

Selection Strategy for Sorghum Targeting Phosphorus-limited Environments in West Africa: Analysis of Multi-environment Experiments

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ABSTRACT

Although sorghum [*Sorghum bicolor* (L.) Moench] in West Africa (WA) is generally cultivated with limited or no fertilization on soils of low phosphorus availability, no assessments of the genetic variation among WA sorghum varieties for adaptation to low soil P are known. We assessed grain yields of 70 diverse sorghum genotypes under –P (no P fertilization) and +P conditions at two locations in Mali over 5 yr. Genetic variation for grain yield under –P conditions and the feasibility and necessity of sorghum varietal testing for grain yield under –P conditions were evaluated. Delayed heading dates (0–9.8 d) and reductions of grain yield (2–59%) and plant height (13–107 cm) were observed in –P relative to the +P trials. High estimates of genetic variance and broad-sense heritabilities were found for grain yield across both –P ($h^2 = 0.93$) and +P ($h^2 = 0.92$) environments. The genetic correlation for grain yield performance between –P and +P conditions was high ($r_G = 0.89$), suggesting that WA sorghum varieties generally possess good adaptation to low-P conditions. However, genotype \times phosphorus crossover interaction was observed between some of the highest yielding genotypes from the –P and +P selected sets, with the variety IS 15401 showing specific adaptation to –P. Direct selection for grain yield in –P conditions was predicted to be 12% more efficient than indirect selection in +P conditions. Thus, selection under –P conditions should be useful for sorghum improvement in WA.

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Abbreviations: aVD, average variance of differences; BLUP, best linear unbiased prediction; $G \times E \times P$, genotype \times environment \times phosphorus-level interaction; $G \times P$, genotype \times phosphorus-level interaction; GCV, genetic coefficient of variation; GEI, genotype \times environment interaction; RYR, relative yield reduction; WA, West Africa.

SORGHUM [*Sorghum bicolor* (L.) Moench] is a staple crop of the Savannah Zone of West and Central Africa. The adaptation of sorghum to the climatic and edaphic conditions of this zone is critical for food security, and increasingly for farm income. Most of Sub-Saharan African soils (75%) show plant nutrient deficiency (IFDC, 2006). Limited soil phosphorus (P) availability is a serious and frequent constraint to sorghum and pearl millet [*Pennisetum glaucum* (L.) R. Br.] growth and productivity across the range of rainfall zones in West Africa (WA) (Buerkert et al., 2001). Although sorghum has a yield potential of several tons per hectare in WA, actual yields average only about 1 t ha⁻¹ since 1960 (FAO, 2010), due in part to low soil fertility and low-input production systems (Vom Brocke et al., 2010). Deficiency in P is known to reduce growth and delay maturity (Fageria et al., 1988; Wissuwa and Ae,

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2001; Chen et al., 2008; Cichy et al., 2008). Doumbia et al. (1998) reported strong correlations between poor sorghum growth and P deficiency and aluminum toxicity in WA soils. In most of these soils, available P contents (Bray-1) are below the critical level of 7 ppm P (= 7 mg P kg⁻¹ soil) (Manu et al., 1991; Doumbia et al., 2003). Although soils may have acceptable total P contents, the quantity of plant-available P is often very limited, because the majority of soil P (70–90%), and the little P applied as inorganic fertilizer, is being fixed in the soil as nonavailable P (e.g., Fe-, Al-phosphate) for plants (Holford, 1997).

The Guinea-race of sorghum originated in the WA savannah (De Wet and Harlan, 1972). The traditional landrace varieties of this race, along with newly bred varieties developed by introgressing exotic germplasm into local Guinea-race materials, are the predominant types of sorghum cultivated in the Sudanian zone from Senegal to Burkina Faso. However, no systematic assessment of the genetic variation among these farmer landrace varieties and newly bred varieties for adaptation to low soil P in WA is available. Further, the lack of knowledge of the extent and nature of genotype × phosphorus interactions and genotype × environment interactions across low-P environments impedes the design of WA sorghum breeding programs to effectively target adaptation to the low-P conditions that are very common for the region's resource-poor farmers.

This study evaluated the grain yields of diverse WA sorghum varieties grown under a sampling of low- and high-P environments. Our goal was to assess the necessity and feasibility of breeding sorghum specifically for low-P conditions in the Sudanian-zone of WA. Our objectives were to (i) describe the genetic variation for grain yield under -P and +P conditions of a diverse sample of cultivated sorghum varieties, (ii) assess the genotypic specificity of -P adaptation, and (iii) compare the relative efficiency of direct selection for grain yield under -P conditions vs. indirect selection, when testing under +P conditions.

MATERIALS AND METHODS

The 70 sorghum varieties used in this study are representative for the diversity of cultivars and breeding lines adapted to the Sudanian zone of Mali (Table 1). Approximately half of the entries were landrace varieties, all of which are classified as Guinea-race, the predominant race in Mali. These accessions are tall (height >3 m) with photoperiod sensitivity and grain size covering the range exhibited by this race in the Sudanian zone of Mali. Four of the latest maturing entries were susceptible to sorghum midge (*Stenodiplosis sorghicola*) and frequently suffered nearly complete grain losses, and were thus excluded from the analyses. The remaining entries were bred from biparental Guinea × Caudatum-race crossing and backcrossing (27 entries) or from a Guinea-race random-mating population (five entries). 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 nonsensitive photoperiod sensitivities. There is almost no genetic relationship between the landrace varieties and the bred varieties, as none of these landrace varieties occur in the pedigrees of varieties derived from biparental crossing, and only one landrace variety was among the 13 landraces parents of the Guinea Population (Rattunde et al., 1997) from which the five population derivatives originated.

