) have a relatively high soil volume exploited. Two genotypes (IT90K-59 and IT89KD-391) have a relatively high P uptake rate, and particularly the uptake rate of non Olsen-P is high. This indicates that these two cowpea genotypes do have a higher intensity of the root-induced processes releasing non-Olsen-P in the rhizosphere.

A strong correlation between N and P uptake was found (r^2=0.95, $P < 0.01$) (data not shown).

The Olsen-P in the rhizosphere soil represents only a small fraction of P uptake. The data in Table 3 show that the total P content in plants (shoots + roots and root hairs) was higher than total P (Q_{total}) in the soil volume exploited by the roots and root hairs 61 DAP, but lower than Q_{total} + Q_2 (Olsen-P diffused to the volume exploited by roots and root hairs). If assumed that non-Olsen-P was absorbed only from the volume of soil exploited by roots and root hairs, Table 3 shows that the fraction of total P absorbed varied from 6 to 85% among the cowpea genotypes. This indicated a considerable variability in the capability to dissolve and absorb non-Olsen-P.

Root morphology

Root length and root hair length, respectively, differed among the eight genotypes (Table 2). The length of the roots varied between 89 and 365 m pot^{-1} and the root hairs varied between 0.23 and 0.38 mm. Thus Danila had 27% longer hairs than IT86D-715, which had the second longest hairs. IT90K-59 and IT89KD-349 had the shortest root hairs. No significant differences in the root diameter 34 DAP (0.21 ± 0.001) were observed

Soil volume exploited by roots and root hairs (Equation (3)) is an important root parameter. As a result of the variation in root and root hair length the soil volume exploited by roots + root hairs showed also differences among the eight genotypes (Table 2). The percentage of soil per pot within the root + root hair zone is shown in Table 4. There was a large difference in soil volume within the root + root hair zone with IT82D-716, and IT86D-715 having the largest soil volume exploited (4.8%), whereas IT89KD-349 the smallest soil volume exploited (0.8%). This root parameter seems to give a useful picture of the root's access to less mobile nutrients in the soil.

Danila was a good example of the large effect it had to use soil volume exploited instead of root length. Danila had the longest root hairs and a moderate length of the root. Even so Danila exploited 4.5% of the total soil volume (Table 4). Due to the considerable variation in root length and root biomass root density varied from 0.022 to 0.091 mm mm^{-3} (Table 2). IT90K-59 and IT82D-716 showed the highest mean biomass production of roots with 1.75 g dry matter pot^{-1}, and IT89KD-349 showed the lowest mean root biomass production with 0.38 g dry matter pot^{-1}. All the genotypes formed nodules (Table 2) indicating N_2-fixation.

Discussion

Phosphorus uptake

The quantity of soil-P extracted as Olsen-P does not account for all the labile P in the soil. The non-Olsen-P fraction is therefore not entirely non-labile, strongly

Table 2. Biomass of cowpea, root length, root hair length, mean root density, volume of soil within the root + root hair zone (Equation (3)), quantity of Olsen-P within the root + root hair zone, Q_1 (Equation (4)), estimated quantity of Olsen-P diffusing into the root hair cylinder, Q_2 (Equation (5)) and plant uptake of non-Olsen-P (Equation (1)) 61 days after planting, mean uptake rate (Equation (9)) and mean rate of non-Olsen P depletion

