Plant and Soil 220: 119–128, 2000.
© 2000 Kluwer Academic Publishers. Printed in the Netherlands.

Phosphorus use efficiency and nitrogen balance of cowpea breeding lines in a low P soil of the derived savanna zone in West Africa

N. Sanginga*, O. Lyasse and B.B. Singh
International Institute of Tropical Agriculture (IITA), Oyo Road, PMB 5320, Ibadan, Nigeria. Mailing address: c/o L.W. Lambourn & Co., Carolyn House, 26 Dingwall Road, Croydon CR9 3EE, England.

Received 3 November 1998. Accepted in revised form 30 December 1999

Key words: arbuscular mycorrhizal fungi (AMF), N_2 fixation, N harvest index, P uptake, cowpea (*Vigna unguiculata*), P use efficiency

Abstract

Differences in growth, nodulation and arbuscular mycorrhizal fungi (AMF) root infection among recent cowpea breeding lines from IITA were examined at low and high P levels in pot (94 lines) and field experiments (43 lines) at Fashola in the derived savanna zone of Nigeria. Based on their growth performance, these lines were subdivided into 5 groups: (i) poor performance under low and high P conditions: (ii) good performance under low P and poor performance under high P; (iii) intermediate performance under high and low P; (iv) good performance under high and low P conditions; and (v) good performance under high P and poor performance under low P. About 42% of the breeding lines (18 out of 43 lines tested) had the same grouping for the field and pot experiments. Eight cowpea lines (4 P-responders and 4 non-P-responders) were selected from the first experiment for subsequent studies on the effect of P supply (0, 20, 40 and 60 kg P ha^{-1}) on P uptake, P use efficiency, dry matter production, N-fixation, AMF infection and N balance. Dry matter production, shoot/root ratio, total shoot N, and total N-fixed of the non-P-responder line, IT81D-715, were strongly related to P uptake efficiency. The P-responder IT81D-849 had a significant (95%) correlation between AMF and P-use efficiency. The cowpea lines fixed on average 22 kg N ha^{-1}, which was 70% of the plant total N. The N balance based on the difference between the amount of N_2 fixed and N exported through the harvest, ranged between −10.6 kg N ha^{-1} and +7.7 kg N ha^{-1}. Based on its adaptability to grow in low P soils and overall positive N balance, the cowpea line IT81D-715 should be recommended for cultivation when P is the limiting factor.

Introduction

Cowpea is of major importance to the livelihoods of millions of people, many of whom are the world's poorest (Quin, 1997). Cowpeas are also important in the nutrient economy of low-input cropping systems since they fix N_2 through symbiotic association with bacteria, thereby improving soil fertility and reducing the need for N fertilizer. The process of biological N_2 fixation by cowpea nodules requires large amounts of P, and its availability is a primary constraint to N_2 fixation and therefore the N economy of many tropical ecosystems (Danso, 1992; Mortimore et al., 1997). No attempt has so far been made to select cowpea genotypes that can fix N_2 at low levels of plant-available P and N in the moist savanna zones of West Africa. Low levels of soil available N and P and large crop responses to N and P fertilizer applications are common for both cereals and legumes in the moist savanna of West Africa (Bationo et al., 1986). Nitrogen and P fertilizers are often expensive due to the lack of locally available resources. Furthermore, fertilizer P can be fixed into forms unavailable to plants by Fe and Al oxides found in tropical soils (Sample et al., 1980). Application of commercially available P fertilizers or amendments can therefore not be relied upon to reasonably redress such nutrient depletion. It would thus be desirable for crop plants to access a greater pro-

* FAX No: 234-2-2412221. E-mail: N.Sanginga@cgiar.org

Table 1. Physico-chemical characteristics of topsoil (0–15 cm depth) at Fashola

Soil characteristics	
Sand (%)	83.00
Silt (%)	16.00
Clay (%)	1.00
pH (H_2O)	6.00
Organic C (%)	0.48
Total N (%)	0.04
Bray I P (mg/kg)	5.33
NH_4-Acetate extractable cations (cmol/kg)	
Ca	4.15
Mg	0.42
Mn	0.03
K	0.11
Na	0.03
Total Acidity (cmol/kg)	0.01

