# Prospects for Sorghum Improvement for Phosphorus Efficiency

N. Seetharama, K. R. Krishna, T. J. Rego, and J. R. Burford

#### Introduction

Phosphorus (P) deficiency is common in sorghum-growing regions of the semi-arid tropics (SAT) (Sallanpaa, 1982), and ranks second in importance only after nitrogen (N) deficiency. In addition to the deficiencies of these two nutrients, other nutrient disorders may be common. For example, zinc (Zn) deficiency is common in India, potassium (K) and sulphur (S) deficiency in West Africa, and aluminum (Al) toxicity in Latin America (Sánchez and Salinas, 1981). Amelioration of P deficiency by application of P fertilizers is costly. Thus, improved farming practices have the best chance of adoption by the small subsistence farmers with limited financial resources if they involve only moderate amounts of low-cost inputs. To achieve this, we need to determine efficient fertilizer practices in conjunction with the development of P-efficient cultivars.

In this paper we will briefly summarize the relevent research at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), near Hyderabad in India. We will report our results from studies on three aspects of P nutrition, viz., soil, plant, and the associated microorganisms, and will discuss the prospects for crop improvement in P-stress (and related) environments.

### Response of sorghum to phosphorus fertilization

Because of the wide variation in response to P fertilizer in farmers' fields reported in SAT India (Pal et al., 1982), much more critical base information is required to predict the occurrence of P deficiency. Both the nutrient demand by crops, and capacity of the

Plant physiologist; microbiologist; soil scientist; and principal soil chemist, respectively, International Crops Research Institute for the Semi-And Tropics (ICRISAT), Patancheru, P.O. 302 324, A.P., India.

soils to supply P are not well understood. Plant demand for P by high-yielding sorghum cultivars is high (Table 1). For information on the soil supply and its adequacy, we rely on fertilizer response experiments, a number of which have been conducted at ICRISAT.

Table 1. Mineral concentration<sup>a</sup> in grain and straw, and the total amounts of minerals removed by the crops of sorghum at a yield level of 5 tons of grain and 10 tons of straw per hectare during the 1979 rainy season crop on slightly acidic Alfisol at ICRISAT.

Mineral	concer	neral atration g/g)	Nutrients removed by a crop yielding 5 tons of grain and 10 tons of straw per ha (kg)			
	Grain	Straw	Grain	Straw	Total	
N	14.6	8.0	73.0	80.0	153.0	
K	5.2	10.3	26.0	103.0	129.0	
P	3.7	1.2	18.5	12.0	30.5	
Mg	2.2	2.2	11.0	22.0	33.0	
Ca	0.3	3.0	1.5	30.0	31.5	
S	1.0	0.9	5.0	9.0	14.0	
	μ	g/g				
Al	213	947	1.07	9.47	10.54	
Fe	55	269	0.28	2.69	2.97	
Mn	21	58	0.11	0.58	0.69	
Zn	28	25	0.14	0.25	0.39	
Cu	6	8	0.03	0.08	0.11	

a. Data on mineral concentration represent average values for 12 cultivars grown at four fertility levels with mean slightly acidic-neutral fertilizer, of 45 kg N, 19 kg P/ha. SOURCE: Seetharama N, and Clark, R. B. Unpublished.

## Comparison of crops for their response to phosphate fertilizer

Most of the sorghum grown in the tropics is intercropped. In order to be able to predict the fertilizer needs of sorghum-based cropping systems, we need to know the response of each of the component crops to P fertilizer. A Neubauer-type pot experiment on a severely P-deficient Alfisol (about 1 µg/g Olsen-P) showed quite clearly the marked difference between sorghum and pigeon

pea in their needs for added P. Without added P, pigeon pea growth was satisfactory over a period of 40 days, but both growth and P uptake by sorghum were severely limited (Table 2). These marked differences between sorghum and pigeon pea provided confirmation of results obtained in the field.

The experiment was located on a slightly acidic (pH 6.0-6.5) Alfisol (details in next section). Applications of water-soluble P caused much larger responses in sorghum and millet than in pigeon peas. The response by these cereals exceeded 100%, and the application of as little as 10 kg P/ha was sufficient to achieve much of the maximum possible response (Figure 1). The benefit to

Table 2. Effect of addition of phosphorus on growth of sorghum and pigeon pea 40 days after emergence in a pot experiment on a P-deficient Alfisol, ICRISAT, 1980.

