

Phosphorus uptake and use efficiency of diverse West and Central African sorghum genotypes under field conditions in Mali

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Abstract

Aims Sorghum [*Sorghum bicolor* (L.) Moench], a staple crop in West and Central Africa (WCA), is mostly cultivated on soils with low phosphorus (P) availability and thus adaptation to those conditions is vital for food security. Assessment of genotypic variation of WCA sorghum for P uptake and P use efficiency is undertaken to understand the diversity available and opportunities for its use.

Method We assessed mature plant yield, P uptake and P use efficiency traits of 70 diverse WCA sorghum genotypes under –P (no P fertilization) and + P field conditions in Mali in 2010, to discover differences among all genotypes tested and between and within specific genotype groups.

Results Large significant genotypic variation for P uptake and P use efficiency traits were observed for all genotypes among and within landrace and researcher bred pools under –P conditions. P uptake traits had a

larger genotypic variation than P use efficiency traits. Landrace genotypes showed generally higher P uptake and grain P concentration while formally bred genotypes exhibited a higher P use efficiency. Photoperiod sensitivity was related to higher P uptake.

Conclusion Genotypic selection for P uptake and P use efficiency traits to improve adaptation to low P soils is possible in sorghum. Use and further study of WCA sorghums for adaptation to low P availability is appropriate as this germplasm shows large variation for P uptake and use efficiency and higher levels of P use efficiency than other important cereals.

Keywords Sorghum · Phosphorus efficiency · Genetic diversity · Plant breeding

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Introduction

Low phosphorus (P) soils are a major constraint to crop production in West and Central Africa (WCA) (Buerkert et al. 2001). Sorghum [*Sorghum bicolor* (L.) Moench], a staple crop in WCA, is mostly cultivated on low-input marginal soils and thus adaptation of sorghum to those conditions is vital for food security (Doumbia et al. 1993). P acquisition plays an important role for crop adaptation to low P soils (Sattelmacher et al. 1994; Wang et al. 2010) and a higher internal P use efficiency could help to limit soil nutrient mining (Ahmad et al. 2001; Rose and Wissuwa 2012), especially in low-input farming conditions.

Significant genotypic variation for traits related to P acquisition and P use efficiency has been observed in various crops e.g. rice, wheat, barley, pigeonpea, clover and maize (Silva et al. 1992; Sattelmacher et al. 1994; Trolove et al. 1996; Subbarao et al. 1997; Römer and Schenk 1998; Wissuwa and Ae 2001; Manske et al. 2001; Rose et al. 2010). However, despite the extensive cultivation of sorghum under low P conditions in WCA, no systematic characterization of traits related to P acquisition and P use efficiency is available for the diverse varieties that are grown there. Significant and agronomically important grain yield differences under low P conditions were observed in a set of sorghum landraces and formally bred varieties from WCA (Leiser et al. 2012b). Furthermore it was shown that this variation can be exploited to breed for higher grain yield and that spatial adjustment methods can be helpful for effective genotypic evaluation under low P availability conditions (Leiser et al. 2012a).

Both traditional landrace varieties of the Guinea-race, originating from West Africa (De Wet and Harlan 1972), and newly bred varieties, developed by introgressing exotic germplasm into local Guinea-race materials, are now cultivated in the Sudanian zone of WCA. As in rice (Wissuwa and Ae 2001), a few of the landrace varieties show specific adaptation to low P soil conditions (Leiser et al. 2012b), raising questions of possible differences for P acquisition and P use efficiency between farmer landrace and researcher-bred materials with introgressed exotic germplasm. Additionally, WCA sorghum varieties differ widely for stem internode-lengths and degree of photoperiod sensitivity, influencing plant height, harvest index, time to flower and the balance between pre- and post-flowering growth periods. Exploring the existence of any relationships between P acquisition or use efficiency and varietal differences for patterns of growth would be of interest, potentially enabling design of more

efficient sorghum improvement strategies for adaptation to low P soils.

In order to better exploit various mechanisms for low P adaptation in sorghum we seek to (i) characterize the genetic diversity for grain and plant P uptake, use efficiency, concentration and partitioning among diverse WCA sorghum germplasm, (ii) determine the relationships among measures of P acquisition, P use efficiency and yield, and (iii) examine the differences among and within genotype groups based on race and growth pattern.

Materials and methods

Genotypes

The 70 sorghum varieties used in this study represent the diversity of cultivars and breeding lines adapted to the Sudanian zone of Mali. Approximately half of the entries are landrace varieties, all belonging to the Guinea-race using the classification of Harlan et al. (1972a) (Table 1). These accessions are representative of the landraces cultivated in the zone, being tall (stem-internode length ≥ 20 cm) with the majority being intermediate- to highly-photoperiod sensitive. Four of the latest maturing entries proved to be susceptible to sorghum midge (*Stenodiplosis sorghicola*), incurring nearly complete grain losses, and were thus excluded from analyses. The remaining entries were bred from biparental Caudatum \times Caudatum and Guinea \times Caudatum-race crossing and backcrossing, respectively, or from a Guinea-race random-mating population. These bred varieties represent a continuum from Guinea- to Caudatum-race phenotypes for grain- and glume-characteristics, with diversity for plant height, and intermediate to non-sensitive photoperiod sensitivities. There

Table 1 Characterization of genotypes based on their breeding history, race, photoperiod sensitivity and internode length