Table 2. Cowpea lines used in experiment I

Cowpea lines	Cowpea lines
1 Kanannado	23 IT89KD-260
*2 Danila	24 IT89KD-245
3 IT82E-32	25 IT92KD-170-1
4 IT82E-18	26 IT92KD-279-3
5 IT88F-2062-5	27 IT88D-345
6 Vita-3	*28 IT82D-849
7 Vita-1	29 IT83D-492
8 TVX-4659-03E	30 IT86D-721
9 TVX-1850-01E	31 IT87D-611-3
10 TVX-2724-01F	*32 IT86D-716
11 TVX-3236	33 IT81D-885
12 IT91K-118-20	34 IT81D-994
13 IT91K-93-10	35 IT85D-385D-2
14 IT90K-284-2	36 IT86D-880
15 IT90K-76	37 IT81D-1228-13
*16 IT90K-59	38 IT84D-449
*17 IT89KD-349	39 IT89KD-288
18 IT89KD-453	40 IT92KD-258-9
19 IT92KD-370	41 IT845-2135
20 IT92KD-405-2	*42 IT81D-715
21 IT89KD-457	*43 IT89KD-374
*22 IT89KD-391	

*The 8 cowpea lines selected for experiment II.

portion of the total soil nutrient pool than is otherwise available to them. Inter- and intraspecific differences in P uptake, accumulation and use are well known for grain legumes such as mungbean (*Vigna radiata*) and soybean (*Glycine max*) (Gunawardena et al., 1993; Abdelgadir, 1998). However, mechanisms by which these legumes exhibit differential abilities to grow at low or high P supply are not completely understood and few have been described to any extent (Singh et al., 1997). A better understanding of leguminous species or cultivar differences in P and N nutrition may help in breeding new cultivars for new areas where fertilizers are not readily available. The objectives of this study were (i) to determine specific differences in growth response, P uptake and P use between recent cowpea lines, (ii) to determine the relationships between plant growth characteristics and P-uptake and P-use efficiency, and (iii) to select lines which have the high nodulation and N_2 fixation potential and therefore the positive N balance at low levels of P in the soil.

Materials and methods

Field experiments were conducted at Fashola for 3 years between 1994 and 1996. Fashola (7° 50′ N, 3° 55′ E, soil type: Oxic Paleustalf) is located in the derived savanna of Nigeria in West Africa and has a bimodal rainfall pattern with about 1200 mm rainfall per annum. A pot experiment was done at the International Institute of Tropical Agriculture (IITA) at Ibadan, Nigeria, using topsoil collected from the field at Fashola. Selected physico-chemical characteristics (0–15 cm depth) of the soil measured according to IITA analytical procedures (IITA, 1989) are given in Table 1.

Experiment I: Screening of cowpea lines under low and high P conditions

Pot experiment

A randomized complete block design with three replications was used. Treatments included 94 cowpea lines and two P levels (without and with 60 mg P kg soil^{-1}). Soil for the pot experiment was collected from 0–15 cm depth from the field at Fashola. The soil was air dried, sieved (<2 mm screen) and weighed (5 kg soil pot^{-1}). A basal application of 60 mg K kg^{-1} soil as muriate of potash and 1 ml of a combination of micronutrients (Vincent, 1970) per kg soil was applied to each pot before planting. Phosphorus was applied as KH_2PO_4 at the rate of 60 mg P kg soil^{-1} where appropriate. The seeds were surface sterilized with 95% ethanol (1 min) and 3% H_2O_2 (5 min), and then

Table 3. Shoot dry weight (g plant^{-1} at mid-podding) and growth characteristics of selected P- and non-P-responder cowpea lines grown in a low P soil

Cowpea lines	P application		Growth characteristics	
	0 kg P ha^{-1}	60 kg P ha^{-1} (SSP)	Days to maturity (d)	Canopy height (cm)
Non-P-responders				
IT 81D-715	24.33	23.11	75–80	50
Danila	7.00	6.49	85–90	20
IT 90 K-59	11.78	3.24	70–75	50
IT 89 KD-349	14.55	11.38	75–80	35
P-responders				
IT89KD-374	13.08	15.16	70–75	30
IT89KD-716	18.01	20.03	75–80	30
IT89KD-391	6.51	9.28	75–80	40
IT82D-849	17.68	25.33	65–70	50
LSD 5% (1)	9.00			
LSD 5% (2)	2.00			

(1) LSD (5%) for comparing cowpea lines within one P level.
(2) LSD (5%) for comparing P levels within cowpea lines.

rinsed with sterile water (Vincent, 1970). Four seeds of each line were sown in each pot and thinned to two plants per pot one week after emergence. All plants were harvested at 8 weeks after planting (WAP), and assessed for dry matter production (shoots and roots), nodulation and mycorrhizal infection. Mycorrhizal infection was rated on fresh roots using the method by Giovanetti and Mosse (1980) after clearing and staining following the procedure described by Phillips and Hayman (1970).