Yield trials were conducted in Mali, WA, at the Kolombada (12°40' N, 7°0' W) research station of the Institut d'Economie Rurale and the Samanko (12°31' N, 8°4' W) station of the ICRI-SAT (Supplemental Fig. 1) from 2006 to 2010. All trials were rain-fed, with rains differing in amount and frequency (Table 2). Two separate trials were conducted at each location and year: one with (+P) and one without (-P) phosphorus fertilization. The +P and -P trials were conducted in adjacent fields at Samanko, or in a single field divided into +P and -P sections at Kolombada. The +P fields were fertilized with diammonium phosphate (18–46–0) at rates of 100 to 200 kg ha⁻¹ as basal fertilizer and urea (50 kg ha⁻¹) (46–0–0) as topdressing. The -P fields received only topdressing with urea at rates that gave approximately equivalent units of nitrogen as received by the +P fields at Samanko 2006 to 2010 and Kolombada 2009. The -P fields at Kolombada in 2006 to 2008 received only the same quantity of urea used as topdressing in the +P experiments. Each trial consisted of 70 genotypes sown in an α -design with four complete replicates, each with 14 incomplete blocks of five plots. Field layouts differed among trials, with column numbers ranging from 15 to 35 and row numbers ranging from 8 to 20. Plots consisted of two 3-m 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 approximately 9.8 plants m⁻². A single border row separated each test plot to minimize neighbor effects. The guard rows were left unsown in 2006 to 2008, whereas they were sown with a common locally adapted variety in 2009 and 2010. In most years soil samples were analyzed after fertilizer application for plant-available P, using the Bray-1 method (Bray and Kurtz, 1945), organic carbon, pH in H₂O and aluminum-saturation (Table 2). The environmental mean plant-available soil P-levels (Bray-1 P) were above 14 ppm (14 mg P kg⁻¹ soil) in the +P and mostly below 10 ppm (10 mg P kg⁻¹ soil) in the -P trials.

DATA ANALYSIS

Analysis of Individual Trials

Each single environment trial was analyzed for grain yield with several spatial models as described in a companion study (Leiser et al., 2012); the optimum model was identified for each trial, and predicted values and standard errors were computed for each genotype, taking the factor genotype as fixed. The repeatability (w^2) of each trial was calculated with a formula adjusted for unbalanced data sets (Eq. [19] in Piepho and Möhring, 2007):

$$w^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{VD}{2}} \quad [1]$$

where σ_g^2 is the genotypic variance component and VD is the average variance of differences between genotype means.

The genetic coefficient of variation (GCV) of each trial was calculated as:

$$GCV = \frac{\sqrt{\sigma_g^2}}{\mu} \quad [2]$$

where σ_g^2 is the genotypic variance component and μ the trial grand mean, to enable comparisons of genetic variance across trials of differing mean yields. As a measure for the extent of error in each trial, the average variance of differences (aVD) between genotypes was estimated and standardized by dividing the square root of aVD (= SEd) with the trial grand mean, to enable comparisons of error extent across trials of differing mean yields. Differences between means for w^2 , GCV, and aVD between means across the -P and +P trials were tested with a two-sided *t* test. The relative yield reduction (RYR) was calculated as: $RYR = 100 \times [1 - (\text{MeanYield}_{-P} / \text{MeanYield}_{+P} \times 100)]$. Genetic correlations between yield performance in the +P and -P trials in each environment (location-year-combination) were calculated according to Cooper and DeLacy (1994), assuming no environmental covariance because of the experimental setup.

Combined Analysis across Environments

Eight of the nine -P trials and seven of the eight +P trials were used in a combined weighted mixed-model Restricted Maximum Likelihood (REML) analysis. Two trials, namely Kolombada 2008 -P and Samanko 2008 +P, were excluded from the analysis, due to a low RYR, height reduction, and heading delay (Table 3), which could be explained by certain environmental constraints. 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. The adjusted means were used as response variate and the reciprocal squared standard error (SE) from each entry as weights (Möhring and Piepho, 2009). The residual variance was fixed, thus the specified residual variance-covariance matrix with the corresponding weights was

Table 1. Number of sorghum genotypes of landrace and research bred origins, and their classification into photoperiod-sensitivity and plant height groups.

Origin	Photoperiod sensitivity			Plant height	
	No.	Strong	Intermediate	Weak	Tall Short
Farmer landrace	34	6	21	7	34 0
Research bred	32	0	15	16	14 18

used as residual term and no extra residual variance component was needed (Piepho, 1999). Smith et al. (2001) proposed a weighting method based on the variance-covariance matrix of the adjusted means specifically for analyses (e.g., incomplete blocks, spatial adjustment) where higher covariances are expected in the variance-covariance matrix. We did not detect high covariances in the single-trial variance-covariance matrixes of the spatially adjusted means or of the adjusted means derived from a model with random incomplete block effects, so we used the simpler method of Piepho (1999). Furthermore we correlated the best linear unbiased predictions (BLUPs) of a one-stage and two-stage analysis across the -P and +P trials. For the one-stage analysis we modeled random incomplete blocks within each trial and variance heterogeneity between trials. The weighted two-stage analysis was conducted with adjusted means from the single trial incomplete block analyses and their corresponding inverse squared SEs as weights. There was a very strong relationship for the -P and +P trials ($r_{-P} = 0.9985$, $r_{+P} = 0.9994$) between the one- and two-stage analysis, suggesting that our weighting method was sufficient. Because BLUP values predict more accurately genotypic differences (Piepho et al., 2008), the genotype effect was considered random for the estimation of each BLUP value. The BLUPs were tested for significant differences against the grand mean and between each other with linear contrasts as implemented in the VTCOMPARISON procedure in Genstat 14 (<http://www.vsn.co.uk/software/genstat> [accessed 11 July 2012]). Broad-sense heritability (h^2) within and across P-levels

Table 2. Characterization of environments for sowing date, rains within the whole year (total rain), rains within the season after sowing (season rain), applied fertilizer, soil pH, soil plant-available P (Bray-1 P), soil total P, soil aluminum saturation (Al³⁺-sat.), and soil organic carbon (C_{org}).

