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Pearl Millet Inbred and Testcross Performance under Low Phosphorus in West Africa

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ABSTRACT

Pearl millet [*Pennisetum glaucum* (L.) R. Br] is a food security crop for millions living in drylands of Africa and Asia. Its production on acid sandy soils of the Sahel is limited by erratic rainfall and poor soil fertility, especially low P soils. We sought to elucidate the genetic variation in West and Central African landrace-derived inbred lines for grain yield under low P conditions, to determine their performance as inbred lines per se and in hybrid combinations, and to determine quantitative-genetic parameters to derive an appropriate breeding strategy to enhance grain yield under low P conditions. We evaluated a total of 155 landrace-derived inbred lines as well as their testcrosses in four locations during two years under two treatments, high P (HP; with P fertilization) and low P (LP; without P fertilization). Results revealed significant effects for genotypes, P-level, genotype × P-level, as well as genotype × environment interactions. Grain yield reductions under LP treatment ranged from 7.9 to 35.5%, and 11.2 to 60.9% for inbred lines and testcrosses respectively, with positive midparent heterosis averaging 43.5% under LP. We conclude that direct selection of testcrosses under LP is more effective and that indirect selection for testross performance from inbred line performance is not desirable.

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Abbreviations: aVD, standardized average variance of a difference; BLUP, best linear unbiased predictor; CV_g, genetic coefficient of variation; DAP, diammoniom phosphate; G × E, genotype × environment interaction; G × L, genotype × location interaction; G × P, genotype × P-level interaction; G × Y, genotype × year interaction; GCA, general combining ability; GY, grain yield; h^2, broad-sense heritability; HP, high-phosphorus treatment; IBL, inbred line; LP, low-phosphorus treatment; MPH, midparent heterosis; OPV, open-pollinated variety; REIS, relative efficiency for indirect selection; r_g, genetic correlations; RS, rainy season; RYR, relative yield reduction; S, selection differential; SCA, specific combining ability; TC, testcross; w^2, repeatability.

Pearl millet (2n = 2x = 14), also known as *Cenchrus americanus* (L.) Morrone, is a food security crop in the arid and semiarid areas of Africa and Asia produced on >10 million ha in Asia and about 16 million ha in Africa (Rai et al., 2009). This is attributed to its unique adaptability to extreme environments such as drought, high temperatures, and poor soils (Payne et al., 1998; van Staveren and Stoop, 1985). In the Sahel region of West Africa, pearl millet

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has been shown to grow under conditions of drought, low soil water holding capacity, poor nutrient availability, low soil pH, and high temperatures (Brück et al., 2003).

Phosphorus is the second most limiting mineral nutrient in crop production after nitrogen (Vance et al., 2003) and it has been shown to be the most limiting soil macronutrient to pearl millet productivity in the Sahel (Bationo and Mokwunye, 1991). Phosphorus is essential for cell growth and cell division in living organisms; hence it is an important inorganic plant nutrient (Hammond and White, 2008). It is taken up by plants either as dihydrogen phosphate ions ($H_2PO_4^-$) or hydrogen phosphate ions (HPO_4^{2-}), depending on soil pH, and these occur in soil solutions at very low concentrations (Hinsinger, 2001; Raghothama, 1999). Hence P acquisition is by diffusion against the gradient. According to Hinsinger (2001), P availability in the soil depends on the types and amounts of clay and metal oxides, soil solution pH, ionic strength, concentrations of P and metals (Fe, Al, and Ca), and the presence of competing anions, including organic acids.

Phosphorus deficit in plants initiates a series of transcriptional, biochemical, and physiological responses that serve either to enhance the plant's ability to acquire P from the soil or improve the efficiency with which plants utilize P internally (Hammond and White, 2008; Hammond et al., 2004; Jain et al., 2007; Vance et al., 2003). Such responses include modifications to root structure (Hammond and White, 2008), the formation of symbioses with mycorrhizae (Smith and Read, 1997), and the production of root exudates such as organic anions and phosphatase enzymes (George et al., 2002; Tadano et al., 1993). This therefore indicates differential responses of plants to P deficit.