Type	Race			Photoperiod Sensitivity ^a			Internode Length ^b			
	Caudatum	Caudatum-Guinea	Guinea	ns	s	vs	s	m	l	
Researcher Bred	32	10	22	0	15	11	6	12	10	10
Landrace	34	0	0	34	1	10	23	0	4	30

^a Based on heading date differences (Clerget et al. 2007) between a 6th June and a 8th July sowing date in 2009, ns: non-sensitive = 19–29 days, s: sensitive = 4.1–18 days and vs: very sensitive ≤ 4 days difference

^b s: short ≤ 14 cm, m: medium = 15–19 cm, l: long ≥ 20 cm

is no strong genetic relationship between the landrace varieties and the bred varieties, as none of these landrace varieties occur in the pedigrees of varieties derived from bi-parental crossing, and only one landrace variety was among the 13 landraces parents of the random mating Guinea population (Rattunde et al. 1997) from which the five population derivatives originated.

Field experiments

Field trials were conducted in Mali, West Africa at the Samanko (12° 31' N, 8° 4' W) station of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in 2010. Two separate trials were planted (sowing date: 26/06/2010) in adjacent fields, one with phosphorus fertilization (denoted “+P”) and one without (denoted “-P”). The + P field was fertilized with 100 kg ha⁻¹ diammonium phosphate (18-46-0) as basal fertilizer and urea (50 kg ha⁻¹) (46-0-0) as top dressing. This field was cultivated with sorghum in 2009 with 100 kg ha⁻¹ DAP, and was in fallow for more than 3 years before 2009. The -P field received only topdressing with urea at rates that gave equivalent units of nitrogen as received by the + P field. This field was cultivated with sorghum for 4 years and mixed legumes for 1 year in the preceding 5 years, all with zero P fertilization, and was fallowed for more than 3 years preceding 2005. Each trial consisted of 70 genotypes sown in an α -design with four complete replicates, each with 14 incomplete blocks of five plots. Plots consisted of two 3-meter rows with 75 cm distance between rows and 30 cm between hills within rows. Hills were thinned to two plants, resulting in a total of ~9.8 plants m⁻². A single border row planted

with a medium tall, medium late maturing genotype separated each test plot to minimize neighbor effects. Five soil samples were taken from each rep in the + P and -P fields and were analyzed for plant available P (Bray-1 P), pH, aluminum saturation and organic carbon. No major differences between the -P and the + P field were observed for these soil parameters except for Bray-1 P, and for organic carbon (0.29 % in -P and 0.38 % in + P; $p < 0.001$). The -P field had a mean Bray-1P value of 5.69 mg P kg soil⁻¹, whereas the + P field showed a mean value of 19.18 mg P kg soil⁻¹. Several P uptake and utilization-efficiency parameters were observed or calculated for physiological mature plant material in both the -P and + P trials (Table 2). Plant material was harvested from the whole plot and air dried until no weight changes were observed. Due to difficulty of measuring the very large stover biomass under the + P conditions it was only recorded in two of the four replications, whereas it was recorded in all four replications under -P. Therefore, all traits calculated with stover yield (SY) differ for level of replication between + P and -P conditions. P concentrations of stover and grain samples were analyzed using an inductive coupled plasma optical emission spectrometer (ICP-OES) as described in VDLUFA (2011).

Data analysis

Single trial analysis

Each trait in the -P and + P trial was separately analyzed with a mixed model REML-analysis considering the genotype factor as fixed and replication and incomplete

Table 2 Phosphorus concentration, uptake and utilization traits of sorghum evaluated at Samanko, 2010 under -P and + P conditions

Trait	Description	Calculation	Unit
GY	Grain yield		t/ha
SY	Stover yield		t/ha
BMV	Total biomass yield	GY + SY	t/ha
PCG	P concentration in grain		mg/g
PCS	P concentration in stover		mg/g
PG	P content of grain	PCG x GY	kg/ha
PS	P content of stover	PCS x SY	kg/ha
PBM	P content of total biomass	PG + PS	kg/ha
PHI	P harvest index	PG/PBM	
PUTIL-G	P-utilization for grain production	GY/PBM	kg/gP
PUTIL-S	P-utilization for stover production	SY/PBM	kg/gP
PUTIL-BM	P-utilization for biomass production	BMV/PBM	kg/gP

block factors as random. If this incomplete-block analysis did not yield repeatability (w^2) values $w^2 \geq 0.75$, several spatial models were fitted as described in a companion study (Leiser et al. 2012a); the optimum model was identified based on *Akaike's information criterion* (AIC), and predicted values and standard errors were computed for each genotype, taking the factor genotype as fixed. The analysis of grain P concentration (PCG) and grain P content (PG) in $-P$ used grain aluminum content as co-variable as fixed regression factor to account for possible contamination of the seeds with soil. This was not necessary in $+P$ since no significant Al effect was detected. PUTIL-G-Hi was calculated using harvest index as a fixed regression factor in a mixed model to account for PUTIL-G independent of harvest index. The genetic coefficient of variation (GCV) and the repeatability (w^2) of each trait were calculated as described in Leiser et al. (2012b). For comparing the different genotypic groups for their mean performance, an analysis of variance was fitted with the genotypic adjusted means as the response variable and the genotype group as a fixed factor.