	IT82D-889	IT82D-849	IT90K-59	IT82D-716	IT86D-715	IT89KD-391	IT89KD-349	Danila±
Biomass stem & leaves (g pot^{-1})	14±1.0	22±0.4	19±1.5	21±1.3	22±0.7	22±2.0	3.9±0.2	6.8±0.5
Biomass pods (g pot^{-1})	6.5±0.9	3.7±1.2	0.00	0.11±0	0.54±0.1	0.24±0	3.9±0.2	3.2±0.7
Biomass roots (g pot^{-1})	0.9±0.1	1.2±0.2	1.8±0.1	1.8±0.1	1.5±0.3	1.5±0.4	0.3±0.04	0.6±0.1
Biomass nodules (g pot^{-1})	0.5±0.2	0.6±0.2	0.6±0.1	0.5±0.3	0.4±0.04	0.6±0.2	0.08±0.01	0.1±0.02
Root length, L_{34} (m)	111±26	135±1	984±8	101±8	105±17	100±11	46±6	81±21
Root length, L_{61} (m)	212±18	290±25	331±32	365±38	368±54	317±53	89±6	237±50
Root density (10^{-2} mm mm^{-3})*	5.3±1.3	7.2±1.7	8.3±2.2	9.1±2.7	9.2±3.8	7.9±2.7	2.2±0.4	5.9±3.5
Root hair length (mm)*	0.29±0.01	0.28±0.01	0.23±0.01	0.30±0.01	0.30±0.1	0.28±0.01	0.23±0.01	0.38±0.02
Soil volume explored (10^3 mm^3 pot^{-1})*	104±12	135 16	117 18	188±27	189±37	148±26	31±3	175±41
Q_1 (mg pot^{-1})	1	2	2	3	3	2	0.43	
Q_2 (mg pot^{-1})	22	27	20	26	27	23	8.6	20
Non-Olsen-P (mg pot^{-1})	23	32	34	31	23	35	8	1
Total (shoot) P uptake (mg pot^{-1})	46	61	56	60	53	60	17	24
Mean P uptake rates** (10^{-3} μg P mm^{-3} day^{-1})	11	13	21	14	12	16	14	5
Mean rate of non-Olsen-P Depletion (10^{-3} μg P mm^{-3} day^{-1})	6	7	13	7	5	9	6	0.2

*61 days after planting; **during 61 days.

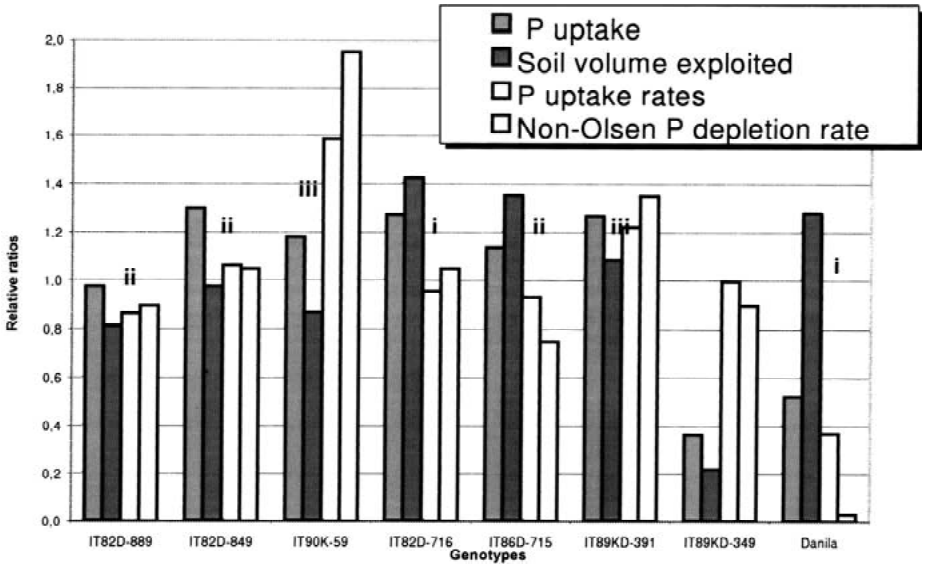

Figure 2. Total P uptake 61 DAP, soil volume exploited 61 DAP, uptake rate of P and the rate of non-Olsen-P depletion per unit soil volume exploited by roots + root hairs as a fraction the means of the eight genotypes.