The varietal differences in nutrient efficiency are based on genetic variation in physiological or morphological characters. Brück et al. (2003) and Faye et al. (2006) reported pearl millet genotypic differences in root and shoot parameters in fields with P deficiency and in hydroponic conditions, respectively. However, these studies only included a few genotypes. Studies investigating the genetic variation for low P tolerance in contrasting environmental conditions in West Africa are generally lacking and therefore the robustness of the genetic component of variation has rarely been tested from a breeding perspective. Furthermore, no study has focused on the performance of inbred lines with a possible aim towards hybrid breeding for low P tolerance.

The high outcrossing nature of pearl millet (85%; Burton, 1974) favors development of open-pollinated varieties (OPVs). These are the predominant pearl millet varieties grown in West Africa (Velu et al., 2011) and have the advantage that the seed can be recycled by farmers due to the absence of inbreeding depression. Whereas improved OPVs partially exploit heterosis, most of these varieties have low grain yields under the harsh conditions of drought, poor soil fertility, and high temperatures (Izge et al., 2007). Single-cross hybrids on the other hand allow for maximum exploitation of heterosis (Velu et al., 2011) but might be less capable of buffering unpredictable environmental variablity. Genetically more heterogeneous hybrid types (3-way, 4-way, top-cross hybrids) may ultimately be the best choice for highly variable environments like the Sahel. Any hybrid breeding requires proper information on combining ability and heterosis of diverse breeding populations to be able to efficiently select appropriate hybrid parents (Izge et al., 2007). Ouendeba et al. (1993) found significant general combining ability (GCA) among 10 crosses from five landrace populations. Such information is generally lacking on a diverse set of landrace-derived West and Central African pearl millet inbred lines.

The objectives of the current study therefore are:

(i) to elucidate the per se performance and genetic variation among West and Central African landrace-derived inbred lines for grain yield under low P conditions,
(ii) to determine the inbred lines' performance in the form of testcrosses with regard to grain yield under low P conditions, and
(iii) to estimate quantitative-genetic parameters such as heritabilities under low and high P conditions, coefficients of correlation between performance under low and high P conditions and between line per se and testcross performance, and extent of genotype × P interaction and to derive recommendations regarding appropriate selection strategies to enhance pearl millet grain yield under low P conditions.

MATERIALS AND METHODS

Genetic Materials

About 180 inbred lines (IBL) were developed from a collection of landraces from West and Central Africa to represent a large part of the diversity of pearl millet in this region, which is also the centre of origin for pearl millet. As the landraces displayed high inbreeding depression and genetic load, the inbred lines were developed by three generations of selfing followed by two generations of sibbing to reduce depression due to inbreeding. The inbred lines were also crossed to a non-male sterile tester (ICML-IS 11033) to produce F_1 testcrosses (TC). One hundred and sixty IBLs together with their TCs and 173 IBLs together with their TCs (choice determined by availability of enough seed for field trials) were evaluated in rainy season (RS) 2011 and RS 2012, respectively, in replicated field trials under LP and HP conditons.

Experimental Conditions

The trials were conducted in four locations in West Africa: Sadoré, Niger (17°36′28.04″ N; 8°4′53.99″ W); Gampela, Burkina Faso (12°25′51″ N; 1°22′18″ W); Bambey, Senegal (14°42′2.66″ N, 16°27′32.8″ W); and Koporo, Mali (14°3′49.9″N; 3°4′31″ W)