Location	Year	P-level	Sowing date	Total rain		Season rain		Fertilizer		pH	Bray-1 P	Total P	Al ³⁺ -sat.	C _{org}
				mm	d	mm	d	N kg ha ⁻¹	P kg ha ⁻¹					
Kolombada	2006	+P	18 July 2006	906	53	611	32	41	20	n.a. [†]	16.60	n.a.	n.a.	n.a.
		-P						23		n.a.	11.44	n.a.	n.a.	n.a.
Kolombada	2007	+P	5 July 2007	880	51	759	37	41	20	5.01	19.48	n.a.	14.35	0.26
		-P						23		4.88	13.85	n.a.	21.02	0.25
Kolombada	2008	+P	10 July 2008	616	52	462	35	41	20	n.a.	16.5 [‡]	n.a.	n.a.	n.a.
		-P						23		n.a.	n.a.	n.a.	n.a.	n.a.
Kolombada	2009	+P	9 July 2009	720	59	587	49	29.5	20	5.14	16.02	108.73	1.58	0.28
		-P						23		5.27	8.88	105.66	2.14	0.24
Samanko	2006	+P	27 June 2006	1008	63	765	57	29	17	5.01	14.44	106.24	8.82	0.33
		-P	28 June 2006					46		4.43	6.51	122.09	20.63	0.28
Samanko	2007	-P	16 July 2007	809	63	622	48	46		n.a.	3.95	n.a.	n.a.	n.a.
Samanko	2008	+P	2 July 2008	1035	63	791	48	45.72	50.8	n.a.	n.a.	n.a.	n.a.	n.a.
		-P	7 July 2008					46		n.a.	8.00 [‡]	n.a.	n.a.	n.a.
Samanko	2009	+P	8 July 2009	1068	66	911	51	59	40	5.18	18.78	111.58	10.69	0.38
		-P						58.42		4.83	7.40	111.70	22.82	0.29
Samanko	2010	+P	26 June 2010	1230	67	954	55	41	20	5.67	19.18	n.a.	8.00	0.37
		-P						40.9		6.41	5.69	n.a.	2.00	0.19

[†] n.a. = missing data.

[‡] Estimated value based on results from previous/next year.

Table 3. Estimates of mean (GY, in gm⁻²), repeatability (w^2), genetic coefficient of variation (GCV), standardized average variance of differences (aVD) for grain yield in nine trials without (–P) and eight trials with P fertilization (+P), as well as the relative yield reduction (RYR), genetic correlation (r_g) between grain yield performance under –P vs. +P, height reduction (HR, in cm), and delay of heading (HD, in days) in –P relative to +P trials.

Location	Year	P-level	GY	w^2	GCV	aVD	r_g	RYR	HR	HD
			gm ⁻²		%	%		%	cm	d
Kolombada	2006	+P	115.8	0.69	19.1	18.0	0.73	27	–36.8	1.95
		–P	84.6	0.69	19.3	18.4				
Kolombada	2007	+P	85.4	0.83	34.1	21.7	0.91	59	–56.4	3.98
		–P	35.2	0.74	21.9	18.2				
Kolombada	2008	+P	157.3	0.77	15.3	11.7	0.99	07	–13.4	0.01
		–P	145.6	0.61	12.7	14.2				
Kolombada	2009	+P	177.4	0.87	24.9	13.6	0.83	43	–67.4	7.95
		–P	100.5	0.76	31.9	25.5				
Samanko	2006	+P	192.2	0.86	22.4	13.0	0.57	38	–66.2	4.14
		–P	118.8	0.87	31.2	16.9				
Samanko	2007	–P	37.1	0.70	34.4	31.5				
Samanko	2008	+P	113.8	0.84	27.0	16.7	0.50	02	–30.3	–1.78
		–P	111.6	0.77	23.9	18.5				
Samanko	2009	+P	299.7	0.84	23.4	14.4	0.78	57	–98.8	9.82
		–P	130.0	0.86	38.3	22.1				
Samanko	2010	+P	202.0	0.81	21.1	14.4	0.78	51	–107.5	7.61
		–P	98.1	0.77	28.8	22.0				
Mean		+P	168.0	0.81	23.4	15.4				
Mean		–P	95.7	0.75	26.9	20.8				
			*	NS†	NS	*				

* $p < 0.05$ in two-sided t test.

† NS = not significant in two-sided t test.

was calculated with an adjusted formula for unbalanced trials with random genotype effects (Cullis et al., 2006):

$$h^2 = 1 - \frac{\bar{v}_{BLUP}}{2\sigma_g^2} \quad [3]$$

where \bar{v}_{BLUP} is the mean variance of a difference between two BLUPs and σ_g^2 is the genotypic variance component. The h^2 estimate was used for describing the heritability of the multi-environment data set, while w^2 was used as measure for repeatability of each individual trial.