Characteristic	No added P	P added (μg/g)	Least significant difference (0.05)
Dry-matter production (g/pot)			•
Sorghum	0.9	3.5	0.3
Pigeon pea	2.5	2.2	0.5
P uptake (mg/pot)			
Sorghum	0.6	3.7	0.3
Pigeon pea	3.4	4.4	0.7

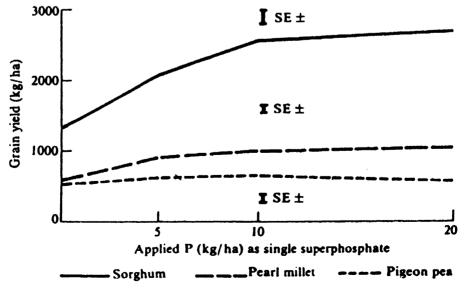


Figure 1. Effect of applied phosphorus on the grain yields of sorghum, millet, and pigeon pea at ICRISAT, 1976 to 1979.

cost ratios from the first increment (5 kg/ha) of P were very attractive. Even more important, was the consistency of sorghum's response to added P on this Alfisol over the years, independent of seasonal rainfall (Figure 2), in contrast to the variability in N responses (Kanwar et al., 1984). In pigeon pea, the response was consistently small in all years; this crop has a small demand, and appears to be efficient in absorbing P from the soil.

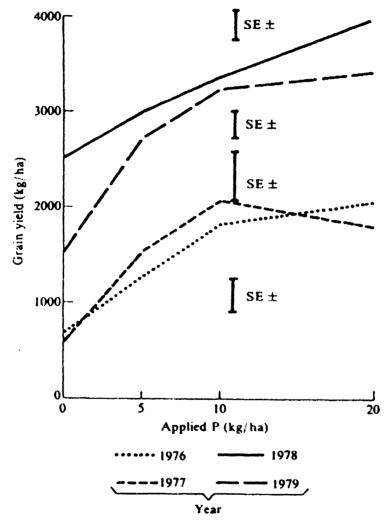


Figure 2. Seasonal variation in the response of sorghum to single superphosphate at ICRISAT.

### Effect of sources of phosphorus

Studies of different sources of P require carefully designed experiments, because residual effects from a single application

may last for several years. Thus, long-term experiments are needed. In such experiments, continuous monocropping is undesirable because of the likelihood of pest and disease buildup. To overcome this problem, we designed a simple two-year rotation of improved cropping systems consisting of an intercrop of millet/pigeon pea in one year in rotation with a sole crop of sorghum in the next year. Duplicate main plots, one for each cropping system (millet/pigeon pea, and sorghum) ensured that each crop could be examined in each year, with a basal dressing of 40 kg N/ha applied to all treatments of millet, and 60 kg N/ha to sorghum.

Using this general design, we commenced an experiment in 1976 on an Alfisol to determine the extent to which rock phosphate could substitute for water-soluble P source. A major reason for studying the effectiveness of the rock phosphate was the shortage of indigenous sulphur sources in India to convert rock phosphate into soluble superphosphate.

Sorghum responded to rock phosphate but to a much smaller extent than to water-soluble P (Figure 3). Applying all the rock phosphate initially for the whole period of 4 years caused a significantly greater response than annual applications, but only at the highest rate. This experiment has two more years to run before completion of its second 4-year cycle. Thorough soil sampling then will indicate the changes in soil nutrient status.

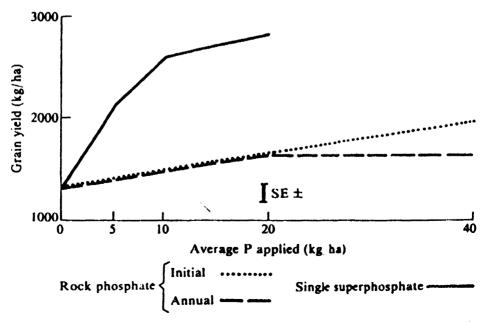


Figure 3. Effect of source and rate of applied phosphorus on sorghum grain yield at ICRISAT, 1976 to 1979.

#### Effect of soil

Preliminary experiments at ICRISAT have also indicated that Vertisols and Alfisols differ markedly in their soil-test/cropresponse relationships for P applied to sorghum. In field experiments conducted in the 1981 and 1982 rainy seasons, sorghum responded appreciably to added P only when the available P in the Vertisol was extremely low (less than about 2 µg/g Olsen-P). Larger responses were observed in the long-term experiment on the nearby Alfisol (described above), with an initially higher available P content (3 µg/g). Thus, the two soils appear to have different critical limits. More rigorous testing was attempted in greenhouse experiments, using four sampling sites for each soil to provide a range in available-P status. Relationships based on the Olsen test differed little between the two soil orders, but when other predictive soil tests were used, very substantial differences were observed (Haile, 1983). Further research is in progress at ICRISAT.

## Variation in sorghum genotypes for phosphorus nutrition physiology

Genotypic variation in nutritional efficiency can be due to one or more characteristics listed in Table 3. Plants adapted to soils of low fertility appear to have characteristics different from those adapted to optimal nutrient supply (Bieleski and Lauchli, 1983). Hence, we should evaluate sorghum genotypes for their nutrient efficiency under two different conditions:

Performance under moderate to adequate nutrient supply; and

performance when nutrient(s) is severely limiting.