Combined analysis across $-P$ and $+P$

A two stage multi-environment combined analysis was conducted so that adjusted means of each entry per trial could be used, where the adjusted means were computed separately for each trial accounting for any specifics such as spatial adjustment if needed. A combined weighted mixed-model REML -analysis, as described in Leiser et al. (2012b), was applied. The genetic correlations between $-P$ and $+P$ performance were calculated assuming no environmental covariance (Cooper and DeLacy 1994). The coefficient of genetic correlation can be stated as:

$$r_G = \frac{r_P}{\sqrt{w_{T1}^2 \times w_{T2}^2}},$$

where r_P is the phenotypic correlation based on adjusted means and w_{T1}^2 and w_{T2}^2 are the repeatabilities (broad sense heritability) of the respective traits.

All analyses were conducted with the statistical software package Genstat 15 (<http://www.vsnl.de/software/genstat>) and R (R Core Team 2013).

Results

Genetic variation for P uptake and P use efficiency traits

Highly significant differences among genotypes and high repeatabilities ($w^2=0.76-0.90$) were observed in $-P$ and $+P$ conditions for P concentration (PCG, PCS), uptake (PG, PS, PBM), and use efficiency (PUTIL-G, PUTIL-S, PUTIL-BM) traits (Table 3). More than two-fold genotypic ranges existed in $-P$ conditions for traits related to P concentration, uptake, and use efficiency. P uptake traits showed somewhat greater genetic variation (GCV) than P use efficiency traits under $-P$ conditions, but tended to be lower under $+P$ conditions. The $-P$ and $+P$ means differed significantly for all traits. There was a significant genotype-by-phosphorus (GxP) interaction for most P uptake and use efficiency traits, but generally the GxP-interaction variance components were smaller than the variance components for G (ratio G:GxP >1). Stover P concentration was the only trait with non-significant genotypic differentiation across the two P treatments, and comparatively large GxP interaction, pointing to highly variable responses of the genotypes to the two P treatments for this trait.

Relationships among yield, P uptake and P use efficiency traits

Grain and stover yields were significantly correlated in $-P$ (Fig. 1) but not in $+P$ (Suppl. 1). Whereas P concentrations in grain and stover exhibited negative correlations to grain yield that were similar in both $-P$ and $+P$, the correlation between grain yield and PHI under $-P$ was non-existent but strongly positive ($r=0.52^{***}$) in $+P$ conditions (Suppl. 1). Correlations between P uptake and P use efficiency were near 0 for grain but significant positive for stover and total biomass production in $-P$ conditions. Under $+P$ conditions, in contrast, they were moderately positive for grain and 0 for total biomass (Suppl. 1). The correlations between PUTIL-G and PCG were highly negative in both P conditions, as were the correlations between PHI and PCS. The harvest index (grain as percent of total biomass; HI) in both $-P$ and $+P$ conditions was highly correlated with PUTIL-G ($r=0.76^{***}$; $r=0.77^{***}$) and PHI ($r=0.82^{***}$; $r=0.69^{***}$).

Genotypic performance in $-P$ and $+P$ conditions were highly related for yield and P use efficiency traits, with genetic correlations ranging from 0.71 to 0.93

Table 3 Yield, P-concentration, acquisition, and utilization trait means (μ), genotype minimum (Min) and maximum (Max), repeatability (w^2) and genetic coefficient of variation (GCV) under low (-P) and high-P (+P) conditions, and estimated genetic (σ^2_G)and genotype by P-level interaction variance ($\sigma^2_{G \times P}$) components across P-levels and genetic correlations (r_G) between -P and +P performance

Trait ^a	-P						+P				Combined		
	μ^b	Min	Max	σ^2_G	w^2	GCV	μ^b	σ^2_G	w^2	GCV	σ^2_G	$\sigma^2_{G \times P}$	r_G
GY	0.98	0.38	1.84	***	0.79	29.2	2.02	***	0.81	20.9	8.8***	3.1*	0.75
SY	2.60	0.70	5.20	***	0.9	39	6.91	***	0.87	31.9	194.3***	45.6**	0.93
BMV	3.54	1.01	5.93	***	0.84	31.8	8.67	***	0.8	25.1	188.8***	34.4 ns	0.91
PCG	3.02	1.89	4.10	***	0.86	14.2	3.58	***	0.92	12.1	108.2***	28.8**	0.75
PCS	0.42	0.23	0.64	***	0.76	16.2	0.77	**	0.57	17.9	2.3 ns	4.0*	0.32
PG	2.83	1.15	5.49	***	0.77	23.8	6.97	***	0.71	16.3	34.9**	30.9**	0.53
PS	1.09	0.21	2.72	***	0.88	44	5.11	*	0.72	27.8	20.7**	14.1 ns	0.54
PBM	3.98	1.99	7.01	***	0.82	25.6	11.53	**	0.64	16.8	74.5*	64.5*	0.48
PHI	0.73	0.58	0.89	***	0.83	9.1	0.57	**	0.67	12.5	0.2***	0.1*	0.66
PUTIL-G	0.25	0.16	0.39	***	0.87	19.4	0.16	***	0.83	20.4	1.3***	0.3**	0.81
PUTIL-S	0.66	0.31	1.12	***	0.81	20.1	0.60	***	0.87	26.1	18.4***	3.7**	0.85
PUTIL-BM	0.90	0.45	1.30	***	0.78	13.6	0.763	***	0.82	19.6	13.2***	5.9***	0.71

^a Trait abbreviations and units in Table 2. ns = non-significant, *, **, *** = significant on 0.05, 0.01 and 0.001 probability levels, respectively^b μ of -P and +P are significantly ($p < 0.05$) different from each other for all traits, except for PUTIL-S ($p < 0.06$)

(Table 3). P-uptake traits showed moderate genetic correlations (0.48 to 0.54) between P-levels. P-concentrations showed a strong genetic correlation over P-levels for grain but not for stover biomass.