Field experiment

The area of the experimental field was 90 m×25 m. The land was cleared of trees, ploughed and then disc-harrowed twice. Before the second disc-harrowing, the field was sprayed with the herbicide gramoxone at a rate of 9.44 L ha^{-1}. A chisel plow was used to establish an inter-row distance of 75 cm. A strip-plot design with 3 replications and two treatments (two P application levels and forty-three cowpea lines) was used. Single super phosphate (SSP) was the source of P (60 kg P ha^{-1}) applied manually by broadcasting. Surface-sterilized seeds of 43 cowpea lines selected for their good growth (Table 2) from the pot experiment were sown by hand at a spacing of 25 cm within and 75 cm between lines. One week after emergence, the plants were thinned to one per hill. The cowpea field was sprayed and weeded according to standard agricultural practices. Plant sampling was carried out at mid-podding and maturity. At the first sampling time, three plants from the middle of each line were dug out. To minimize damage to the root system, the soil around the plant was loosened using forks. However, at the harvesting stage (when pods browned), 10 plants from the middle of each line were harvested. Plant samples were processed for shoot dry weight, root dry weight, number and dry weight of nodules. Mycorrhizal infection rate on the roots was determined at mid-podding as described in the pot experiment. The plants were left to dry in a greenhouse. When the pods were dry, they were threshed by hand. The seeds were then dried for 24 h at 40 °C and weighed. Plant shoots, roots, nodules and straw were dried in an oven at 80 °C for 3 consecutive days before weighing.

Experiment II: Response of selected cowpea lines to different P levels under field conditions

Eight cowpea cultivars (Table 3) selected from the field experiment conducted in 1994 were planted for two seasons in 1995 and 1996 at a spacing of 25 cm within rows and 75 cm between rows. A split-plot design with 3 replications was used for the experiment. Main treatments were four levels of SSP (0, 20, 40 and 60 kg P ha^{-1}) and the cowpea lines were the subtreatments. The subplots measured 10×5 m. Each plot received a basal application of 30 kg K ha^{-1} as muriate

Table 4. Effect of P application on shoot dry matter (g per 5 plants) and shoot/root ratio of cowpea lines grown in the field at Fashola in 1995

Cowpea lines	P application (kg P ha^{-1})							
	0	20	40	60	0	20	40	60
	Shoot dry weight [g (5 plants)$^{-1}$]				Shoot/root ratio			
Non-P-responders								
IT81D-715	109	75	88	108	30	21	23	38
Danila	87	81	77	92	23	21	17	34
IT90K-59	74	75	68	87	22	24	26	20
IT89KD-349	77	94	81	108	21	28	15	33
P-responders								
IT89KD-374	51	82	69	63	18	26	24	13
IT86KD-716	52	60	53	61	21	12	17	13
IT89KD-391	65	75	95	71	15	17	28	20
IT82D-849	82	114	92	107	18	31	47	27
LSD (1)	13				7			
LSD (2)	18				10			

(1) LSD (5%) for comparing cowpea lines within one P level.
(2) LSD (5%) for comparing P levels within cowpea lines.

of potash. No N fertilizer or bradyrhizobia inoculation was applied. Two seeds were sown per hill and the seedlings thinned to one per hill one week after emergence. Maize was used as a reference plant to allow estimation of N_2 fixation by the difference method (Hardarson et al., 1984). The net contribution of N_2 fixation to the N balance of the soil has been calculated as follows (Peoples and Craswell, 1992): Net N balance=Nf–Ns, where Nf is the amount of N_2 fixed and Ns represents the total N in the seeds. The plots were weeded by hand; spraying the crops with appropriate insecticides controlled insect pests. Plants were sampled at mid-podding and at maturity as described earlier, and the same parameters were measured in addition to total N and P in the plant tissues.

Table 5. Arbuscular mycorrhizal fungi infection rate (%) cowpea lines grown at different levels of P application at Fashola in 1995

Cowpea lines	P application (kg P ha^{-1})			
	0	20	40	60
Non-P-responders				
IT81D-715	26	30	16	07
Danila	28	24	07	04
IT90K-59	25	28	05	04
IT89KD-349	25	33	16	07
P-responders				
IT89KD-374	28	34	12	04
IT82D-716	27	32	16	06
IT82KD-391	22	28	17	07
IT82D-849	28	31	16	05
LSD (1)	1.7			
LSD (2)	2.4			

(1) LSD (5%) for comparing cowpea lines within one P level.
(2) LSD (5%) for comparing P levels within cowpea lines.