in the RS 2011 and RS 2012. The IBL and TC trials were grown side by side under HP and LP conditions. For the RS 2011, 160 IBLs and the 160 TCs were evaluated together with two checks in an 18 by 9 α-lattice with three replications in each treatment (P-level). In RS 2012, 173 IBLs and their TCs were evaluated together with two checks in a 35 by 5 α-lattice with three replications per treatment (P-level). For the IBLs, the checks included the tester (ICML-IS 11033) and ICML-IS 11197, an inbred line developed from the popular improved cultivar 'Sosat-C88', which has relatively short plant height (avoiding competition effects). The checks for TCs included equally Sosat-C88 and one local variety provided by the collaborator at each test site. We did not have prior information concerning performance under LP of the checks. One hundred and fifty five genotypes were common between the RS 2011 and RS 2012 trials. In each of the trials, a single row of seven hills per plot with 0.8m intra- and 0.75m interrow spacing was used resulting in a final plot area of 3.6 m^2. Border rows were used to separate the IBL trials from the TC trials to avoid competition. Soil samples were taken in each trial, sampling the top 20 cm. The samples were analyzed for pH, total nitrogen, organic carbon, Bray 1 P, and exchangeable potassium ions at ICRISAT, Niger. In RS 2011, the HP treatment received 100 kg ha^{-1} diammonium phosphate (DAP) (corresponding to 20 kg ha^{-1} P and 18 kg ha^{-1} N) at sowing, whereas the LP treatment received a basal application of 39 kg ha^{-1} urea (corresponding to 18 kg ha^{-1} N). Both treatments were then supplied with two topdressings (30 and 45 d after sowing) of 35 kg ha^{-1} urea (corresponding to 16 kg ha^{-1} N). Due to concerns about the possible masking of the P effect, the P level was doubled in RS 2012 by providing an extra 255.56 kg ha^{-1} single super phosphate (corresponding to 20 kg ha^{-1} P) in addition to 100 kg ha^{-1} DAP (corresponding to 20 kg ha^{-1} P) while the urea amount required at sowing remained the same as for RS 2011 (39 kg ha^{-1} urea~18 kg ha^{-1} N). The N-level was also balanced accordingly by increasing the number of top dressings with urea to four (i.e., 25 kg ha^{-1} urea, corresponding to 11.4 kg ha^{-1} N) at 3, 5, 7, and 9 wk after sowing. Although the P treatment was recommended to be applied at sowing, the fertilization was actually based on moisture availability in the soil (to avoid burning of the seedlings) and was sometimes delayed by up to 2 wk after sowing due to the erratic nature of rainfall within the region. The summary of the environmental conditions as well as fertilization of the trials is shown in Table 1. The trials were conducted under rainfed conditions.

Data Collection

Data collected in each plot include days from sowing to 50% flowering (with flowering defined as full female stigma emergence on 50% of the main panicles), plant height (from soil surface to panicle tip) after flowering taken as an average of three representative plants, and grain yield converted to g m^{-2}.

Statistical Analyses

Analysis was done on the basis of REML mixed models using GENSTAT 15th edition. Each trait in each environment was analyzed separately with genotypes as well as blocks nested in replications considered as random effects in the analysis of variance. Data was transformed if residuals were not normally distributed. For a combined analysis within one P-level, locations

Table 1. Growing conditions for yield trials evaluated under high phosphorus (HP) and low phosphorus (LP) conditions during 2011 and 2012 rainy seasons in West Africa.

Location†	Year	Treatment	Sowing date	Total rain		Rain during first 3 wk		Rain during flowering		Fertilizer		pH-H_2O	Total N	Carbon-org‡	Bray1 P	K+ exc§
				mm	d	mm	d	mm	d	N kg ha^{-1}	P kg ha^{-1}	1:2.5	mg-N kg^{-1}	%-C.	mg-P kg^{-1}	cmol+ kg^{-1}
Sadore	2011	HP	11 July	466	34	163	10	50	4	50	20	4.6	175	0.21	3.3	0.12
		LP	11 July					50	4	50		4.6	184	0.21	3.4	0.12
Gampela	2011	HP	29 July	893	61	247	15	86	10	50	20	6.6	370	0.41	7.7	0.38
		LP	29 July					50	8	50		6.3	251	0.24	6.2	0.47
Koporo	2011	HP	10 July	308	26	49	6	36	5	50	20	5.3	83	0.11	3.2	0.19
		LP	10 July					36	5	50		4.6	111	0.12	3.5	0.17
Bambey	2011	HP	18 July	584	35	62	4	97	9	50	20	6.1	305	0.25	5.5	0.13
		LP	18 July					97	9	50		5.9	214	0.25	4.5	0.11
Sadore	2012	HP	2 July	634	28	113	5	186	11	64	40	4.8	219	0.25	3.0	0.13
		LP	2 July					161	10	64		4.7	190	0.23	3.5	0.11
Gampela	2012	HP	21 July	950	–	–	–	100	–	64	40	6.6	268	0.27	4.2	0.31
		LP	21 July					100	–	64		6.6	270	0.26	6.2	0.34
Bambey	2012	HP	9 July	601	51	114	9	219	31	64	40	5.8	184	0.23	3.9	0.09
		LP	9 July					300	35	64		5.6	219	0.23	4.0	0.09

†Sadore in Niger, Gampela in Burkina Faso, Koporo in Mali, and Bambey in Senegal.