## Selection for nitrogen and phosphorus efficiency under adequate nutrient supply

The differential response of sorghum genotypes to the same level of applied nutrients suggests the existence of genotypic differences in the efficiency of nutrient absorption and distribution in the

#### Table 3. Possible components of genetic variations for nutrient efficiency.

- 1. Acquisition from the environment
  - 1. Efficient root system.
    - a) High root to shoot ratio, under nutrient deficiency.
    - b) Greater lateral and vertical spread of roots.
    - c) High root density or absorbing surface, more root hairs, especially under stress.
  - 2. Physiological efficiency of nutrient uptake per unit root length.
  - 3. Generation of reducing and chelating power (e.g., Fe).
  - 4. "Extension" of the root systems by mycorrhizae.
  - 5. Longevity of roots.
  - 6. Ability of roots to modify rhizosphere to overcome low/toxic levels of minerals.
- II. Nutrient movement across roots and delivery to the xylem
  - 1. Lateral transfer through endodermis.
  - 2. Release to xylem.
  - Control of ion uptake distribution by either root or shoot systems, or by both.
    - a) Delivery to root or shoot under deficiency.
    - Overall regulation of nutrient uptake and use at whole plant level.
- III. Nutrient distribution within plants
  - 1. Capacity for rapid storage when nutrient is available, for later use.
  - 2. Degree of retranslocation and reutilization under stress.
  - 3. Release of ions from vacuoles under nutrient deficiency.
  - 4. Natural iron chelating compounds in xylem.
  - 5. Rate of leaf abscission and rate of hydrolysis (of organic P, for example).
- IV. Growth and metabolic efficiency under nutrient limitations
  - 1. Capacity for normal functioning, even under relatively low tissue nutrient concentration.
  - 2. Element substitution (e.g., Na+ for K+).
- V. Polyploidy and hybridity levels.

SOURCES: Chaplin, F. S. 1980.
Gerloff, G. C. and Gabelman, W. H. 1983.
Goodwin, D. C. and Wilson, E. J. 1976.
Saric, M. R. 1983.

plant. We have observed considerable variation for different characteristics concerned with both N and P uptake and utilization (Table 4). Our studies also showed that N and P uptake were highly correlated with crop total dry matter production, and the efficiency of translocation (proportion of the total above-ground plant nutrient in the grain) of these minerals was also highly correlated to harvest index (Figure 4). This suggested that: selection for crop growth may automatically include selection for efficient N and P uptake; and that genotypes with reasonable harvest index will also have a reasonable ability to transfer these minerals to the grain.

Several experiments were conducted under different fertility levels and soil types to study the genotypic differences in nutrient uptake and utilization. We found that genotypes with approximately the same biomass and harvest index could vary significantly in N and P uptake as well as in transfer of nutrients to the grain. Such differences are usually masked when the data for the whole set of heterogeneous genotypes are analyzed together. Table 5 shows the variability for such characters in a set of five selected genotypes falling within a comparable maturity class (except IS 6380). Note, for example, that both P 721 and DL 642 have similar

Table 4. Range of variability for nitrogen and phosphorus and translocation in 14 sorghum genotypes in an Alfisol, postrainy season, 1976.

Variable	Maximum	Minimum	Mean	Coefficient of variation
Grain yield (g/plant)	54	8	35	30
Dry weight (g/plant)	130	51	79	26
Harvest index (HI) (%)	66	12	42	27
N in grain/plant (g)	1.02	0.16	0.51	33
N/plant (g)	1.25	0.51	0.74	. 23
N translocation index <sup>a</sup> (NTI) (%)	83	25	69	21
P in grain/plant (g)	0.60	0.07	0.26	44
P/plant (g)	0.65	0.19	0.33	32
P translocation index <sup>a</sup> (PTI) (%)	93	33	79	20

a. Calculated as the percentage of the total above ground N/P in the grain.

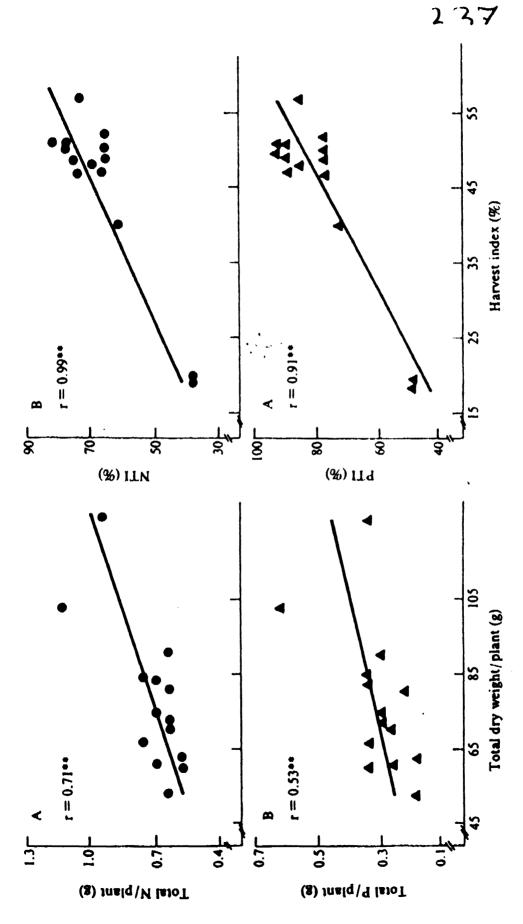


Figure 4. (A) relationships between plant dry weight and N or P per plant; and (B) relationships between harvest index and N translocation index (NTI), or P translocation index (PTI).