Differences among specific genotype groups for P uptake and P use efficiency

The landrace (LR) and researcher-bred (RB) genotype groups differed significantly for most P uptake and use-efficiency traits (Fig. 2). The landrace group had higher P uptake (PCG, PG, PS, PBM) and PUTIL-S, but lower PHI and PUTIL-G. Trends corresponding to extent of Guinea- or Caudatum-race genetic background were seen, with PCG, and both PCS and PUTIL-S increasing with more Guinea background, and PHI and PUTIL-G increasing with more Caudatum background (Table 4). Generally the extent of within group genetic variation for P concentration, uptake and use efficiency was large and did not differ much among the germplasm groups (data not shown). For grain yield, however, the researcher-bred group showed 40 % higher variation than the landrace group based on standard deviations of the genotypic means (data not shown), and the Caudatum-race group had 26 %

and 32 % higher mean GY compared to the Guinea and Caudatum-Guinea race group, respectively (Table 4).

The three photoperiod sensitivity (PS) classes, specifically the very sensitive and the non-sensitive one, differed significantly for all traits except for GY, PCS and PUTIL-BM (Table 5). Whereas the P uptake traits and PCG showed an increasing trend with higher photoperiod sensitivity, a decreasing trend was observed for PHI and PUTIL-G. Genotype groups based on stem-internode length (SIL) however did not exhibit any clear trends for P uptake. PCG did show an increasing trend with longer stem internodes however, whereas PUTIL-G showed a decreasing trend. Genetic variation within each class, both for PS and SIL classes, were generally similar for all P uptake and use efficiency traits (data not shown).

Although the top ranked genotypes for PUTIL-G were Caudatum, dwarf, photoperiod insensitive researcher-bred lines, there was one taller, photoperiod sensitive Guinea landrace among the top 10 % (Table 6). More landraces and breeding lines with Guinea race background were included in the top 10 % when PUTIL-G was adjusted for harvest index (HI used as covariate in a mixed model). The reverse pattern was observed among the top genotypes for total P uptake,