‡Carbon-org, organic carbon.

§K^+ exc, exchangeable potassium ions.

were treated as fixed whereas genotypes, years, and all interactions as well as blocks nested in replications within locations were treated as random. For a combined analysis across treatments (P-levels), the treatment (P-level) was considered as fixed whereas genotypes, environments (location–year combination), and all interactions were considered random. We had to drop Koporo 2012 trials because the trials had been virtually washed away due to too much rainfall and concomitant soil erosion directly after sowing. Bambey 2012 trials were dropped due to too much missing data (caused by too much raifall and water stagnation in the field during the season) that could not be corrected for by the standardized average variance of a difference (aVD). Gampela 2011 TC trial was also dropped due to too much missing data following drought after sowing. As a measure for the extent of error in each trial so as to be able to compare the extent of error across trials of differing mean yields, the standardized aVD was calculated according to Leiser et al. (2012) as:

$$\text{aVD} = \left(\text{VD}\right)^{1/2}/\mu$$

where VD is the average variance of a difference between means of genotypes, and μ is the trial mean. For each single trial, repeatability (w^2) was calculated according to Piepho and Möhring (2007) as:

$$w^2 = \sigma_g^2 / \left[\sigma_g^2 + \left(\text{VD}/2\right)\right]$$

where VD is the average variance of a difference between means of genotypes and σ^2_g is the genetic variance component. For combined analysis, broad-sense heritability (h^2) was calculated according to Cullis et al. (2006) as follows:

$$h^2 = 1 - \left(V_{\text{BLUP}} / 2\,\sigma_g^2\right)$$

where V_{BLUP} is the mean variance of a difference of two best linear unbiased predictors (BLUPs) and σ^2_g is the genetic variance component. To allow for comparison of genetic variance components across trials with different means, the genetic coefficients of variation were calculated as:

$$CV_g = \left(\sigma_g^2\right)^{1/2}/\mu$$

where σ^2_g is the genetic variance component and μ the population mean.

Relative yield reduction (RYR) in LP vs. HP treatment was calculated according to Venuprasad et al. (2007) as:

$$\text{RYR} = \left[1-\left(\mu\text{LP}/\mu\text{HP}\right)\right]100$$

where μLP is the mean under LP and μHP is the mean under HP.

Genotypic correlations were computed on the basis of BLUPs from all single trials and the genetic coefficients of correlation between HP vs. LP and/or IBL vs. TC (for simplicity marked as x and y) were calculated according to Cooper et al. (1996) and Kebede et al. (2013) assuming no environmental covariance between the LP and HP trials due to the experimental set up as:

$$r_{g(xy)} = r_{p(xy)} / \left(h_x^2 \times h_y^2\right)^{1/2}$$

where $r_{p(xy)}$ is the correlation of the traits measured in setting x and y (in this case either LP and HP and/or TC and IBL), whereas h_x^2 and h_y^2 are the broad-sense heritabilities of traits measured in setting x and y, respectively.

Midparent heterosis (MPH) was calculated according to Huang et al. (2006) as:

$$\text{MPH} = \left(F_1 - \text{MP}\right)/\text{MP}$$

where F_1 is the mean performance of the testcross and MP is the average performance of the two parents. Since the F_1 performance is not completely independent of the parental performance, the difference of the F_1 mean from the mid-parent mean was assessed using a paired *t* test.

The selection diffential (*S*) was calculated as:

$$S = \mu\text{-select} - \mu\text{-pop}$$

where μ-select is the mean of the selected individuals at 10% selection intensity and μ-pop is the grand mean (population mean) (Leiser et al., 2012). The significance of this difference from the grand mean was tested using an independent *t* test.