Chemical analysis

Analysis of P in the shoots was done using the vanado-molybdate yellow method, and total N was determined by an automatic N analyzer following wet acid digestion (IITA, 1989).

Statistical analysis

Analysis of variance (ANOVA) was done using the SAS program (SAS, 1989) to determine treatment and interaction effects. Least significant differences (LSD) were calculated at the 5% level to assess treatment differences. Correlation coefficients were computed for selected character pairs.

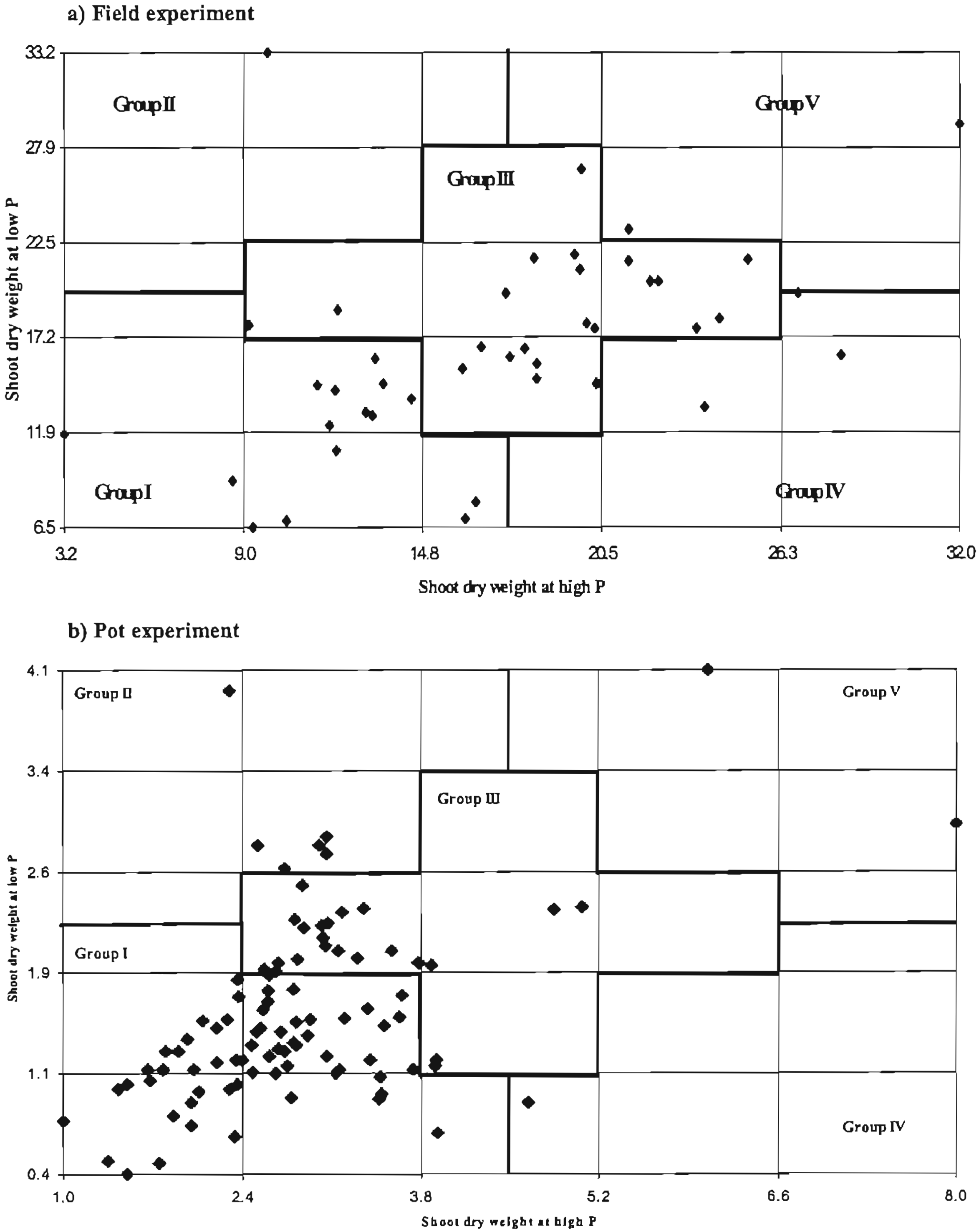

Figure 1. Shoot dry weight variability of cowpea lines to low (no P applied) and high P (60 kg P/ha) application.