Mixed models were fitted within each P-level to estimate genotype \times environment interaction (GEI) and environmental factors contributing to GEI (Table 4). To detect the GEI pattern a three-way-interaction model was fitted with genotypes and years considered as random and locations as fixed. The existence of any major definable mega-environments needing to be considered for characterizing genotypic performance across –P or +P environments was examined by the extent to which GEI could be explained by various environmental parameters using a model that included genotype, trials, and environmental factors (Table 4), all considered as random effects.

The model within one P-level and environmental factors can be stated as:

$$Y_{ijk} = \mu + G_i + E_j + GE_{ij} + F_k + e_{ijk}, \quad [4]$$

where Y_{ijk} is the adjusted mean of the i th genotype in the j th environment within the k th class of the environmental factor, μ is the grand mean, G_i is the effect of the i th genotype, E_j the effect of the j th environment, F_k the effect of the k th environmental parameter for explaining GE, and e_{ijk} is the error of each Y_{ijk} considered by the reciprocal squared SE as weights.

A combined analysis across P-levels was conducted with P-level as fixed and genotypes and environments (location–year–combination) as random. The factorial model can be stated as:

$$Y_{ijk} = \mu + P_i + EP_{ij} + GP_{ik} + GEP_{ijk} + e_{ijk}, \quad [5]$$

where Y_{ijk} is the adjusted mean of the k th genotype (G) in the j th environment (E) and the i th P-level (P). An unstructured variance–covariance model was fitted for P-level (P) in each interaction. The reciprocal squared SE of each Y_{ijk} were considered as weights. A four-way-interaction model with P-level, year, location, and genotypes had convergence problems and thus will not be presented. Assuming covariances between trials the genetic correlation of grain yield between +P and –P across all environments was calculated as:

$$r_g = \frac{\sigma_{G(-P+P)}}{(\sigma_{G(-P)}\sigma_{G(+P)})} \quad [6]$$

where $\sigma_{G(-P+P)}$ is the covariance of genotype means in –P and +P and $\sigma_{G(-P)}$ and $\sigma_{G(+P)}$ are the genotypic standard deviations within the –P and the +P fertility level, respectively.

For the 15% best yielding genotypes (top 10) within each P-level a linear regression of grain yield against the trial mean soil Bray-1 P (mg P kg⁻¹ soil) was conducted with 13 trials having measured and two trials having estimated Bray-1 P values (Table 2).

Genotypic superiority for grain yield across –P and +P trials was calculated as the selection differential ($S = \mu_{\text{select}} - \mu_{\text{grand}}$) of the 5, 10, and 15% top yielding genotypes in –P and +P. The relative efficiency of response to indirect vs. direct selection for grain yield under –P conditions was estimated as:

$$R_{id}/R_d = r_G \times h_{+P}/h_{-P} \quad [7]$$

where R_{id} and R_d are the indirect and direct response to selection, respectively, r_G the genetic correlation coefficient between +P and -P and h_{+P} and h_{-P} the square root of the broad-sense heritability (h^2) within the +P and -P environments, respectively (Atlin and Frey, 1989). All data analyses were conducted with the Genstat 14 software.

RESULTS

Mean Performance Under High- and Low-Phosphorus Soil Conditions

The -P trials generally exhibited reduced grain yields, plant heights, and delayed heading, relative to the corresponding +P trials (Table 3). The mean grain yield across the -P environments was significantly lower than across the +P environments, although there was a rather big range (2–59%) for RYR in -P vs. +P conditions, with some pairs of trials (Kolombada 2008 and Samanko 2008) showing almost no yield difference between -P and +P. High RYR in -P experiments was strongly associated with large delay of heading ($R^2 = 0.75^{**}$) and large height reduction ($R^2 = 0.67^{**}$).

Examination of RYR, plant heights, and delayed heading levels identified two environments that appeared to be inappropriate for assessing differential genotypic performance under contrasting P conditions. The Kolombada 2008 -P trial was in a field that had been fallow for many years and had relatively high mean yield (1.45 t ha⁻¹), and no yield reduction or delay in flowering compared to the +P trial. The Samanko 2008 +P trial appeared to suffer from shallow soil depth, with very poor plant growth throughout the season in three of four replicates despite high and repeated fertilization and achieved a mean yield of only 1.1 t ha⁻¹ (Table 2 and Table 3). Therefore these two trials were excluded from the combined analyses.

Genetic Variation Under Low- and High-Phosphorus Conditions

The mean repeatability (w^2) estimates for grain yield in the -P trials were slightly but nonsignificantly lower than in the +P trials (Table 3). Although there was a significant higher error (aVD) in the -P trials, the GCV tended to be higher in -P relative to +P, which resulted in nearly the same level of repeatability in -P as in the +P conditions (Table 3). We observed medium to high genetic correlations ($0.5 \leq r_G \leq 0.99$) for grain yield between -P and +P in each environment. No relationship was observed ($r = -0.22$ n.s.) between r_G for grain yield and RYR across the pairs of -P and +P trials over all environments, even if Samanko 2008 was excluded.

Table 4. Environmental factors and their factor classes.

Factor class	Sowing date	Grain yield	Rain amount	Days with rain	Bray-1 P
		g m ⁻²	mm yr ⁻¹	d yr ⁻¹	mg P kg soil ⁻¹
1	20–30 June	0–50	600–800	50–55	3–7
2	01–10 July	50–100	800–900	55–60	7–10
3	10–20 July	100–150	900–1000	60–65	10–13
4		150–200	1000–1100	>65	13–17
5		>200	>1100		17–20

Table 5. Variance components for grain yield (\pm SE) within eight trials without (-P) and seven trials with P fertilization (+P) analyzed with a mixed-model Restricted Maximum Likelihood approach, as well as the standardized average variance of differences (aVD), genetic coefficient of variation (GCV), and broad-sense heritability (h^2) estimates.