Table 3. P content in shoots (Q_p), total soil P (Q_{total}) within the soil volume exploited by roots and root hairs, Olsen-P moved by diffusion to the volume exploited by roots and root hairs (Q_2, Equation (5), and estimated percentage of total P absorbed from the volume exploited by roots and root hairs 61 DAP

	IT82D-889	IT82D-849	IT90K-59	IT82D-716	IT86D-715	IT89KD-391	IT89KD-349	Danila
Total P in shoot (mg P pot^{-1})	45.8±0.9	61.1±4.8	55.5±4.2	59.8±2.4	53.4±2.2	59.6±8.1	16.9±1.4	24.4±0.9
Total P in roots + hair zone, Q_{total} (mg P pot^{-1})	38	49	42	68	69	54	11	69
Q_{total} + Q_2 (mg P pot^{-1})	60	76	62	94	96	77	20	84
Percentage of total P absorbed*	63	69	85	50	38	69	70	6

*Assuming that non-Olsen-P was only absorbed from the volume exploited by roots and root hairs.

bound P solely. The isotope exchangeable P accounts for approximately 10% of the total P in P-exhausted soils (Wild, 1988), which can be considered a better indication of labile P than Olsen-P. However, the large fraction of non-Olsen-P absorbed by the cowpea genotypes (Tables 2 and 3) in this experiment indicated that plant roots were able to induce transformation and uptake of non-labile soil-P within the soil volume exploited by roots + root hairs. This is in accordance with findings in other legumes such as pigeonpea (Ae et al., 1990; Subbarao et al., 1997) and common bean (Beebe et al., 1997).

The main strategies of soil-P acquisition by plants are the development of roots and root hairs, establishment of concentration gradient over root membrane, root induced processes dissolving soil-P and association with mycorrhiza. From Figure 2 it appears that the eight cowpea genotypes can be grouped (I, II and III) in accordance with soil P acquisition strategies, such as development of root/root hairs and root induced processes dissolving soil-P.

Group I is IT82D-716 and Danila that have a relatively high volume of soil exploited by roots + root hairs, but a low P uptake rate. These genotypes use the strategy of root interception to acquire soil-P. It is notable that Danila is also considered very drought tolerant (Table 5).

Group II is IT82D-889, IT82D-849 and IT86D-715, which have a moderate volume of soil exploited by roots + root hairs and a moderate P uptake rate. These genotypes express more and less equal activity into both strategies.

Table 4. Volume of soil within the root + root hair zone in percentage of the total soil volume in the pot

	IT82D-889	IT82D-849	IT90K-	IT82D-716	IT86D-715	IT89KD-391	IT89KD-349	Danila
%RZ of pot soil volume	2.6	3.4	3.0	4.8	4.8	3.8	0.8	4.5

Table 5. Information on the selected cowpea varieties (Singh, 1999, pers. comm.)

Variety	Growth season	Growth	Resistance	Photosensitivity*	Origin of germplasm	Response to rock P-app.**	Seed color
IT82D-889 (Popular variety)	Extra early (60 days)	Erect	Multiple diseases, 8 viruses	PIS	Nigeria, Tanzania, USA, India	Not known	Red, smooth
IT82D-849	Early (70 days)	Erect, broad leaves	Major diseases, striga	PIS	Nigeria, Tanzania	P response	Brown, smooth
IT90K-59	Medium (75 days)	Semi erect	Multiple disease, stiga, electra	PIS	Nigeria, Tanzania, Botswana	No P response	Brown, rough
IT82D-716	Medium (75 days)	Very erect	Multiple disease	PIS	Nigeria, Tanzania	P response	White, brown eye
IT86D-715	Medium (75 days)	Long peduncles over canopy	Multiple disease	PIS	Nigeria, USA, Tanzania	No P response	White, rough
IT89KD-391	Late (80–85 days)	Semi erect	Aphids, bruchids	PIS	Nigeria, Tanzania	P response	Brown, rough
IT89KD-349	Late (80 days)	Semi spreading	Aphids, thrips, bruchids,	PS	Kananandndo, Nigeria, Tanzania	No P response	White, rough
Danila (Local variety)	Late (80–85 days)	Spreading	Very draught	PS	Nigeria	No P response	White, rough

*PIS – photo insensitive; PS – photosensitive.
**Studied by Sanginga et al. (2000).

Group III is IT90K-59 and IT89KD-391, which have a relatively low volume of soil exploited by roots + root hairs but a high P uptake rate particularly from non-Olsen-P. These genotypes to a large extent use the root-induced processes to acquire P from the strongly bound pools of soil-P, and invest less in root development.