The relative efficiency of indirect selection compared with direct selection (REIS) was calculated according to Zhao et al. (2006) as:

$$\text{REIS} = r_{g(xy)} \left(h_x^2 / h_y^2\right)^{1/2} \times 100$$

where $r_{g(xy)}$ is the genotypic correlation between the direct and indirect criterion x and y (in this case, HP vs. LP and/or IBL vs. TC), while h_x^2 and h_y^2 are the respective broad-sense heritabilities.

RESULTS

Trait Means and Performance Comparison between Low P and High P Treatments

We observed a general reduction in grain yield and plant height and a delay in flowering for all LP trials in the inbred line trials as well as testcross trials. The grain yield ranged from 25.2 to 71.7 g m^{-2} under LP and from 39.1 to 91.3 g m^{-2} under HP for the inbred line trials. The testcross means ranged from 43.9 to 118.4 g m^{-2} under LP and from 83.5 to 140.1 g m^{-2} under HP (Table 2). The single environment grain yield BLUPs under LP for the 155 inbred lines common between RS2011 and RS2012 evaluation trials are shown in Supplemental Table S1. Reduction in plant height ranged from 2.0 to 14.7 cm for inbred lines and from 0.4 to 24.7 cm for testcrosses, whereas flowering delay ranged from 1.5 to 6.7 d in inbred lines and 1.1 to 10.4 d in testcrosses (Table 2). For a combined analysis within one treatment (P-level), the inbred lines had a

Table 2. Grain yield means ± SE (μ ± SE), repeatabilities (w^2), coefficient of genetic variation (CV_g), standardized average variance of a difference (aVD), pairwise genetic correlation between low phosphorus (LP) and high phosphorus (HP) trials (r_g), relative yield reduction under LP (RYR), height reduction (–HT) and flowering delay (FD) under LP.

	Location†	Year	Treat	μ	w^2	CV_g	aVD	r_g	RYR	–HT	FD
				g m^{-2}						cm	d
Inbred lines	Sadore	2011	HP	58.8 ± 7	0.84	29.3	17.9	0.96	8.4	–10.7	4.3
			LP	53.8 ± 2	0.59	22.0	26.0				
	Gampela	2011	HP	91.3 ± 9	0.76	42.3	33.5	0.87	37.4	–10.5	2.1
			LP	57.2 ± 9	0.63	27.4	29.5				
	Koporo	2011	HP	77.9 ± 4	0.68	22.3	21.6	0.98	7.9	–6.4	1.5
			LP	71.7 ± 3	0.64	20.7	22.0				
	Bambey	2011	HP	69.5 ± 4	0.84	39.0	24.1	0.93	29.5	–2.0	2.9
			LP	48.9 ± 3	0.82	24.6	9.5				
	Sadore	2012	HP	39.1 ± 7	0.71	37.0	33.1	0.96	35.5	–12.2	6.7
			LP	25.2 ± 3	0.79	38.0	27.9				
	Gampela	2012	HP	66.9 ± 6	0.69	42.8	40.3	0.94	19.3	–14.7	3.6
			LP	54.0 ± 6	0.70	34.0	31.6				
	μHP				0.75	35.3	28.4				
	μ LP				0.70	27.7	24.4				
Testcrosses	Sadore	2011	HP	83.5 ± 10	0.63	17.9	19.4	0.86	25.2	–0.4	3.2
			LP	62.5 ± 3	0.62	17.6	19.3				
	Koporo	2011	HP	122.4 ± 8	0.59	14.4	17.0	0.84	26.6	–20.3	3.2
			LP	89.9 ± 6	0.57	12.9	15.8				
	Bambey	2011	HP	93.8 ± 7	0.67	20.4	20.5	0.81	11.2	–5.9	1.1
			LP	83.3 ± 9	0.64	24.1	25.7				
	Sadore	2012	HP	112.2 ± 20	0.59	17.4	20.4	0.90	60.9	–24.7	10.4
			LP	43.9 ± 8	0.59	22.9	27.2				
	Gampela	2012	HP	140.1 ± 9	0.62	17.8	19.6	0.82	15.5	–7.1	3.1
			LP	118.4 ± 8	0.61	17.5	19.8				
	μ HP				0.62	17.6	19.4				
	μLP				0.61	19.0	21.6				