Table 5. Nitrogen and phosphorus uptake, translocation, grain and plant dry weights in selected genotypes. Means of three environments with moderate or high N and P fertilization at ICRISAT.

	Genotype						Standard error
Attributes	P 721	IS 858	IS 2223	DL 642	IS 6380	Mean	of mean (SE) ±
Grain yield (g/plant)	18.3	27.2	21.8	24.1	5.1 .	19.3	3.8
Total dry weight (g/plant)	60.6	<b>79</b> .1	53.6	61.5	70.2	65.0	4.4
Harvest index (%)	30.2	34.4	40.7	39.2	7.3	32.0	2.6
Total N (g/plant)	0.78	0.77	0.48	0.56	0.67	0.65	0.06
Nitrogen translocation index (%)	44.9	46.8	56.3	42.9	23.9	43.1	4.1
g grain/g N taken up by the plant	23.5	35.3	45.4	43.0	7.6	29.7	13.1
g dry wt/g N in the plant	77.7	102.7	111.7	109.8	104.8	100.0	14.1
Total P (g/plant)	0.19	0.38	0.4 i	0.43	0.31	0.34	0.05
Phosphorus translocation index (%)	63.2	60.5	41.5	23.3	35.5	44.1	5.8
g grain/g P in the plant	96.3	71.6	53.2	56.0	16.5	56.8	12.9
g dry wt/g P in the plant	318.9	208.2	130.7	143.0	226.5	191.2	31.4
Days to 50% flowering	65	67	67	69	82	70	10

dry weights, but P 721 takes up 39% more nitrogen than DL 642, and has 9% greater nitrogen transfer ability. Similarly, IS 858 and DL 642 have nearly the same harvest index, but the P translocation index for IS 858 is 22% greater than for DL 642.

In order to conclude whether or not the selection for dry weight and harvest index also includes selection for nutrient uptake and translocation to the grain, crosses were made between parents listed in Table 5.  $F_2$  plants were selected for a range of dry weight per plant and harvest index, and in  $F_3$  progenies estimates of dry weight, grain yield, as well as N and P in grain and whole plants, were determined. The correlations between biomass and total nutrient taken up by the different groups of  $F_3$  progenies were again very high (P>0.01). Similar relationships were observed between harvest index and the N and P transfer efficiency.

Thus, the selection for biomass and harvest index under adequate nutrient supply also includes selection for traits concerned with nutrient (N and P) uptake and translocation to the grain. Under moderate to high soil-fertility status, breeding programs specifically aimed at increasing the efficient use of major nutrients are not needed because the inefficient entries will be culled out in the routine process of multilocational trials, or when tested under different fertility levels (Rao et al., 1981; Seetharama et al., 1984; also unpublished data of G. Alagarswamy on pearl millet at ICRISAT: personal communication).

## Genotype evaluation under low soil phosphorus and without fertilization

The variability among the few selected genotypes in physiological nutrient use efficiency is shown in Table 5. Dry matter produced per unit P taken up by the plant was more variable than the dry matter production per unit N. In 1977, we selected 140 germplasm entries from a drought-screening nursery consisting of 1200 entries originating from drier regions of the SAT. While most of the lines showed severe P deficiency, these selected lines were free of such symptoms, and have comparatively high grain yields. Later they were repeatedly screened in a field of low soil P status (2 µg/g Olsen-P; an Alfisol, with soil-P further depleted by repeated cropping with maize) for comparing their ability to grow and produce reasonable yields. Table 6 shows the variations in a few selected germplasm and check entries for several characteristics.

Table 6. Genotypic differences in P use efficiency and mycorrhizal colonization in an Alfisol with Oben P>0.5 µg/g during the 1983 rainy season at