Table 6. Total P accumulation in shoot and seeds of cowpea lines grown at different levels of P application at Fashola

Cowpea lines	P application (kg P ha^{-1})				Means*
	0	20	40	60	
	Total shoot P (kg ha^{-1})				Total seed P (kg ha^{-1})
Non-P-responders					
IT81D-715	3.8	3.3	3.6	4.7	2.3^{b}
Danila	3.4	3.9	3.4	5.1	2.4^{ab}
IT90K-59	2.6	4.3	3.8	4.9	3.3^{a}
IT89KD-349	3.1	5.3	3.8	5.8	2.9^{ab}
P-responders					
IT89KD-374	2.0	4.0	3.5	2.8	1.8^{c}
IT86KD-716	2.6	3.0	2.8	3.9	2.3^{bc}
IT82KD-391	3.1	4.4	4.8	4.8	2.8^{ab}
IT82D-849	3.1	4.8	4.8	5.4	3.3^{a}
LSD (1)	0.8				
LSD (2)	1.1				

(1) LSD (5%) for comparing cowpea lines within one P level.
(2) LSD (5%) for comparing P levels within cowpea lines.
*Values followed by the same letter are not significantly different at $p \leq 0.05$.

Table 7. P use efficiency (g shoot dry weight per mg P in shoots) and P uptake (mg of P taken up in shoot biomass per g of dry roots) as a response to P application in 1995

Cowpea lines	P application (kg P ha^{-1})							
	0	20	40	60	0	20	40	60
	P-use efficiency				P-uptake efficiency			
Non-P-responders								
IT81D-715	0.37	0.24	0.27	0.26	97	90	88	155
Danila	0.30	0.24	0.24	0.19	78	95	74	169
IT90K-59	0.31	0.19	0.19	0.20	70	123	138	106
IT89KD-349	0.27	0.19	0.25	0.20	85	149	60	163
P-responders								
IT89KD-374	0.30	0.22	0.21	0.25	64	119	115	51
IT82D-716	0.23	0.21	0.21	0.18	96	55	87	79
IT82KD-391	0.23	0.20	0.21	0.16	64	89	132	124
IT82D-849	0.29	0.26	0.21	0.21	59	125	227	127
LSD (1)	0.02				33			
LSD (2)	0.03				47			

(1) LSD (5%) for comparing cowpea lines within one P level.
(2) LSD (5%) for comparing P levels within cowpea lines.

Table 8. Effect of P application on total N accumulated and N_2 fixed by cowpea lines grown in Fashola (1995)

Cowpea lines	P application (kg P ha^{-1})								
	0	20	40	60	Means	0	20	40	60
	Total shoot N (kg N ha^{-1})					Total N_2 fixed (kg ha^{-1})			
Non-P-responders									
IT81D-715	27.1	22.5	27.8	30.3	26.9^a	24.5	20.3	24.3	28.2
Danila	25.3	24.3	25.2	26.0	25.2^a	22.6	22.1	21.7	23.9
IT90K-59	24.6	20.6	20.8	27.2	23.3^a	21.9	18.4	17.2	25.1
IT89KD-349	21.2	27.2	24.9	32.5	26.4^a	18.5	25.1	21.3	30.4
P-responders									
IT89KD-374	15.7	24.3	22.4	20.0	20.6^{bc}	13.1	22.2	18.8	17.9
IT82D-716	15.8	19.3	18.2	17.8	17.8^c	13.1	17.1	14.6	15.7
IT82KD-391	20.6	21.5	30.2	21.7	23.5^b	17.9	19.4	26.6	19.6
IT82D-849	22.5	29.4	29.7	34.0	28.9^a	19.9	27.3	26.2	31.9
LSD (1)	4.0					3.9			
LSD (2)	5.6					5.6			

(1) LSD (5%) for comparing cowpea lines within one P level.
(2) LSD (5%) for comparing P levels within cowpea lines.