† Sadore in Niger, Gampela in Burkina Faso, Koporo in Mali, and Bambey in Senegal.

mean of 54.0 g m^{-2} under LP and 61.8 g m^{-2} under HP, whereas the combined LP mean for testcrosses was 77.9 g m^{-2} against 109.1 g m^{-2} combined HP mean (Table 3). We observed consistently high positive genetic correlations (r_g) between LP and HP treatments in all pairwise trial analyses ranging from 0.87 to 0.98 for inbred lines and 0.81 to 0.90 for testcrosses. There was a wide range for RYR in both inbred line and testcross trials, with RYR ranging from 7.9 to 35.5% for inbred lines and from 11.2 to 60.9% for testcrosses (Table 2). High relative yield reduction was associated with lower genetic correlation between LP and HP in both testcross and inbred line trials ($r = -0.72$ and $r = -0.67$, respectively; $P < 0.001$: data not shown). The RYR was also correlated with number of days with rain during flowering of $r = 0.89$ under HP, $r = 0.85$ under LP in inbred lines; $P < 0.001$, and $r = 0.51$ and $r = 0.75$ under HP and LP; $P < 0.001$, respectively, in testcrosses (data not shown). There was positive correlation between grain yield (GY) and soil pH ($r = 0.79$ and $r = 0.56$; $P < 0.001$) for both inbred lines and testcrosses, respectively (data not shown). For combined analysis across locations, the genetic correlation between LP and HP was 0.92 and 0.69 for inbred lines and testcrosses, respectively. The RYR under LP across all locations was relatively lower in the inbred lines than in testcross trials (23.5 and 29.2% respectively) (Table 3).

Repeatability, Broad-Sense Heritability, and Genetic Variation

Repeatability estimates w^2 per single trial were higher for inbred trials than for the testcross trials (Table 2). The w^2 for inbred line trials ranged from 0.59 to 0.82 with a mean of 0.70 under LP and from 0.68 to 0.84 with a mean of 0.75 under HP. For testcrosses, the w^2 range was 0.57 to 0.64 with a mean of 0.61 under LP and 0.59 to 0.67 with a mean of 0.62 under HP (Table 2). Except for two locations in the inbred line trial, there was a consistent reduction in w^2 under LP for both inbred line and testcross trials, although in most cases, the difference was minimal between HP and LP w^2 values (Table 2). The coefficient of genetic variation (CV_g) was lower under LP in inbred lines trials, ranging from 20.7 to 38.0% with a mean of 27.7%, compared with HP trials with CV_g range of 22.3 to 42.8% and a mean of 35.3%. The extent of error was also lower in LP inbred line trials, with a mean of 24.4% compared with 28.4% aVD in HP inbred line trials.

Table 3. Variance components for grain yield (σ^2 ± SE), best linear unbiased predictor means (μ), broad-sense heritability (h^2), genetic coefficients of variation (CV_g), standadized average variance of a difference (aVD), relative yield reduction under low phosphorus (RYR), genetic correlation between low phosphorus (LP) and high phosphorus (HP) treatments (r_g), and the treatment (P-level effect) effect (Treat) from a combined analysis within one P-level (left) and across P-levels (right) in both testcross and inbred lines trials.

Random term†	σ^2 ± s.e				Random term	σ^2 ± s.e	
	Testcrosses		Inbred lines			Testcrosses	Inbred lines
	LP	HP	LP	HP		Combined HP and LP	
	σ^2 ± s.e	σ^2 ± s.e	σ^2 ± s.e	σ^2 ± s.e		σ^2 ± s.e	σ^2 ± s.e
G	229*** ± 82	352*** ± 56	357*** ± 77	559*** ± 123	G	438*** ± 149	681*** ± 93
G × Y	122*** ± 45	188*** ± 49	200*** ± 54	441*** ± 93	G × P	42* ± 17	31* ± 15
G × L	55ns ± 35	29ns ± 72	150 ** ± 65	200*** ± 73	G × E	253*** ± 79	351*** ± 34
G × Y × L	26ns ± 28	52ns ± 94	41ns ± 70	92ns ± 82	G × P × E	151ns ± 167	10ns ± 43
Mean (μ)	77.2	109.1	54.0	61.8	Mean	102.1	62.9
h^2	0.57	0.62	0.75	0.78	h^2	0.74	0.93
CV_g	19.6	17.2	35.0	38.3	CV_g	18.3	42.0
aVD	18.2	15.0	24.7	25.4	aVD	14.7	16.0
RYR	29.2		23.5		Treat	*	*
r_g	0.69		0.92				