Term	-P	+P
σ^2_G	387.3** \pm 85.0	734.6** \pm 186.1
$\sigma^2_{G \times Y}$	90.3* \pm 35.2	250.1** \pm 84.0
$\sigma^2_{G \times L}$	51.5 \pm 27.0	318.9** \pm 91.7
$\sigma^2_{G \times Y \times L}$	139.0** \pm 36.8	173.5* \pm 81.9
aVD	8.50	5.84
GCV	22.85	15.21
h^2	0.93	0.92

* Significant at $p < 0.05$.

** Significant at $p < 0.01$.

Variance Components Under Low- and High-Phosphorus Conditions

Significant but rather small genotype \times environment interaction (GEI) was detected across the -P trials (Table 5). The GEI variance components were smaller than the genotypic components, which contributed to the high heritability estimate (h^2) over all -P trials. Most of the GEI in -P was of more complex nonexploitable three-way interaction ($G \times Y \times L$). The GCV and aVD estimates across the -P trials were higher than for the +P trials (Table 5) and the heritability estimate was comparable to that of the +P trials, similar to the single trial repeatability estimates. Inclusion of environmental factors (Table 4) generally explained relatively small portions of GEI across -P environments (Table 6). The amount of total annual rainfall proved to be the most important factor explaining 43% of GEI in -P. However, the amount of rainfall or days with rain during the growing season (after sowing) explained less GEI than total seasonal rainfall (data not shown). The GEI was reduced by 18% by including a factor for the trial mean yield level and by only 9% by including factors for date of sowing (late-June to mid-July sowings) or soil plant-available P, as estimated by Bray-1 P. Therefore all -P trials were considered as one population of environments for further analyses since a subdivision of our environmental sample for controllable environmental factors was of no explanatory value.

The GEI across +P trials was significant and appeared to be somewhat more important in +P than in -P trials, with the

Table 6. Variance components for total genotype \times environment interaction (GEI) and residual GEI after accounting for genotypic interactions with specific environmental factors, and the absolute difference between total and residual variance components, using mixed-model Restricted Maximum Likelihood analyses across environments with P fertilization (+P) and without fertilization (–P).

P-level		Total	Residual GEI after accounting for				
			Sowing date	GY [†]	Rain amount	Days with rain	Bray-1 P
+P	GEI	596.9	500.4	608.1	503.2	291.1	587.6
–P	GEI	249.6	226.4	204.8	142.6	234.3	226.3
					Δ GEI [‡]		
+P	Δ GEI		–96.4	11.2	–93.6	–305.8	–9.3
–P	Δ GEI		–23.2	–44.8	–106.9	–15.3	–23.3

[†] GY = Trial grain yield class, Rain amount, and Days with rain over the entire year (see Tables 2 and 4);

[‡] Δ GEI = residual GEI – original GEI.

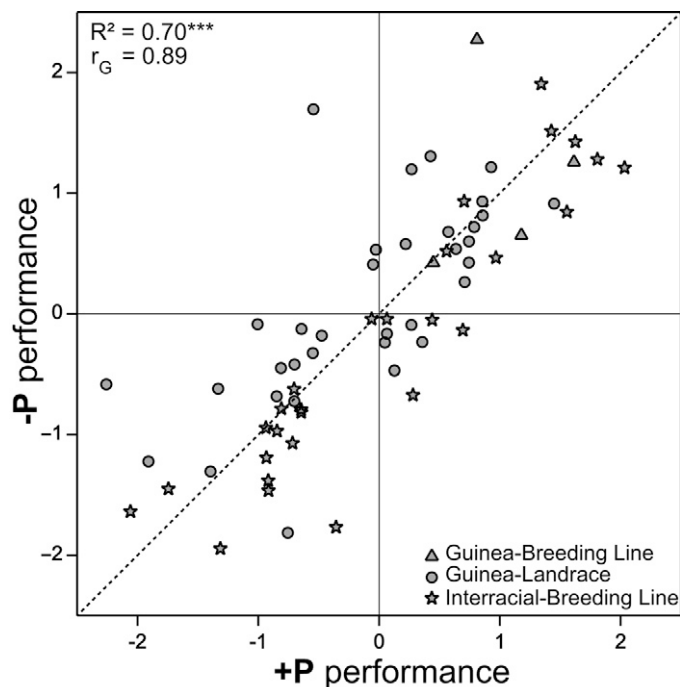


Figure 1. Grain yield performance as standardized best linear unbiased predictions ($\mu = 0$; $\sigma = 1$) of 66 sorghum genotypes across eight trials without (–P) and seven trials with P fertilization (+P), with the corresponding coefficient of determination (R^2) and genetic correlation (r_G).

sum of all GEI components equaling the genotype variance component (Table 5) and contributed to the h^2 estimate across all +P environments not exceeding that of the –P environments. The +P trials showed relatively higher two-way interactions ($G \times Y$, $G \times L$). Especially the genotype \times location interaction ($G \times L$) was much more important in the +P trials as seen in the variance component ratio of $G : G \times L$ in +P (1:0.43) vs. –P (1:0.13). Trial yield level and sowing date explained only very little of GEI in the +P trials, similar to the –P trials (Table 6). More GEI in the +P trials was explained by the annual total number of rain days (51%) than by rain days during the growing season (27%) (data not shown). A genotypic grouping factor based on photoperiod sensitivity could explain 27% of GEI in +P, whereas it explained only 10% in –P conditions (data not shown).