Sorghum genotype	Origin	Days to flower	Grain	Biomass	Harvest index	Phosphorus translocation index (PTI)	P uptake	P use c	P use efficiency in plant	Root o	Root colonized by mycorrhizaed
			(g/m²)	<b>(g</b> / m³)	<b>%</b>	<b>%</b>	(g/plant)	Grain Ge	in Biomass (g/g P)	Fieldb	Pot studya
Germplasm entries											
IS 10734	Chad	62	145	\$	28.5	73.4	0.41	366	1773	;	
IS 10747	Chad	<i>L</i> 9	*	337	24.9	2 89	7	3 2	243	<b>\$</b> ;	57(22)4
15 7501	Nigeria	102	35	1564	3.0	} <u>e</u>	70.0	<u> </u>	<b>X</b> :	\$ 5	(52)
15 1320	Nigeria	8	61	929	· ·	7 81	<b>5</b> 5	<b>?</b> ?	1501	<b>70</b>	(8) (8)
IS 3860	Mali	98	23	518	4.2	27.3	0.37	۲ ج	762	<b>5</b> 2	65(33)
Breeding lines								}		ξ.	(7)07
DL 642	India	8	•		•						
7 130		? ;	0	20 20 7	2.9	13.4	0. <b>7</b>	<b>£</b>	1358	25	2410)
	India	8	113	531	22.0	73.6	0.58	3	Š	;	
SAS	India	<b>3</b>	7	28	2.5	~	0 33	? ?	3 5	î	T
P 721	NSA	08	4	9	3.5	) ·	0.32	7 6	200	i	Ţ
Mean for 24 entriesd		78	40.2	415	10.7	35.0	0.42	7 [0]	917 1015	1 \$	<u> </u>
Standard error of										<b>!</b>	5
mean (SE) (±)		2.5	14.8	112	2.3	8.6	0.08	23	<b>%</b>	•	15
Coefficient of											
variation (CV) (%)		4.5	34.4	38	30.2	34.7	28.7	33	23	8	4
Minimum		19	2.7	110	0.41	9	0.13	•	973	,	1
Maximum		<u>8</u>	15.7	1264	28.5	73.6	0.89	355	<u>1</u> 231	3 6	23 <b>2</b> 5
4. Sampled at 40 days after planting	atine										

Sampled at 40 days after planting.

Sampled at phytiological maturity.

The figures in parentheses represent percent colonization when the pots are irrigated with 10 to solutions. Entries studied totaled & except for root colonized by mycorrhizae-which totaled 7 for field & 6 for pot study. ت- ن غمله

While differences in maturity and harvest index hinder accurate measurements of efficiency, the superiority of some genotypes (e.g., IS 10734 or IS 10747 over DL 642 and CSV 5) is clear both in grain yield and P uptake (Table 6). Among the released cultivars, the common Indian hybrid CSH 6 showed comparable efficiency to IS 10734 or IS 10747, indicating that the conventional breeding program has also resulted in fairly P-efficient cultivars.

No relationship was observed between concentration of P in plants and either grain or biomass productivity (Figure 5). For identifying the efficient genotypes, we need to consider both high P uptake as well as high efficiency of P utilization in grain and biomass productivity (Table 6). However, utilization quotients can vary widely within a genotype depending upon the quantity and pattern of nutrient supply (Myers and Asher, 1982; also see following section).

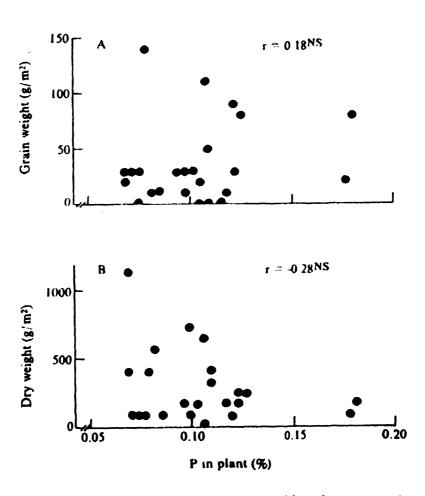


Figure 5. Relationships between the concentration of P in plant at maturity and grain (A), or dry matter yields (B) at ICRISAT during the 1983 rainy season.

## Mycorrhizae

### Differences among host genotypes

A survey of sorghum grown at ICRISAT in Alfisol soils showed extensive colonization of the roots by vesicular-arbuscular mycorrhizae (VAM). We found spore types of the following four major genera of VAM fungi: Glomus, Gigaspora, Acaulospora, and Sclerocystis. The extent of root colonization varied with location and plant cultivar, suggesting a possible cause for differences in the amount of benefits that the crop derives from such a symbiotic association under different conditions. The mycorrhizal root colonization, plant growth, and P-uptake response to inoculation vary with isolate of the mycorrhizal fungus used (Krishna and Diart, 1984). The dependence of symbiotic efficiency on the fungal isolate and soil environment is now well known (Abbot and Robson, 1982; Hayman, 1982) but differences between host genotypes are poorly understood.

Differences between host genotypes for percentage root colonization were detected both in field, and in pot culture using low P Alfisol (lµg/g soil; extracted with NaHCO<sub>3</sub>) (Table 6). Addition of P resulted in a decrease in colonization rates, but the "efficient" genotypes such as IS 10734, IS 10747, and IS 1320 still showed higher colonization than "inefficient" hosts such as DL 642. Some interactions between P levels and host genotypes were apparent; the interactions between P levels and isolate efficiency (Howeler and Sieverding, 1983) have not yet been investigated.

#### Response to mycorrhizal inoculation

In a pot trial, using Alfisol mixed with sand, 1:1 v/v, inoculating sorghum hybrid CSH 5 with five separate species of mycorrhizal fungi increased growth by 15% to 120% (Table 7). Different mycorrhizal cultures varied widely in their ability to stimulate plant growth. The percentage of mycorrhizal colonization and the inorganic P in the xylem exudate correlated significantly, just as the correlation between colonization rate and plant P content (Figure 6). This indicates that P in xylem exudate can be used to select plants and fungus isolates for effectiveness of the symbiosis, in terms of P uptake by the plant.