Results

Experiment I: Screening of cowpea lines under low and high P conditions

Plant growth, nodulation and AMF root infection

There were highly significant differences ($P < 0.001$) in shoot dry weight among cowpea lines at high (60 kg P ha^{-1}) and low P (0 kg P ha^{-1}) P levels both in the pot and field experiments (Figure 1). Phosphorus application increased nodule weight (from 61 to 131 mg plant^{-1}) but reduced AMF root infection rate (from 44 to 24%), but large differences in these root parameters occurred between cowpea lines both at low P and high P (data not shown). Five major P efficiency groups of cowpea lines were distinguished. Group 1, which grew poorly under both low and high P, included about 51% and 35% of the cowpea lines, respectively under potted and field conditions (Figure 1). At the other extreme, Group 5 comprised only 2 cowpea lines in both test conditions, with high growth vigor under both low and high P. Five cowpea lines grew well under low P and their growth was depressed by high P (Group 2) in the pot trial and one line expressed this feature in the field. About 2.3% of the lines in pots and 7% in the field grew poorly at low P conditions but had better growth at high P (Group 4). The other cowpea lines (30% for the pots and 51% in the field) showed no or slight responses to P addition and were considered as intermediate (Group 3). Eighteen out of the 43 cowpea breeding lines (42%), which were grouped as described above, ended in the same groups under both pot and field conditions. Based on shoot dry matter response to P application, eight lines were selected and subdivided into two groups according to P response observed (Table 3). These lines were used for further field studies in 1995 and 1996.

Experiment II: Response of selected cowpea lines to different P levels under field conditions

Growth response and AMF root infection

The non-P-responders did not show any significant benefit of the P fertilization whereas the shoot dry weight of the P-responders increased significantly with P addition in 1995 (Table 4). Significant differences in shoot biomass production between breeding lines occurred especially in the P-responder group. Increasing the level of P from 0 to 20 kg P ha^{-1} increased shoot dry matter production of lines IT82D-849 (39%) and IT89KD-374 (61%), but further P addition did not result in any significant increase in shoot dry matter. Root dry weight of the P-responders varied with P addition, whereas the non-P-responders had no significant variation with application of P (data not shown). Significant differences in shoot/root ratio were observed in the P-responder group while the non-P-responders maintained a similar shoot/root ratio at different levels of P (Table 4). At very low (0 P) and very high levels of P (60 P), the P-responders showed a relative increase of the root biomass as compared to the shoots. The highest shoot/root values were obtained at 40 kg P ha^{-1}. AMF root infection was significantly affected by P application in both groups but it was only slightly affected by cowpea lines (Table 5). The highest infection was obtained at 20 kg P ha^{-1} after which it declined significantly ($P \leq 0.05$) at higher rates of P application.

Phosphorus accumulation, uptake and use efficiency

Application of 20 kg P ha^{-1} significantly increased total P accumulation of the P-responders (Table 6). The non-P-responder group had the highest P accumulation at 60 kg P ha^{-1}. Phosphorus accumulation in seeds did not vary between groups, but differences between breeding lines were observed, and were most pronounced in the P-responder group (Table 6). All cowpea lines showed a decrease in P-use efficiency (g shoot dry weight per mg P in shoots) with increasing amount of P applied up to 60 kg P ha^{-1} (Table 7). Phosphorus-use efficiency (PUE) was significantly different among lines within each group. IT81D-715 had the highest PUE within the non-P-responder group, while IT89D-374 and IT82D-849 had the highest PUE among the P-responders. In contrast to PUE, P uptake efficiency (mg of P in shoot biomass per g root dry weight) of both groups increased with P application (Table 8). The non-P-responders attained a maximum at 60 kg P/ha, whereas the P-responders exhibited the highest level of P uptake efficiency at 40 kg P/ha.

Nitrogen fixation, N balance and seed production

Total N accumulation in the shoots ranged from 15.7 to 34 kg N ha^{-1} (Table 8). The average total N values were significant ($P \leq 0.05$) in the P-responder group at 20 and 40 kg P/ha, while the non-P-responders had no significant effect with P addition. Total N in the shoots did not differ significantly within the non-P-responder group, while strong varietal differences were observed in the P-responder group. No response to P was observed for total N in seed (data not shown). Differences in seed total N between cowpea lines ranged between 16.3 and 29.0 kg N/ha. All cowpea lines nodulated profusely, the number and weight of nodules increasing with the addition of P (data not shown). The percentage of N derived from the atmosphere was on average 70% over the 2 years, and was only significantly influenced by P addition within the P-responder group. The amount of N_2 fixed in 1995 varied between 13.1 and 31.9 kg N ha^{-1}. The N balance calculated on the basis of N fixed and N exported through the seed harvest ranged between −10.6 and 11.1 kg N ha^{-1} (Table 9).

Table 9. Effect of P application on the N-balance of cowpea lines grown in a low P soil

Cowpea lines	P application (kg P ha^{-1})			
	0	20	40	60
	Nbalance (kg N ha^{-1})*			
Non-P-responders				
IT81D-715	−2.9	0.1	5.5	11.1
Danila	3.2	−5.8	−2.3	6.3
IT90K-59	−2.6	−10.6	−9.3	−3.6
IT89KD-349	−2.4	−4.0	−8.4	8.1
P-responders				
IT89KD-374	−1.6	7.6	−0.1	0.9
IT82D-716	−9.3	1.9	−9.0	−2.1
IT82KD-391	−4.8	0.9	2.8	−5.0
IT82D-849	−10.4	−6.4	−1.8	7.7
LSD (1)	6.0			
LSD (2)	8.5			

(1) LSD (5%) for comparing cowpea lines within one P level.
(2) LSD (5%) for comparing P levels within cowpea lines.
*N balance is calculated from the difference between total N fixed and total N exported in seeds.