IT89KD-349 does not fit into any of these groups. IT89KD-349 and Danila were the photosensitive genotypes, which were put in a dark chamber for 12 h every day. This resulted in early pod setting and a very low biomass production compared to the studies of Sanginga et al. (2000). By comparing just these two genotypes, it is seen that they express very different activity in the two strategies for P uptake. Danila has a low P uptake rate but a relatively high soil volume exploited, and IT89KD-349 has a relatively low volume of soil exploited but a high P uptake rate. It seems obvious that the P uptake efficient cowpea genotypes possess both the root interception strategy and the strategy of root-induced processes as the expression of activity within only one of these strategies does not result in a high P uptake as seen in the case of Danila and IT89KD-349.

The genotypes in group I are cowpea varieties from Nigeria. The genotypes in group II have different origins; IT82D-849 is a breed from Nigerian and Tanzanian lines. IT86D-715 and IT82D-889 are breeds originating in USA, India, Nigeria and Tanzania lines. The genotypes in group III are all breeds from the same parent IT84S-2246-4, which may indicate that root-induced mechanisms dissolving non-Olsen P are inherited from this genotype. However, IT90K-59 is a combination of an African selection and a cowpea line from Botswana. IT90K-59 is the only tested variety that possesses the Botswanan germplasm. Hence, the high uptake of non-Olsen-P may come from this line. IT90K-59 is considered a non-P responder (Table 5).

It can be concluded that the studied cowpea genotypes differed in root length, root hair length, and in

the intensity of root induced processes transforming non-labile soil-P to labile soil-P. A more P uptake efficient plant would be a combination of the high uptake rate seen in IT90K-59 and the extended root system seen in IT82D-716. Hence, traits of more P uptake efficient cowpea plants exist, opening the possibility to breed for more P uptake efficient varieties. This seems to be one way to bring more sparingly soluble soil-P into cycling in crop production and obtain capitalisation of the soil P reserves to benefit for the poorest people who rely on this crop in the tropics.

References

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

Barber S A 1995 Soil Nutrient Bioavailability, 2nd edn. Wiley, New York.

Barraclough P B and Tinker P B 1981 The determination of ionic diffusion coefficient in field soils. I. Diffusion coefficient in sieved soils in relation to water content and bulk density. J. Soil Sci. 32, 225–236.

Beebe S E, Lynch J P, Galwey N, Tohme J and Ochoa I 1997 A geographical approach to identify phosphorus-efficient genotypes among landraces and wild ancestors of common bean. Euphytica 95, 325–336.

Bonser A M, Lynch J P and Snapp S 1996 Effect of phosphorus deficiency on growth angle of basal roots in *Phaseolus vulgaris*. New Phytol. 132, 281–288.

Engels C, Neumann G and Gahoonia T S 2000 Assessment of the ability of roots for nutrient acquisition: Anonymous, v. *In* Root Research: A handbook. Eds. A L Smit, A G Bengough, C Engels, M van Noorwijk, S Pellerin and S C van de Geijn. pp. 403–460. Springer, Berlin.

Gahoonia T S and Nielsen N E 1995 Phosphorus mobilization in the rhizosphere as influenced by plant–soil interaction. pp. 208–216. Eds: F Cook Hadian and C Lee Howard. Wye College Press: Wye College, University of London, Kent.

Gahoonia T S, Nielsen N E, and Raza S, 1994, Phosphorus depletion in the rhizosphere as influenced by soil moisture: Plant Soil 159, 213–218.

Gahoonia T S, Nielsen N E and Lyshede O B 1999 Phosphorus (P) acquisition of cereal cultivars in the field at three levels of P fertilization. Plant Soil, 211, 269–281.

Jungk A 1996 Dynamics of nutrient movement at the soil-root interface. *In* Plant Roots – The Hidden Half. Eds. Y Waisel, A Eshel and U Kafkafi. pp. 529–556. Marcel Dekker, New York.

Lynch J P, Epstein E, Läuchli A and Weigt G I 1990 An automated greenhouse sand culture system suitable for studies of P nutrition. Plant Cell Environ. 13, 547–554.