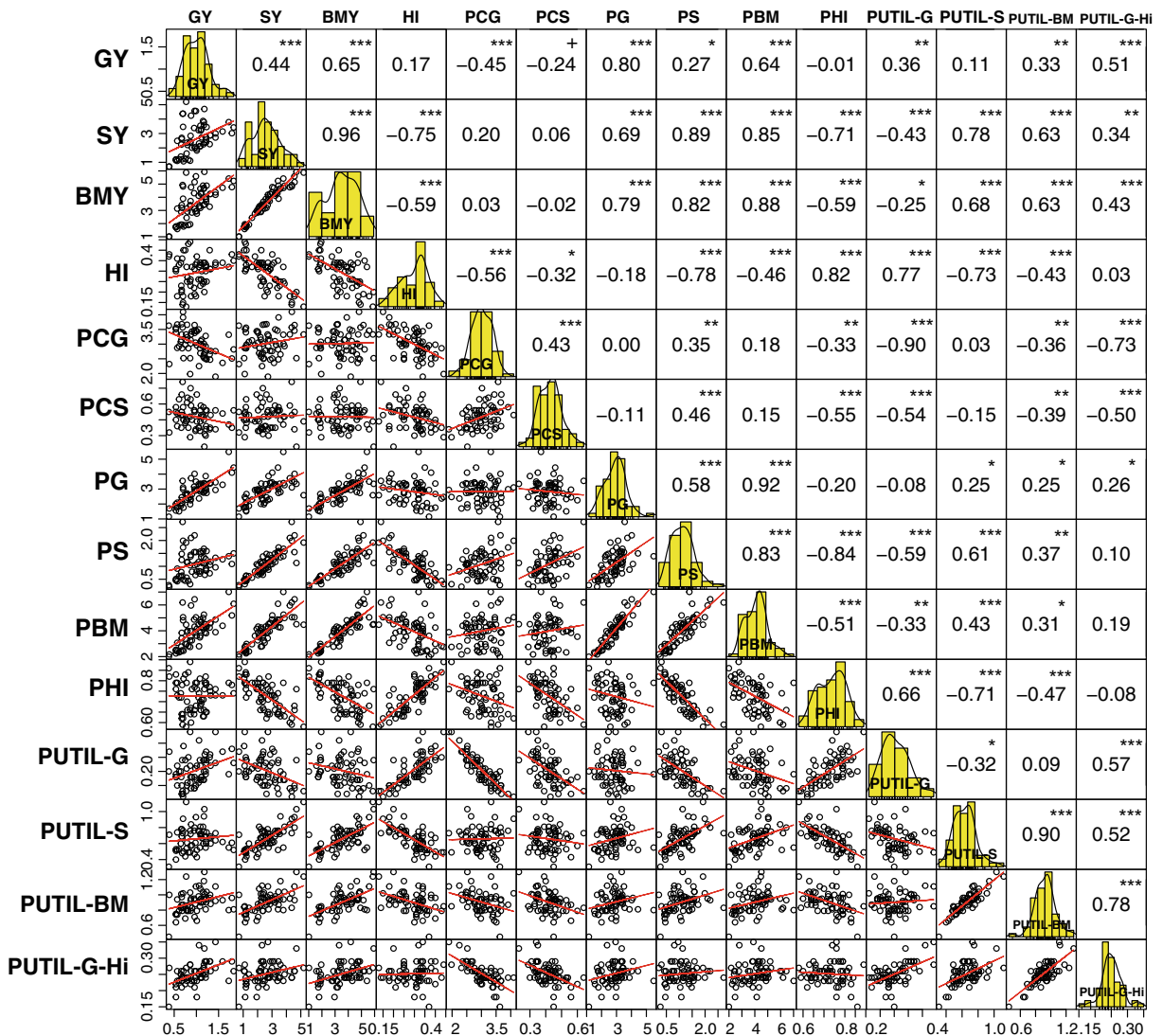


Fig. 1 Relationships of adjusted genotypic means of yield, P concentration, P uptake and P use efficiency traits in -P conditions. Linear regressions among traits (*below diagonal*), distribution of genotypic means for each trait (*diagonal*) and correlation

coefficients with significance levels of two-sided test (*above diagonal*) are shown. Trait abbreviations and units are shown in Table 2. +,*,**,** denote significance at 0.1, 0.05, 0.01 and 0.001 probability levels, respectively

with the highest ranked entries being Guinea landrace types, but with Caudatum and Guinea-Caudatum bred genotypes still included in the top 10 %. The three top ranked genotypes for grain yield were among the highest 10 % of entries for total P uptake. One of these, NAFALEN P6, was also among the highest ranked genotypes for PUTIL-G. Thus genotypic variation for P use efficiency was exhibited among the genotypes with highest P uptake and vice versa.

Discussion

This study provides the first assessment of diverse sorghum varieties from West and Central Africa for their P uptake and P use efficiency under contrasting soil P conditions. The low P field in our study, with a Bray1-P value of 5.69 mg P kg soil⁻¹, had plant P availability that corresponds to values frequently encountered in farmer's sorghum fields in Mali (Leiser et al. 2012b).

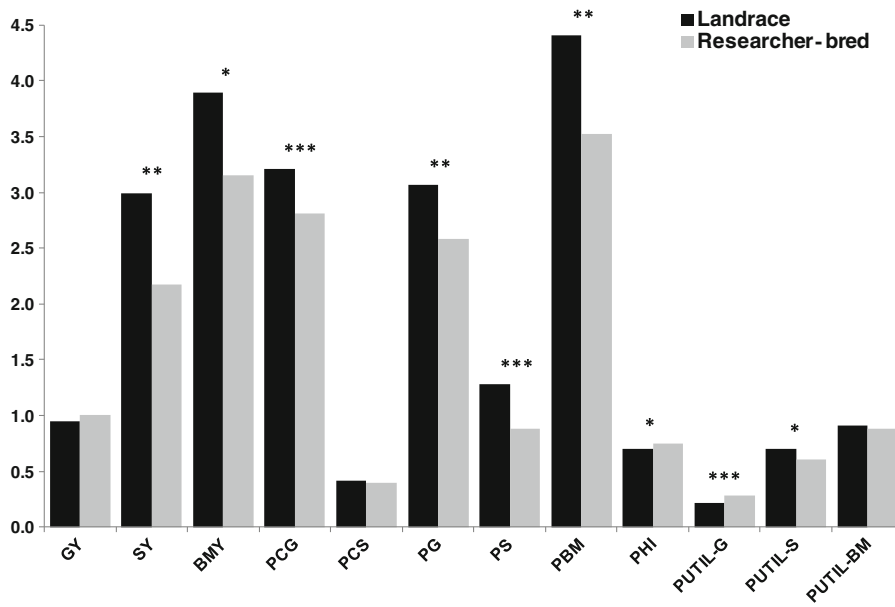


Fig. 2 Means of genotypic groups based on breeding history for yield, P-concentration, acquisition and utilization in –P conditions. Trait abbreviations and units can be seen in Table 2. If indicated

genotype groups are significantly different in a two-sided *t*-test for the respective trait (*, **, ***=*p*<0.05, <0.01, <0.001, respectively)

This level is below the level of 7 mg kg⁻¹ which is considered to be the threshold for sufficiency for sorghum (Manu et al. 1991; Doumbia et al. 2003). Likewise

Table 4 Means of genotypic groups based on race for yield, P-concentration, acquisition and utilization in –P conditions

Trait ^a	Guinea	Guinea-Caudatum	Caudatum
GY	0.95 ab	0.91a	1.2 b
SY	2.99 b	2.09 a	2.38 ab
BMY	3.89 b	2.97 a	3.59 ab
HI	0.25 a	0.31 b	0.35 b
PCG	3.21 b	2.96 b	2.44 a
PCS	0.42 a	0.41 a	0.39 a
PG	3.07 b	2.44 a	2.90 ab
PS	1.28 b	0.85 a	0.96 ab
PBM	4.41 b	3.39 a	3.83 ab
PHI	0.70 a	0.74 a	0.76 a
PUTIL-G	0.22 a	0.26 b	0.32 c
PUTIL-S	0.70 a	0.61 a	0.60 a
PUTIL-BM	0.91 a	0.87 a	0.92 a