Table 7,	Influence of mycorrhizal inoculation on shoot dry matter phosphorus
	concentration in the tissue, and the extent of mycorrhizal colonizationa.

Fungal culture	Shoot dry matter (g/plant)	P concentration in tissue (mg/g dry wt)	Root colonization by mycorrhizae (%)
Glomus fasciculatum	1.93	5.1	66
Glomus mosseae	2.20	3.5	52
Gigaspora margarita	2.07	4.9	48
Glomus fasciculatum (E3)	1.43	1.8	40
Gigaspora calospora	1.14	3.1	36
Acaulospora laevis	1.33	2.2	32
Control	0.98	1,7	25
Standard error of			
mean (SE) (+)	0.20	0.2	0.5
Coefficient of variation			
(CV) (%)	21	13	11

a. 54-day-old plants, all values are means of 5 replicate pots each with one plant grown in 1:1
 v/v sand: Alfisol soil mixture steam sterilized before sowing sorghum hybrid CSH 5.

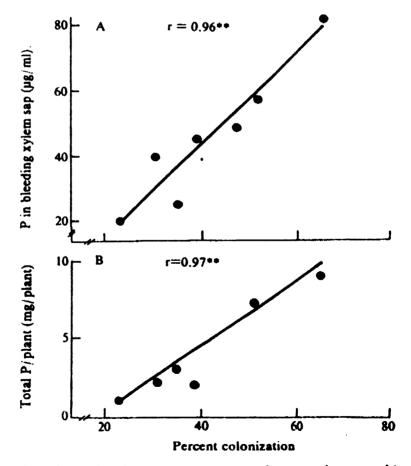


Figure 6. Relationships between percent root colonization by mycorrhizal fungi and inorganic phosphate (P) determined by vanadium molybdate method in bleeding xylem sap (A), or total P/plant (B) from pot experiments at ICRISAT, 1984.

#### Discussion

Our current understanding of the nature of crop adaptation to low levels of natural or added inputs is incomplete. On the one hand, some have unreasonable expectations that crops can be grown continuously without fertilizer; but, on the other hand some have the concern that use of "efficient" genotypes may "mine and squander" limited soil nutrients (Lambert and Arnason, 1982).

Clearly, the problems of P stress cannot be easily resolved, but they can be reduced to manageable proportions if many different aspects—pedological, soil amendment, fertilization, foliar feeding, ecological (e.g., intercropping), and plant breeding—are studied in concert (Fox, 1979). The efficient uptake of the soil P by plants (directly or through mycorrhizae) offers only a temporary solution in the absence of input of external P into the system. In the case of N, at least when high yields are not important, farmers with limited resources can minimize fertilizer N application by introducing legumes into their cropping systems. In the case of P, fertilization can, at best, be only delayed, but its eventual need is unavoidable. Hence, our aim should be to search for more specific combinations of plant genotypes, soils, and soil fertility practices to optimize net returns (Foy, 1983).

Breeding for P stress can be most efficiently carried out in the well-defined target areas, within narrower limits of the theoretical maximum stress and optimum growing conditions (Buddenhagen, 1983). Extremely high levels of efficiency (or stress resistance) may not be a realistic goal, as the different mechanisms involved in adaptation of plants to nutrient stress countervail (trade off) for each other. Plant breeders must be conscious of, and responsive to, both the specific local features of the environment and the possibility of better management techniques. For example, with acid soils of low P status, the soil acidity can be an advantage, in one way: the cheaper rock phosphate may be almost as efficient as the more costly water-soluble P. As P deficiency in crops on acid soils is commonly associated with a variety of other stresses (including drought or disease stress), breeders must carefully select and characterize their test locations.

Because the inheritance of traits related to P nutrition in sorghum is more complex than that of resistance to Al toxicity (Clark, 1982), screening and breeding for the former is likely to be more difficult. A nutrient culture system may supplement field

evaluations to a much greater extent for screening for mineral toxicity (Duncan et al., 1983), but its usefulness for screening for P uptake, especially with mycorrhizal involvement, has been questioned (Howeler, 1981) However, considering the case with which nutrient stress can be quantified, and the possibility of creating uniform stress for screening, it should be easier to breed for resistance to mineral stress, than for resistance to drought or most other biotic stresses.

In addition to improving P uptake in P deficient or high-P-fixing soils, mycorrhizae are believed to assist plants to absorb other nutrients which may be limiting under acid soil conditions (Hayman, 1982) Mycorrhizae also confer drought resistance by increasing the water uptake, and confer disease resistance either indirectly by preventing predisposition of host plants to weak parasites, such as stalk rots (Jordan et al., 1984), or directly by competing with the soil-borne pathogens (Gerdemann, 1975). Mycorrhizae could also be helpful in overcoming the negative interaction between efficiency of uptake of different minerals (Brown et al., 1977) such as the interaction between the uptake of P and that of iron (Fe) or copper (Cu) (Timmer and Layden, 1980).