Manske G G B, Ortiz- Monaterio J I, Ginkel M v, González R M, Fischer R A, Rajaram S and Vlek P L G 2001 Importance of P uptake efficiency versus P utilization for wheat yield in acid and calcareous soils in Mexico. Eur. J. Agron. 261–274.

Mortimore M J, Singh B B, Harris F and Blade S F 1997 Cowpea in traditional cropping systems. *In* Advances in Cowpea Research. Eds. B B Singh, D R Raj Mohan, K E Dashiell and L E N Jackai. pp. 99–113. International Institute of Tropical Agriculture and JIRCAS, Ibadan, Nigeria.

Murphy J and Riley J P 1960 A modified single solution method for determination of phosphate in natural waters. Anal. Chim Acta 27, 31–36.

Nielsen N E, 1993 Bio-availability, cycling and balances of nutrients in the soil-plant system. *In* Integrated Plant Nutrition Systems. FAO Fertilizer and Plant Nutrition Bulletin 12. Eds. R Dudal and R N Roy. pp. 333–348. FAO, Rome, Italy.

Nielsen N E and Barber S A 1978 Difference among genotypes of corn in kinetics of P uptake. Agron. J. 70, 965–968.

Nielsen N E and Schjørring J K 1983 Efficiency and kinetics of phosphorus uptake from soil by barley genotypes. Plant Soil 72, 225–230.

Nye P H and Tinker, P B, 1977 Solute Movement in the Soil–Root System. Blackwell Scientific Publications, Oxford, England.

Oberson A, Friensen D K, Tiessen H, Morel C and Stahel W 1999 Phosphorous status and cycling in native savanna and improved pastures on an acid low-P Colombian Oxisol. 77–88.

Padulosi S and Ng N Q 1990 Wild Vigna species in Africa: Their collection and potential utilization. *In* Cowpea Genetic Resources. Eds. N Q Ng and L M Monti. pp. 59–77. International Institute of Tropical Agriculture, Ibadan, Nigeria.

Sample E C, Soper R J and Racz G J 1980 Reactions of phosphate fertilizers in soils. *In* The role of phosphorus in agriculture. Eds. F E Khasawneh, E C Sample and E J Kamprath. pp. 263–310. ASA, CSSA, SSSA. Madison, WI.

Sanchez PA, S KD, Soule M J, Place F M, Buresh R J, Izac A N, Mokwunye A U, Kwesiga F R, Ndiritu C G and Woomer P L 1997 Soil Fertility Replenishment in Africa: An investment in natural resource capital. *In* Replenishing Soil Fertility in Africa. Eds. R J Burest, P A Sanchez and F G Calhoun. pp. 1–46. ASA, SSSA, Madison, WI.

Sanginga N, Lyasse O and Singh B B 2000 Phosphorus use efficiency and nitrogen balance of cowpea breeding lines in low P soil of the derived savanna zone in West Africa. Plant Soil 220, 119–128.

Subbarao G V, Ae N and Otani T 1997 Genetic variation in acquisition, and utilization of phosphorus from iron-bound phosphorus in pigeonpea. Soil Sci. Plant Nutr. 43, 511–519.

Tinker PB and Nye P H 2000 Solute Movement in the Rhizosphere. Oxford University Press, New York.

Wild A 1988 Plant nutrients in soil: phosphate. *In* Russell's Soil Conditions and Plant Growth (11) Wild A. Ed. pp. 695–742. Longman Scientific & Technical, Harlow.

Williams R F 1948 The effect of phosphorus supply on rates of intake of phosphorus and nitrogen and upon certain aspects of phosphorus metabolism in gramineous plants. Aust. J. Sci Res 1B, 333–361.

Willigen P, Nielsen N E, Claassen N and Castrignanó A M 2000 Modelling Water and Nutrient Uptake. *In* Root Methods: A Handbook. Eds. A L Smith, A G Bengough, C Engels, M Noordwijk, S Pellerin and S C Geijn. pp. 509–544. Springer, Berlin.

Yan X, Lynch J P and Beebe S E 1995 Genetic variation for phosphorus efficiency of common bean in contrasting soil types: I. Vegetative response. Crop Sci. 35, 1086–1093.

Section editor: H. Lambers