^a Trait abbreviations and units in Table 2. Means within the same row and having different letters are significantly different at *p*<0.05 based on Tukey-HSD

the mean grain yield in the low P trial of 1 t ha⁻¹ aligns with Malian farmer’s yield levels (FAO 2010). The high P field can be considered as sufficiently supplied with P, with an average Bray-1 P value of 19.18 mg P kg soil⁻¹ and a P application rate of 20 kg ha⁻¹ (Wortmann et al. 2013). The grain and stover yields in our –P environment, averaging approximately 40 % of those in the + P environment, are at the level at which severe P stress responses should be expressed (Rose and Wissuwa 2012). Since the expression of P uptake and use efficiency are dependent on the context of P availability (Rose and Wissuwa 2012), our results are expected to be pertinent for the targeted environments in West African farmer’s fields. Although the P uptake and use efficiency measures in this study are only from a single year, their repeatability estimates were very acceptable in both –P and + P environments and therefore indicate reliability of the data (Table 3), although multi-environment testing would be necessary to fully confirm this. There were no indications of insufficient moisture during grain filling, even for the late varieties, with one of the latest varieties IS15401 ranking 16 out of 64 for grain yield (Table 6), and a total October rainfall of 81 mm received in six rainfall events.

Table 5 Means of genotype groups based on photoperiod sensitivity and stem internode length for yield, P-concentration, acquisition and utilization in $-P$ conditions

Trait [†]	Photoperiod sensitivity class			Stem-internode length class		
	Very sensitive	Sensitive	Non sensitive	Long	Medium	Short
GY	1.02 a	0.96 a	0.93 a	0.92 a	1.04 a	1.08 a
SY	3.06 b	2.47 ab	1.94 a	2.54 a	3.02 a	2.30 a
BMV	3.97 b	3.43 ab	2.89 a	3.42 a	3.99 a	3.41 a
HI	0.25 a	0.31 b	0.33 b	0.28 a	0.28 a	0.32 a
PCG	3.21 b	3.01 ab	2.70 a	3.16 b	2.90 ab	2.65 a
PCS	0.42 a	0.40 a	0.41 a	0.42 a	0.38 a	0.43 a
PG	3.00 b	2.96 b	2.36 a	2.86 a	2.91 a	2.63 a
PS	1.29 b	1.02 ab	0.81 a	1.08 a	1.17 a	1.02 a
PBM	4.35 b	4.07 b	3.20 a	4.01 a	4.11 a	3.68 a
PHI	0.70 a	0.74 ab	0.75 b	0.72 a	0.71 a	0.74 a
PUTIL-G	0.22 a	0.25 ab	0.29 b	0.23 a	0.26 ab	0.29 b
PUTIL-S	0.71 b	0.63 ab	0.59 a	0.65 ab	0.73 b	0.59 a
PUTIL-BM	0.92 a	0.88 a	0.88 a	0.88 a	0.98 a	0.87 a

^a Trait abbreviations and units in Table 2. Means within the same row and genotype grouping with different letters different significantly at $p < 0.05$ based on Tukey-HSD

Genetic variation of P uptake and use efficiency

Large significant genotypic differences for P uptake and P use efficiency traits were observed for this set of WCA sorghum varieties. The more than two-fold differences for P use efficiency traits and up to five-fold differences for P uptake traits in low P soils correspond to reports of higher genotypic variation for P uptake relative to P use efficiency traits in wheat, maize and rice (Jones et al. 1989; Wissuwa et al. 1998; Parentoni et al. 2010), although P uptake traits may have an overriding impact on biomass production in screening experiments and thus influence other P use efficiency traits (Rose and Wissuwa 2012). The P uptake traits showed higher genetic variation in $-P$ than in $+P$ conditions, as was found by Wissuwa and Ae (2001), and thus selection gain is expected to be higher in $-P$ conditions.

Genetic variation among and within genotype groups

The important and fairly similar levels of genetic variation for P uptake and use efficiency parameters among farmer's landraces and researcher's bred varieties suggests that historical selection both by farmers and formal breeders have retained variation for these traits, and that selection gains can be made in both pools. Nevertheless, differences for trait means and frequency among the top

ranked genotypes were observed between groups classified on breeding history, race, photoperiod sensitivity or stem-internode lengths. The higher P uptake and lower PUTIL-G of the landrace sorghums relative to researcher bred materials is similar to observations made in rice (Wissuwa and Ae 2001). These results correspond to reports of increasing PUTIL-G with increasing harvest index (HI) in wheat and rice genotypes (Jones et al. 1989; Manske et al. 2002; Rose and Wissuwa 2012). However, following adjustment of PUTIL-G for harvest index, the difference between the two groups decreased (from 0.06 to 0.02 kg g⁻¹P) but was still significant ($p < 0.05$). The higher PCG we observed in Guinea-race relative to Caudatum-race genotypes (Table 4) suggests that racial differences may extend beyond the grain and glume form used for their classification (Harlan and de Wet 1972) or that WCA Guinea-race varieties (here only landraces) have undergone long term farmer- and natural-selection for a higher total P uptake and higher PCG, which can be of benefit for early plant establishment on low P soils (White and Veneklaas 2012) and is often found in species naturally occurring on severely P-impoorished soils (Groom and Lamont 2010).