The efficiency of mycorrhizal fungi in promoting nutrient or water uptake may depend on a wide variety of factors. Fungus adapted to an alkaline soil may be less effective in acid soils. It is necessary to have an understanding of the effects of environmental stresses (e.g., temperature or waterlogging), and cultural practices (e.g., application of fungicides or lime) on the mycorrhizal association of sorghum plants. Research at ICRISAT is being directed to select sorghum lines showing higher colonization rates under a wide range of environmental conditions (inluding soil P levels), and to quantify the mycorrhizal benefit to the host plant when grown in soils with low P status, especially in lateritic soils.

Research on several aspects of P nutrition of sorghum is urgently needed. Better definition of the efficiency of mycorrhizal colonization, and the efficiency of use of P taken up by the plant for its growth and grain yield are required for practical applications. However, gross agronomic evaluation of genotypes under representative field environments should precede selection based on physiological criteria. Evaluation and improvement of methodologies are needed for characterizing the critical limits of nutrients in different soil types. The role of mycorrhizal colonization in determination of critical levels of P in the soil should also

be researched. Critical tissue concentrations in sorghum genotypes, along with the possible interaction with other factors affecting crop growth (Myers and Asher, 1982) and health, also need to be investigated before starting any large-scale breeding efforts to increase nutrient efficiency. Such work on critical concentrations is currently in progress in Australia (C. J. Asher and D. G. Edwards, University of Queensland, personal communication).

As seen in Table 6, the sorghums collected in West Africa seem to be more efficient in P uptake and utilization. Genotypes with the best developed nutritional efficiency traits can be expected to be found in the local cultivars from the most infertile soils, e.g., the leached, Alfisol regions of West Africa (S. W. Buol, North Carolina State University, Raleigh, NC, USA, personal communication). It is worthwhile to screen more sorghum germplasm from the sub-Saharan West Africa, especially from the mediumhigh rainfall areas, and from similar regions in Tanzania, Thailand, and the hilly areas of eastern India.

### Summary

Phosphorus (P) deficiency is common in the tropics. Because the need for added P depends upon characteristics of both the crop and the soil, systematic studies are being made in our experiments at ICRISAT, India. Sorghum and pearl millet on an Alfisol responded substantially to added P fertilizer, but the response of pigeon pea was small. Only 10 kg P/ha was needed to achieve most of the maximum possible response; rock phosphate was much less effective than water-soluble P, as the soil was only slightly acidic. Indications have been obtained that Vertisols differ from Alfisols in their soil test/crop response relationships for P applied to the sorghum.

Where fertility is adequate or nearly so, no special breeding program for increasing the efficiency in uptake or utilization of P appears to be needed; plant performance gives an adequate index of P efficiency. However, because there is significantly more genotypic variation in the efficiency of P uptake and utilization under very low P supply than under a moderate supply, breeding cultivars for low P soils is worth pursuing.

Genotypes adapted to low P conditions showed a greater degree of root colonization by mycorrhizal fungi. Response to inoculation with different mycorrhizal fungi increased dry matter and P content of sorghum plants more than two-fold. Estimation of inorganic P in the bleeding xylem sap can be a quick test for rate of colonization. The significance of the above findings for improvement of sorghum grown on low-nutrient status soils is discussed.

#### References

- Abbott, L. K. and Robson, A. D. 1982. The role of vesicular-arbuscular mycorrhizal fungi in agriculture and the selections of fungi for inoculation. Aust. J. Agric. Res. 33:389-408.
- Bieleski, R. L. and Lauchli, A. 1983 Synthesis and outlook. In: Lauchli, A. and Bieleski, R. L. (eds.). Encyclopedia of plant physiology, New Series, Vol. 15B. Springer-Verlag, Berlin, Germany, p. 745-755.
- Brown, J. C.; Clark, R. B.; and Jones, W. E. 1977. Efficient and inefficient use of phosphorus by sorghum. Soil Sci. Soc. Am. J. 41.747-750.
- Buddenhagen, I. W. 1983. Breeding strategies for stress and disease resistance in developing countries. Ann. Rev. Phytopathol. 21:385-409.
- Chaplin, F. S. 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11:223-260.
- Clark, R. B. 1982. Mineral nutritional factors reducing sorghum yields: micronutrients and acidity. In. ICRISAI (International Crops Research Institute for the Semi-Arid Tropics), sorghum in the eighties: Proceedings of the International Symposium on Sorghum, ICRISAT, 1981, Patancheru, A.P., India, p. 179-190.
- Duncan, R. R.; Clark, R. B.; and Furlani, P. R. 1983. Laboratory and field evaluations of sorghum for response to aluminum and acid soil. Agron. J. 75:1023-1026.
- Fox, R. L. 1979. Comparative responses of field grown crops to phosphate concentrations in soil solutions. In: Mussell, H. and Staples, R. (eds.). Stress physiology in crop plants. John Wiley and Sons, New York, NY, USA p. 81-106
- Foy, C. D. 1983. Plant adaptation to mineral stress in problem soils. Iowa State J. Res. 57:339-354.
- G. and Clarkson, D. T. (eds.). The development and function of roots. Academic Press, London, England p. 575-591.