Relationship Between Performance Under Low- and High-Phosphorus Conditions

The significant but rather small genotype \times P-level interaction ($G \times P$) variance component estimate from the combined analysis over all 15 trials shows strong correspondence of genotypic performance between +P and –P conditions (data not shown). The genotype variance component explained most of the variation and had a ratio of 1:0.13 to $G \times P$. Most of the GEI was of a more complex three- or four-way interaction (data not shown), as also seen in the large variance component for genotype \times environment \times P-level interaction ($G \times E \times P$) and the variance component ratio of $G : G \times E \times P$ (1:0.7). The close relationship between genotypic grain yield performance in –P and +P conditions is also indicated by the large estimate of broad-sense heritability ($h^2 = 0.96$) across P-levels and a rather high genetic correlation ($r_G = 0.89$) between grain yield performance under –P and +P conditions. The generally strong agreement between genotypic performance in +P and –P conditions is seen by plotting grain yield BLUPs of –P vs. +P, using standardized values with only a few genotypes showing major deviations from the 1:1 line that suggest some specific adaptation to +P or –P conditions (Fig. 1) and genotype \times phosphorus cross-over interactions (Fig. 2). Generally, the Guinea-landraces showed a better adaptation toward –P, whereas the interracial breeding lines were more adapted to the +P conditions.

Direct vs. Indirect Selection for Grain Yield Under –P and +P Conditions

There was close correspondence between the top 10 (15%) ranked genotypes for grain yield under –P and under +P conditions, with 60% of the genotypes being in common (Table 7). All 10 top-ranked genotypes under –P had grain yield BLUPs that were significantly ($P < 0.01$) larger than the overall –P mean (Table 7).

However, the relative effectiveness of indirect selection in +P for –P grain yield was predicted to be only 88% as effective as direct selection in –P ($R_{id}/R_d = 0.89^* [0.95/0.96] = 0.88$). Additionally, the selection under +P conditions missed some of the highest ranked genotypes for –P grain yield (data not shown). Although selection under +P conditions retained

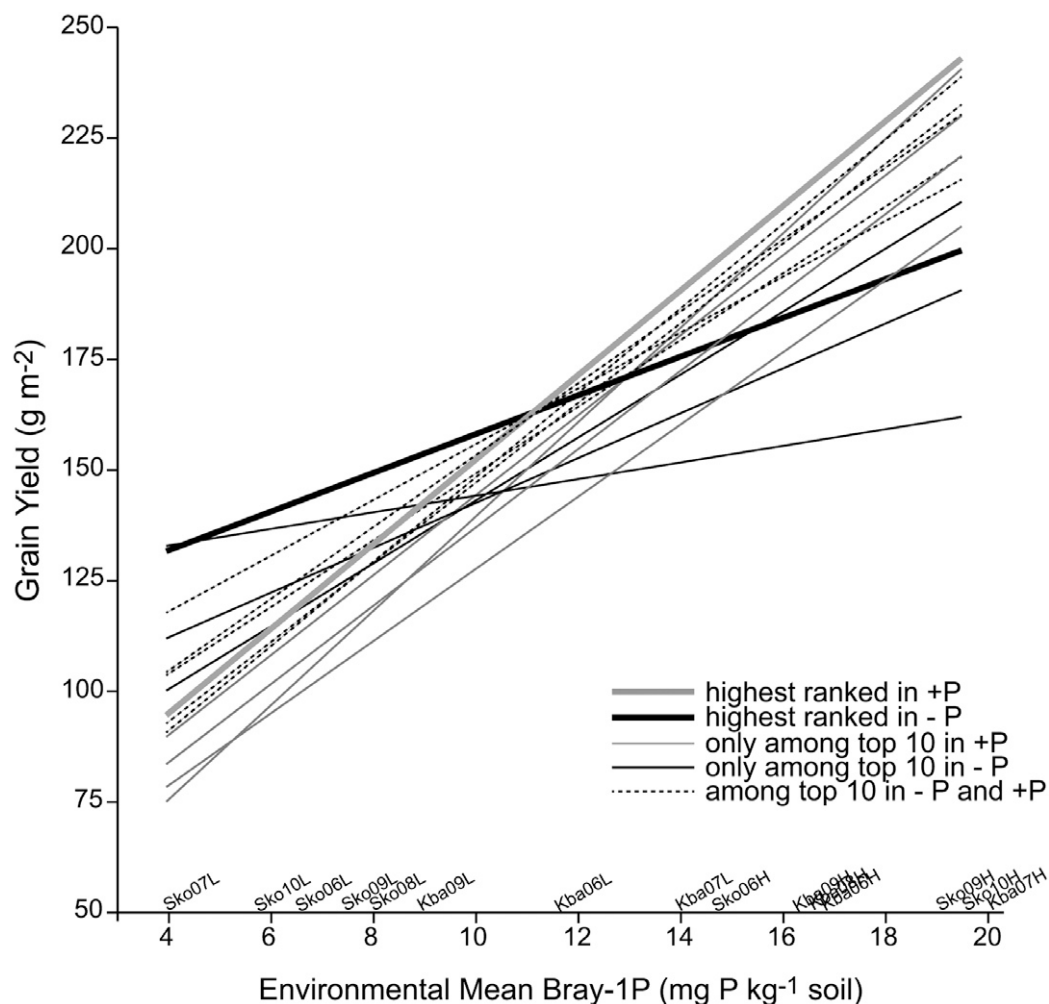


Figure 2. Linear regression of grain yield of 10 best-yielding sorghum genotypes in $-P$ (without P fertilization) and $+P$ (with P fertilization) conditions against the environmental mean Bray-1 P soil value. Slope estimates are significant (t -prob. ≤ 0.05), except for genotypes NAFALNP6, IS 15401, and B2-5.

all five of the interracial breeding lines from the top $-P$ set, it retained only one of the five Guinea-race breeding lines and landrace genotypes (data not shown). Further, higher selection intensity under $+P$ accentuated the loss of the highest ranked genotypes for $-P$ conditions. Thus, there is evidence of significant genotype \times phosphorus crossover interaction among the top 10 yielding genotypes across the $-P$ and the $+P$ environments (Fig. 2). This was particularly the case for the top three genotypes ($\sim 5\%$) from $-P$ and $+P$ selections (Table 7). The genotypes NAFALNP6 and IS15401 showed especially superior yields relative to the other genotypes in very poor environments (< 7 mg P kg $^{-1}$ soil), with an apparent crossover point between 9 and 11 mg P kg $^{-1}$ soil (Bray-1 P) (Fig. 2).