Correlation of AMF, P and uptake and plant growth

P-use efficiency and % AMF were not significantly correlated to most of the growth parameters (data not shown). In comparing the two high yielding lines IT81D-715 (non-P-responder) and IT82D-849 (P responder), dry matter production, shoot/root ratio, total shoot N and total N-fixed of the non-P-responder line (IT81D-715) were strongly related to P uptake efficiency. The P uptake efficiency of the high yielding P-responder (IT82D-849) was only correlated to root biomass and shoot/root ratio.

Discussion

This study showed pronounced differences in P nutrition between the cowpea breeding lines. Different types of growth response to P application were illustrated by cowpea lines such as IT81D-715 and IT82D-849. With line IT82D-849, maximum yield

Table 10. Correlation matrix between P uptake and plant characteristics of cowpea lines grown in the field at Fashola in 1995 (d.f.=10; * 95% correlation. ** 99% correlation)

Cowpea lines	P uptake						
	Sht	Rt	Sht/Rt	TN	NF	PUE	AMF
Non-P-responders							
IT81D-715	**0.72	*−0.58	**0.94	**0.75	**0.74	ns	ns
Danila	ns	*−0.65	**0.95	ns	ns	ns	ns
IT90K-59	ns	*−0.63	**0.83	ns	ns	ns	ns
IT98KD-349	*0.70	*−0.64	**0.96	*0.64	*0.65	*−0.58	ns
P-responders							
IT89KD-374	**0.75	*−0.65	**0.93	*0.64	*0.59	ns	ns
IT82D-716	ns	*−0.60	**0.88	ns	ns	ns	ns
IT82KD-391	*0.66	ns	**0.89	*0.68	*0.68	ns	ns
IT82D-849	ns	**−0.75	**0.98	ns	ns	ns	ns

Sht: Shoot dry matter; Rt=root dry matter; S/R=shoot to root ratio; TN=total N; NF=N_2 fixed; PUPT=P uptake; PUE=P-use efficiency; AMF=Arbuscular mycorrhizal fungi.

was obtained when 60 kg P ha^{-1} was added to the soil. On the other hand, line IT81D-715 did not respond to P indicating that the inherent soil P concentration in Fashola was adequate for its growth. Similar lack of response of soybean lines to P application in low P soils has also been reported at the same site (Abdelgadir, 1998). Our data clearly show that the P requirement for cowpea to achieve maximum growth varies widely within the germplasm. It can be argued that if the ability to grow in low P soils (as in Fashola) is one of the major selection criteria, lines such as IT82D-849 that require P application for maximum biomass production would be at a disadvantage compared to IT81D-715. There are three broad categories of mechanisms by which plants can increase their access to native or applied soil nutrients: i) by increasing absorptive areas, ii) by favorably modifying the absorption mechanisms to increase uptake from low ambient concentrations, and iii) by rhizosphere modification to increase nutrient availability (Bar-Yosef, 1991). We have shown that the breeding lines within the P-responder group are able to adjust their shoot/root ratio under different levels of P, i.e. under P stress, these plants invest relatively more energy to proliferate their root biomass in order to increase the soil-root contact area. Our investigation shows that differences between the two cowpea lines (IT81D-715 and IT82D-849) in their ability to absorb and use P efficiently for biomass production, could largely account for the difference in adaptation of these lines to low P soils. For example, line IT81D-715 had higher PUE at both low and high P rates compared to 849 (Table 8). In contrast to IT82D-849, P uptake of line IT81D-715 was strongly related to growth. Data indicate that P uptake was the most important physiological mechanism for this line as shown by the higher uptake values and poor allocation of P from shoot to seeds (Table 7). Mechanisms by which line IT81D-715 exhibited a similar ability to grow at low or high P supply were not established. However, our results show that N_2 fixation was not affected by P stress, which illustrates the fact that even under low soil P conditions, effective nodulation and N_2 fixation can occur in the case of cowpea. The data presented here indicate that the cowpea lines differ in their ability to fix N_2 under low P conditions. Percentage of N_2 fixed by these legumes was generally high (average over the 2 years: 70%) and is above values reported earlier for cowpea in the moist savanna zone (Eaglesham et al., 1982). The best cowpea line in terms of N balance under a low soil P condition was IT81D-715. This line should be better suited to N- and P-deficient soils. Although other lines such as IT82D-849 presently being adopted by farmers in some areas of the moist savanna showed comparable % N_2 fixation, their optimum amount of N_2 fixation and shoot dry matter production strongly depend on the application of P fertilizer.