However there was confounding between our different genotype groups (Table 1). For example, 30 % of the Guinea LR genotypes were both highly photoperiod

Table 6 Best genotypes (top 10 %) for P use efficiency (PUTIL-G), P use efficiency adjusted for harvest index (PUTIL-G-Hi) and total P uptake (PBM) with their means (rank) for different traits (see Table 2) in -P and their genotypic classification for race, variety type, photoperiod sensitivity class (PS) and stem-internode-length class (SIL)

Variety	Race	Type	PS	SIL	PUTIL-G	PUTIL-G-Hi	PUTIL-BM	PBM	GY	PCG	HI	PHI
PUTIL-G	01-BE-F5P-15	C	RB	ns	m	0.38 (1)	0.34 (1)	1.10 (6)	3.88 (36)	1.42 (6)	1.89 (64)	0.34 (15)
	00-CZ-F5P-25	C	RB	ns	s	0.38 (2)	0.27 (12)	0.84 (41)	2.74 (54)	0.85 (41)	1.97 (63)	0.43 (1)
	KALABAN	C	RB	ns	s	0.35 (3)	0.33 (2)	1.11 (4)	2.80 (52)	1.05 (27)	2.24 (62)	0.31 (25)
	MALISOR-92-1	C	RB	ns	m	0.33 (4)	0.25 (30)	0.83 (43)	2.45 (58)	0.70 (48)	2.51 (54)	0.39 (4)
	NAFALENP6	G-C	RB	vs	m	0.32 (5)	0.28 (9)	0.95 (20)	5.18 (7)	1.80 (2)	2.5 (56)	0.37 (7)
	SGBA-E	G	LR	s	l	0.32 (6)	0.27 (14)	0.99 (14)	2.16 (63)	0.39 (63)	2.31 (61)	0.38 (6)
	DARRELL KEN	G-C	RB	s	l	0.32 (7)	0.28 (6)	0.95 (19)	3.81 (40)	1.21 (12)	2.5 (57)	0.33 (21)
	01-BE-F5P-15	C	RB	ns	m	0.38 (1)	0.34 (1)	1.10 (6)	3.88 (36)	1.42 (6)	1.89 (64)	0.34 (15)
	KALABAN	C	RB	ns	s	0.35 (3)	0.33 (2)	1.11 (4)	2.80 (52)	1.05 (27)	2.24 (62)	0.31 (25)
	IS 15401	G	LR	vs	m	0.29 (15)	0.32 (3)	1.30 (1)	4.51 (19)	1.17 (16)	2.52 (53)	0.19 (55)
PUTIL-G-Hi	KENIKEBA	G-C	RB	vs	l	0.31 (9)	0.29 (4)	1.01 (12)	3.86 (38)	1.19 (15)	2.69 (48)	0.34 (13)
	5147 OR	G	LR	s	l	0.30 (10)	0.28 (5)	0.99 (15)	4.59 (18)	1.31 (8)	2.47 (59)	0.30 (34)
	DARRELL KEN	G-C	RB	s	l	0.32 (7)	0.28 (6)	0.95 (19)	3.81 (40)	1.21 (12)	2.5 (57)	0.33 (21)
	N'TENIMISSA	G-C	RB	ns	l	0.30 (12)	0.28 (7)	0.96 (18)	4.25 (29)	1.29 (9)	2.65 (51)	0.39 (5)
	IS 26077	G	LR	s	l	0.24 (34)	0.23 (51)	0.80 (50)	7.00 (1)	1.72 (3)	3.32 (21)	0.31 (26)
	DOUA-G	G	LR	vs	l	0.18 (59)	0.25 (29)	0.92 (30)	6.44 (2)	0.95 (34)	3.64 (6)	0.18 (57)
	BOBODJÉ	G	LR	vs	l	0.17 (60)	0.23 (44)	0.82 (46)	6.18 (3)	0.68 (51)	3.56 (8)	0.13 (63)
	TIANDOUGOU	C	RB	s	s	0.27 (21)	0.25 (28)	0.80 (48)	6.08 (4)	1.84 (1)	2.81 (44)	0.35 (12)
	SGBA-D	G	LR	s	m	0.18 (57)	0.26 (20)	0.94 (23)	5.95 (5)	0.87 (37)	3.32 (19)	0.18 (58)
	LINA 3	G-C	RB	s	m	0.21 (47)	0.26 (16)	0.93 (25)	5.24 (6)	1.17 (17)	3.01 (32)	0.24 (48)
PBM	NAFALENP6	G-C	RB	vs	m	0.32 (5)	0.28 (9)	0.95 (20)	5.18 (7)	1.80 (2)	2.5 (56)	0.37 (7)
												0.75 (25)

Race: C and G denote Caudatum and Guinea; Type: RB and LR denote research bred and landrace; PS and SIL classes defined in Table 1

sensitive and showed long stem-internodes. Thus the higher total P uptake of landrace Guinea materials was apparently related not only to differences for P acquisition mechanisms but also to their slightly longer mean growth duration ($r=0.20^{***}$ over all genotypes) and taller plant heights ($r=0.34^{***}$), with corresponding higher stover yield (Table 5).

The possible role of photoperiod sensitivity in adaptation to infertile soils was suggested by Clerget et al. (2008a). They found expression of photoperiod sensitivity in WCA sorghums to cover an ensemble of phenological processes, including not only flowering date response, but also major reductions of rate of leaf initiation after 18 to 25 leaves (under non-inducing conditions), and simultaneous reductions of leaf appearance, stem-internode and leaf development, and senescence rates. They suggested that changes in vegetative growth rates may result in reductions in demand of resources for vegetative growth relative to root growth, which show indications of continued linear growth rates (Clerget pers. communication). Similar findings on phenological delay, root growth duration and adaptation to low P conditions were also reported for *Arabidopsis thaliana*, suggesting that this topic merits further research (Nord and Lynch 2008).