DISCUSSION

Appropriateness of Test Environments for Assessing Efficiency of $-P$ and $+P$ Selection

Our series of $-P$ environments showed rather large yield and height reductions and heading delays relative to environments receiving P fertilization, suggesting that the $-P$

and $+P$ environments did differ for P stress. Yield reduction, heading delay, and reduced height in $-P$ compared to $+P$ have been reported for several crops (Rossiter, 1978; Fageria et al., 1988; Atlin and Frey, 1989; Wissuwa and Ae, 2001; Manske et al., 2001; Turk et al., 2003; Chen et al., 2008; Cichy et al., 2008; Parentoni et al., 2010), suggesting that our environmental selection based on yield differences, height reduction, and heading delay was appropriate. Furthermore, the yield levels in our $-P$ trials were within the range common in Malian farmers' fields (FAO, 2010). Although the $-P$ environments in Kolombada 2006 to 2008 received less total nitrogen (N) than the corresponding $+P$ fields, the 2008 $-P$ trial was not included for the combined analysis due to lack of yield reduction, and the relative yield reductions of 2006 and 2007 were within the range of other pairs of trials with equivalent N in both $+P$ and $-P$. Also, genotype main effects and genotype \times environment interaction (GGE) biplots (Yan and Kang, 2002) of $-P$ environments did not reveal any distinct environment grouping relating to amounts of N fertilization (data not shown). The majority of our $-P$ trials had Bray-1 P-levels

Table 7. Ranks and best linear unbiased predictions for grain yield under –P (GY –P) and +P (GY +P) conditions of the 10 sorghum genotypes having the highest rank for grain yield across the eight –P trials and the corresponding selection differentials of the top 10 (15%), 7 (10%) and three (5%) genotypes selected under –P conditions.

Genotype	GY –P	Rank –P	GY +P	Rank +P
NAFALENP6	134.6***	1	202.4***	14
TIANDOUGOU	127.1***	2	218.4***	8
IS 15401	122.8***	3	161.8*	41
GRINKAN	119.1***	4	220.9***	7
01-BE-F5P-15	117.3***	5	226.9***	3
B2-5	114.9***	6	190.9 NS†	26
04-KANIKO-F5DT-26	114.3***	7	232.4***	2
WELI	113.9***	8	226.5***	4
SAKOYKA-BA	113.0***	9	206.0**	11
00-SB-F5DT-5	112.9***	10	239.1***	1
Selection differential 15%	30.7		34.4	
Selection differential 10%	33.1		29.5	
Selection differential 5%	39.8		16.1	
Grand mean	88.3		178.1	

* Significantly different from grand mean in same column at $p < 0.05$ in Wald-statistics in comparison contrasts.

** Significantly different from grand mean in same column at $p < 0.01$ in Wald-statistics in comparison contrasts.

*** Significantly different from grand mean in same column at $p < 0.001$ in Wald-statistics in comparison contrasts.

† NS = nonsignificant.

below 10 ppm P (10 mg P kg⁻¹ soil), thus within the range where P stress for WA sorghums is expected (Doumbia et al., 1993) and the range commonly observed in farmers' sorghum fields in Mali ($N = 207$, range = 1.6–36.2, mean = 7.4, median = 5.5; unpublished data, 2012). Thus, our –P environments appear to be relevant to Malian low-input sorghum production conditions.

Contrary to studies in maize by Parentoni et al. (2010), we did not detect a clear relationship between RYR and the genetic correlation (r_G) between yield in –P vs. +P conditions. This result may indicate that WA sorghums show generally fairly good adaptation to low-P conditions, even though general high yield differences between –P (88.3 gm⁻²) and +P (178.1 gm⁻²) existed. In fact, WA farmers consider sorghum as a crop for poor soils, and its capacity to produce yield without fertilization is one major factor contributing to its extensive cultivation and its importance as a staple cereal.

Selection in –P Conditions is Feasible

Heritabilities and/or repeatabilities for grain yield under low-input conditions are generally observed and expected to be lower due to higher error levels relative to high-input conditions (Ceccarelli, 1989, 1996; Atlin and Frey, 1990). Studies with contrasting P fertility levels showed significantly lower h^2 in the –P environments (Atlin and Frey, 1989; Ding et al., 2012). We also observed higher error levels (aVD) within and across the –P trials compared to +P trials. However, the

greater genetic variation (GCV) under –P conditions, especially those below the crossover point (at 11 ppm P [11 mg P kg⁻¹ soil]), contributed to similarly high h^2 estimates across both –P and +P trials. Greater genetic variation and better genotypic discrimination for grain yield in environments below crossover points was also observed in simulations and GEI studies by Simmonds (1991) and Ceccarelli (1996), respectively. The observed high h^2 estimates across our –P and +P trials were partly due to the rather large number of trials with little GEI and to the exclusion of some trials which showed environmental constraints.