Conclusions

Large differences between cowpea lines were observed for most of the plant parameters (growth, N accumulation, nodulation and N_2 fixation). Cowpea lines differed widely in their P requirements for growth and N_2 fixation. Line IT81D-715 with a positive N balance and high P-use efficiency under low-P conditions could be ideal for low-P soils in the savanna region. However, as IT81D-715 also removed the largest amount of P from the soil, further testing is needed to examine its effect on the soil P status and the long-term effect it will have on the P nutrition of subsequent crops. The possibility to use less soluble and much cheaper P sources (e.g. low-reactive rock phosphate) in combination with selected P-efficient cowpea breeding lines could alleviate this P depletion. A line such as IT82D-849, which requires P application for maximum yield, will be more suitable for soils with high available P. These results suggest the need to take the P requirements of these cowpea lines into account when selecting and introducing certain genotypes in the moist savanna zone.

References

Abdelgadir A H 1998 The role of mycorrhizae in soybean growth in P–deficient soil in the humid tropics. PhD. Thesis. Cornell University. 255 p.

Bationo S. Mughogho S K and Mokwunye A 1986 Management of nitrogen fertilizers for tropical African soils. *In* Management of nitrogen and phosphorus fertilizers in sub-saharan Africa. Eds A Mokwunye and P L G Vlek. pp 283–318. Martinus Nijhoff Publishers. Dordrecht. The Netherlands.

Danso S K A 1992 Biological Nitrogen fixation in tropical agrosystems: Twenty years of biological nitrogen fixation research in Africa. *In* Biological Nitrogen Fixation and Sustainability of Tropical Agriculture. Eds K Mulongoy. M Gueye and D S C Spencer. pp 3–13. John Wiley & Sons Ltd., Chichester. UK.

Eaglesham A R J. Ayanaba A. Rao V R and Eskew D L 1982 Mineral N effects on cowpea and soybean crops in a Nigeria soil. Plant Soil 68. 171–181.

Giovannetti M and Mosse B 1980 An evaluation of techniques for measuring Vesicular-arbuscular mycorrhizal infection in roots. New Phytol. 84. 489–500.

Gunawardena S F B N, Danso S K A and Zapata F 1993 Phosphorus requirements and N_2 accumulation by three mungbean (*Vigna radiata* (L) Wewlzek) cultivars. Plant Soil 147. 267–274.

Hardarson G and Danso S K A 1993 Methods for measuring biological nitrogen fixation in grain legumes. Plant Soil 152, 19–23.

International Institute of Tropical Agriculture (IITA) 1989 Automated and semi-automated methods for soil and plant analysis. Manual series No 7. IITA. Ibadan. Nigeria.

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 Mohan Raj. K E Dashiell and L E N Jackai. pp 99–113. IITA. Ibadan. Nigeria.

Peoples M B and Craswell E T 1992 Biological nitrogen fixation: Investments, expectations and actual contributions to agriculture. *In* Biological Nitrogen Fixation for Sustainable Agriculture. Eds J K Ladha. T George and B B Bohlool. pp 13–40. Kluwer Academic Publishers. Dordrecht. The Netherlands.

Phillips J M and Hayman D S 1970 Improved procedure for clearing roots and staining parasitic and Vesicular arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Brit. Myc. Soc. 55. 158–161.

Quin F M 1997 Introduction. *In* Advances in Cowpea Research. Eds B B Singh. D R Mohan Raj. K E Dashiell and L E N Jackai pp ix-xv. IITA. 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. Am. Soc. Agron.. Madison. Wisconson. USA.

Singh B B. Chambliss O L and Sharma B 1997 Recent advances in cowpea breeding. *In* Advances in Cowpea Research. Eds B B Singh. D R Mohan Raj. K E Dashiell and L E N Jackai. pp 30–49. IITA. Ibadan. Nigeria.

Statistical Analysis System Insititute Inc. 1989 SAS/STAT User's Guide. 4th edn., Vol. 1. SAS. Cary. NC. USA

Vincent J M 1970 A manual for the practical study of the root nodule bacteria. Blackwell Scientific Publications. Oxford.

Section editor: Z Rengel