The higher P uptake of photoperiod sensitive sorghums in this study invites further investigation on possible contributions of photoperiod sensitivity to adaptation to low P conditions. Actually, the June 26 sowing date as in this study limits the period in which photoperiod sensitivity mediated changes of growth processes occur (Clerget et al. 2008). As the consequences of such changes may be cumulative, even greater impact may accrue for the early to mid-June sowing dates which are frequent for WCA farmers in more humid areas.

Relationship among P uptake, P use efficiency and grain yield under low P availability

The absence of negative correlations between P uptake and P use efficiency, either for grain or stover, under low P conditions (Fig. 1) suggests the possibility of making selection progress for both traits. However, P use efficiency is expected to be confounded with P uptake under field conditions (Rose and Wissuwa 2012), and thus cannot be clearly distinguished. Even though correlations indicate that HI is likely a major determinant of PHI and PUTIL-G, as noted by (Rose and Wissuwa 2012), the top genotypes for P use efficiency exhibited differences for HI

(Table 6). Furthermore, the very strong correlation between PCG and PUTIL-G suggest that PUTIL-G is most influenced by P concentration and less by HI. Additionally, PUTIL-G adjusted for HI showed a significant correlation to non-adjusted PUTIL-G ($r=0.57^{***}$) and PCG ($r=0.73^{***}$), confirming the contribution of PCG to P efficiency independent of HI. This suggests the possible use of low PCG as a simple measure for P use efficiency. The effectiveness of simultaneous selection for high GY and low PCG would be aided by their negative correlation. Our PHI values under -P conditions, ranging from 58 to 89 %, are similar to findings in mature wheat and rice plants (Batten 1992; Rose et al. 2010) and thus show a high P remobilization (Veneklaas et al. 2012). In order to avoid confounding effects by HI, Rose et al. (2011) suggested to use the inverse of the shoot P concentration as a measure of internal P use efficiency. Since shoot P concentration is steadily declining with maturity (Schultz and French 1978), only data from the same developmental stages can be compared. PUTIL-BM, the inverse of P concentration in all tissue combined, was used to assess total P use efficiency, although selection on this trait would tend to favor genotypes with a lower HI due to the negative correlation between PUTIL-BM and HI. Further, the comparison between crops for their total P use efficiency using PUTIL-BM can only appropriately be done if they have similar levels of HI. Rice, therefore, with a much higher HI than sorghum should not necessarily be classified as less P use efficient than sorghum based on PUTIL-BM. However, our sorghum results at maturity show higher P use efficiencies (PUTIL-BM) than were observed for maize (Parentoni and Souza Jr. 2008) with similar HI levels under low P conditions, thus confirming the good adaptation of WCA sorghum germplasm to low P conditions as suggested by Leiser et al. (2012b).

Although P uptake traits showed stronger correlations to final grain and stover yields, selection for a higher internal P use efficiency (e.g. lower PCG) should be pursued, to minimize or reduce soil P mining that is occurring in most sub-Saharan African countries (Stoorvogel et al. 1993). Even though selection for PUTIL-G was proposed in recent decades as a selection criterion, its use is questionable due to the confounding effect of HI. Using PUTIL-G-HI or PCG seems promising, especially for identifying efficient LR genotypes that have a lower HI but still rather high grain yields in low P conditions (Table 6). The high genotypic variation for PUTIL-G-HI and PCG and the good correlation to GY ($r=0.51^{***}$, $r=-0.45^{***}$) encourage genotypic selection

for these traits to enhance grain yield and reduce soil-P mining under low input conditions. Although selecting for lower PCG might have a negative impact on early plant development, especially on low P soils (Raboy 2009; White and Veneklaas 2012), the likely reduction of phytic acid content in the grain could increase Zn and Fe bio-availability (Hurrell et al. 2003), which would be of importance in WCA where most grain is used for food. Since soil-P mining can also be caused by soil-erosion, improved cropping system e.g. inter-cropping of legumes with shallow roots and thus better low P soil adaptation (Henry et al. 2010), should be considered as an additional way to minimize soil-P mining in WCA.

Relationships of P uptake, P use efficiency and grain yield assessed in the same field trial are prone to auto-correlations, which is the case in this study (Table 2 and Fig. 1) and others (Jones et al. 1989; Manske et al. 2001; Araújo and Teixeira 2003; Ozturk et al. 2005; Cichy et al. 2008; Parentoni et al. 2010; Rose et al. 2010). Using grain yields from an independent set of environments is crucial for validating genetic relationships of P uptake and use efficiencies with grain yield under low P conditions and formulating promising selection approaches. Our ongoing examination of relationships between P uptake and P use efficiency measured in this study with grain yields across a range of low P environments should help determine the feasibility and usefulness of indirect selection on P-related parameters to enhance low P grain yields and P use efficiency of WCA sorghums.

The diversity exhibited by the WCA sorghum varieties for both P uptake and use efficiency, including a genotype combining high P uptake, P use efficiency and grain yield, supports the conclusion of Lynch (2007) that exploiting natural variation among genotypes, rather than specific gene manipulation, is the preferred tool to select for higher P uptake under –P conditions.

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