- Gerloff, G. C. and Gabelman, W. H. 1983. Genetic basis of inorganic plant nutrition. In: Lauchli, A. and Bieleski, R. L. (eds.). Encyclopedia of plant physiology, New series, Vol. 15B. Springer-Verlag, Berlin, Germany. p. 453-480.
- Goodwin, D. C. and Wilson, E. J. 1976. Prospects for selecting plants with increased P efficiency. In: Blair, G. L. (ed.). Prospects for improving efficiency of phosphorus utilization: Proceedings of a symposium held at the University of New England, 1976, Armidale, S.S.W. Australia p. 131-139.
- Haile, M. 1983. Comparison of soil test/plant response relationships for phosphorus applied to sorghum on Vertisols and Alfisols at International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). M.S. dissertation. Addis Ababa University, Addis Ababa, Ethiopia.
- Hayman, D. S. 1982. Practical aspects of vesicular-arbuscular mycorrhizae. In: Subbarao, N. S. (ed.). Advances in agricultural microbiology. Oxford and IBH Publishing Company, New Delhi, India. p. 325-373.
- Howeler, R. H. 1981. The effect of mycorrhizal inoculation on the phosphorus nutrition of cassava (Manthot esculenta Crantz). In: Russell, R. S; Igue, K.; and Mehta, Y. R. (eds.). The soil/root system in relation to Brazilian Agriculture. Fundação Instituto Agronomico do Paraná, Londrina, Paraná, Brazil. p. 243-258.
  - and Sieverding, E. 1983. Potential and limitations of mycorrizal inoculation illustrated by experiments with field-grown cassava. Plant Soil 75:245-261.
- Jordan, W. R.; Clark, R. B.; and Seetharama, N. 1984. The role of edaphic factors in disease development. In: ICRISAT (International Crops Research Institute for the Semi-Arid Tropics): sorghum root and stalk rots: a world review. Proceedings of the Consultative Group discussion on research needs and strategies for control of sorghum root and stalk rots, 1983, The Rockefeller Foundation, Bellagio Study and Conference Center, Bellagio, Italy. p. 87-97.
- Kanwar, J. S.; Rego, T. J.; and Seetharama, N. 1984. Fertilizer and water-use efficiency in pearl millet and sorghum in Vertisols and Alfisols of semi-arid India. Fertilizer News 29(4):42-52.
- Krishna, K. R. and Diart, P. J. 1984. Effect of mycorrhizal inoculation and soluble phosphorus fertilizer on growth and phosphorus uptake of pearl miliet. Plant Soil 81:247-256.
- Lambert, J. D. H. and Arnason, D. T. 1982. Nitrogen distribution in hybrids and local corn varieties and its possible relationship to a

- declining soil nitrogen pool under shifting agriculture at Indian Church, Belize. Plant Soil 67:119-127.
- Myers, R. J. K. and Asher, C. J. 1982 Mineral nutrition of grain sorghum, macronutrients. In: ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) sorghum in the eighties: Proceedings of the International Symposium on Sorghum, ICRISAT, 1981, Patancheru, A.P., India, p. 161-177.
- Pal, U. R.; Upadhyay, U. C.; Singh, S. P., and Umrani, N. K. 1982. Mineral nutrition and fertilizer response of grain sorghum in India-a review over the last 25 years. Fort. Res. 3:141-159.
- Rao, K.; Rao, S. S.; and Rao, N. G. P. 1981. Genotype X input management interactions on sorghum. Indian J. Genet. Plant Breed, 41:54-58.
- Sallanpaa, M. 1982. Micronutrients and the nutrient status of soils a global study. FAO Soils Bull. 48:444 FAO, Rome, Italy.
- Sánchez, P. A. and Salinas, J. G. 1981. Low-input technology for managing Oxisols and Ultisols in tropical America. Adv. Agron 34:279-406.
- Sarie, M. R. 1983. Theoretical and practical approaches to the genetic specificity of mineral nutrition of plants. In. Sarie, M. R. and Loughman B. C. (eds.). Genetic aspects of mineral nutrition. Martiaus Nijhoff/Dr J. Junk Publishers. The Hague, Netherlands p. 1-14.
- Seetharama, N.; Nath, B.; and Verma, P. K. 1984. Selection for grain yields in low nitrogen fertility conditions. Cereal Res. Comm. 12(1-2): 47-52.
- Timmer, L. W. and Layden, R. F. 1980. The relationship of mycorrhizal infection to phosphorus induced copper deficiency in sour orange seedlings. New Phytol. 85:15-23