Also, GEI in –P was rather small compared to the genotypic variance component, with little indication of high two-way interactions ($G \times L$, $G \times Y$) that otherwise needed to be considered for achieving more effective –P selection. Although rainfall was an important factor explaining GEI, it actually explained more GEI in +P. Most of the GEI in –P was of a complex $G \times Y \times L$ structure and was therefore not exploitable by further subdivision in mega-environments, as pointed out by Atlin et al. (2000, 2001). Therefore, the limited GEI observed across our –P environments despite ample sampling of years, sowing dates, and productivity levels suggests that BLUPs across –P trials may be used for selecting genotypes with superior –P adaptation and yield stability. However, a grouping of environments by rainfall zones may be helpful and testing in different rainfall zones should be considered for yield stability estimation.

The relatively lower GEI in –P vs. +P, especially for location, may be due in part to consequences of differential flowering responses of photoperiod-sensitive and less sensitive materials. Genetic variance for date of heading was higher in +P compared to –P environments. Although all varieties showed delayed flowering in –P, the less photoperiod-sensitive materials tended to have greater delays (data not shown), and thus reduced flowering time differences between these normally early-flowering materials and the typically later-flowering photoperiod-sensitive varieties under the –P conditions.

Therefore, genotypic selection for grain yield in researcher managed –P environments appears to be feasible and relevant to farmer's low-P conditions for sorghum in Sudanian WA, especially in test environments with Bray-1 P values below 9 and 11 ppm (9 and 11 mg P kg⁻¹ soil). The application of spatial adjustment methods (as in this study) can increase the repeatability in single trials (Leiser et al., 2012) and the broad-sense heritability across environments (data not shown) and, thus, further enhance the precision and efficiency of genotypic selection in low-input conditions.

Direct Selection in –P Conditions is More Efficient and There is a Need for Specific Adaptation to –P Conditions

The correspondence of sorghum varieties' yield performances under –P and +P conditions was surprisingly high relative to

observations in other crops like oat (*Avena sativa* L.), common bean (*Phaseolus vulgaris* L.), rape (*Brassica napus* L.) seeds, and maize (*Zea mays* L.) (Atlin and Frey, 1989; Beebe et al., 1997; Hammond et al., 2009; Parentoni et al., 2010; Ding et al., 2012). The high genetic correlation over P-levels and the small $G \times P$ variance component suggest that selection for general grain yield performance could be done either under $-P$ or $+P$ conditions. Also, these results suggest that the Guinea-race sorghum germplasm tested in this study has fairly good adaptation to low-P conditions. This may reflect the history of WA farmer's cultivation and selection of this race of sorghum over millennia under low-input conditions. Even today Malian farmers in intensifying production zones with >900 mm annual rainfall still extensively cultivate sorghum in the less fertile fields, knowing that sorghum can more dependably produce grain than can maize under such conditions. The rather weak relationship between RYR and r_G in this study compared to maize (Parentoni et al., 2010) also points to a general good adaptation of WA Guinea-race germplasm to low-P conditions.

However, specific adaptation to $-P$ conditions was shown by certain varieties in our study, such as IS 15401, and higher expected gains for grain yield in $-P$ conditions were predicted via direct selection under $-P$ conditions. Therefore, the careful identification of breeding objectives and target environments for which improvements are sought will be important for deciding on which testing environments to emphasize.

In this paper we have compared indirect selection under $+P$ conditions to direct selection under $-P$ conditions. These two strategies imply that in a future breeding program only one of the two types of trial will be used. If for some reason both types of trial will be conducted, the most efficient strategy may be to combine data from both types of trials. This is implemented most conveniently by fitting Model [5] and computing BLUPs of GP for the $-P$ condition. These BLUPs will combine the information across P-conditions in an optimal way, exploiting the genetic correlation between $+P$ and $-P$ conditions (Piepho and Möhring, 2005; Przystalski et al., 2008). We predicted grain yield BLUPs with both approaches and found a very strong agreement between $-P$ ($r = 0.9942$) as well as $+P$ ($r = 0.9895$) BLUPs derived from a model, not exploiting genetic correlations (as used in Table 7), and Model [5], respectively. In the $-P$ conditions all top 10 genotypes (as in Table 7) remained the same with slight rank changes, whereas in $+P$ only nine out of 10 genotypes remained within the 10 top ranked genotypes (data not shown).

Low P availability in WA soils is very prevalent (<7 ppm Bray-1 P [7 mg P kg^{-1} soil]) (unpublished data, 2012), especially in sorghum and pearl millet fields (Buerkert et al., 2001). Furthermore, inadequate infrastructure, high prices, lack of credit, and risk aversion limit many African farmers' use of fertilizers, resulting in average annual

fertilizer application rates of 5 to 8 kg NPK ha^{-1} (Jayne et al., 2003; Morris 2007; Bekunda et al., 2011). The fact that our $-P$ environments appeared to better reflect farmers' conditions than the $+P$ environments encourages more extensive sorghum varietal testing under $-P$ conditions for WA. Further, assessments of flowering delay and plant height under low-P variety testing could help avoid risks of poor grain fill with early cessation of seasonal rains and transhumant livestock damage of shorter height plants under low-P field conditions in WA. The long-term perspective of depleting worldwide P resources (50–370 yr) and rising fertilizer prices (Cordell et al., 2009; Van Kauwenbergh, 2010; Bekunda et al., 2011; Cooper et al., 2011; Jasinski, 2012), combined with continued population growth, point to the importance of crop breeding for $-P$ conditions on a worldwide scale (Gregory and George, 2011).

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