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

†G, genotype; G × Y, genotype × year interaction; G × L, genotype × location interaction; G × Y × L, genotype × year × location interaction; G × P, genotype by P-level interaction; G × E, genotype × environment interaction; G × P × E, genotype × P-level × environment interaction.

In testcross trials, however, the CV_g was slightly higher under LP than HP, ranging from 12.9 to 24.1% with a mean of 19.0% under LP compared with HP trials with CV_g range of 14.4 to 20.4% and a mean of 17.6%. The aVD in testcross trials was also higher under LP compared with HP (21.6 and 19.4% for LP and HP, respectively) (Table 2). In the combined analysis across locations within one treatment (P-level), h^2 under LP was relatively lower than that under HP for both testcross and inbred trials (0.57 vs. 0.62 and 0.75 vs. 0.78 for testcross and inbred trials, respectively) (Table 3). The genetic coefficient of variation was lower under LP than HP for inbred trials (35.0 vs. 38.3%), whereas it was relatively higher under LP than HP for testcross trials (19.6 and 17.2% respectively), though the extent of error was also higher under LP than HP in testcrosses (Table 3). Across P-levels, the broad-sense heritability was lower in testcrosses than in inbred lines (0.74 and 0.93 respectively). The genetic variance appeared to have been reduced by about 50% in the testcrosses compared with inbred lines, on the basis of the genetic coefficients of variation (18.3 and 42.0% respectively) (Table 3).

Variance Components and Patterns of Genotype × Environment Interaction

Most of the variance was explained by the genotypic component for both testcross and inbred line trials. For the combined analysis within one P-level, most of the genotype × environment interaction (G × E) was in the two-way interaction forms (genotype × year [G × Y] and genotype × location [G × L] interactions), while the threefold interaction component G × L × Y was mostly relatively smaller and nonsignificant. The G × Y variance component was more important than G × L interaction. The G:G × Y variance component ratios under LP were 1:0.53 and 1:0.56 for testcrosess and inbred lines, respectively, whereas under HP, the G:G × Y ratios were 1:0.53 and 1:0.79 for testcross and inbred line trials, respectively. The G:G × L ratios were 1:0.24 and 1:0.42 for testcross and inbred line trials, respectively, under LP compared with G:G × L ratios of 1:0.13 and 1:0.36 under HP for testcross and inbred line trials, respectively. The three-way interaction (G × L × Y) was nonsignificant under both LP and HP for the two sets of experiments (inbred and testcross trials) (Table 3). For the performance across P-levels, the P-level treatment effect as well as the genotype × P-level (G × P) interaction were significant at $P < 0.05$ for both testcross and inbred line trials. The G:G × P ratios were 0.10 and 0.05, respectively, for testcross and inbred line trials. The two-way interaction (G × E) was significant whereas the three-way interaction (G × P × E) was not signifcant.

Response to Direct vs. Indirect Selection for Low P Tolerance

The correspondence of ranks at 10% selection intensity between HP and LP was 60 and 47% for inbred lines and testcrosses respectively (data not shown). Selection for low P tolerance under HP therefore missed out 40 and 53% of the best genotypes under LP in inbred lines and testcrosses, respectively. This would therefore imply differential response of genotypes to LP as evidenced by the

Table 4. Best linear unbiased predictors of the best 15 (10%) testcrosses under high phosphorus (μHPTC) and low phosphorus (μLPTC), ranks based on selection under high (HP) and low phosphorus (LP), selection differential (S) under HP and LP selection and midparent heterosis under HP (HPMPH) and under LP (LPMPH).

Testcrosses												
Selection under LP							Selection under HP					
Genotype†	μHPTC	μLPTC	Rank HP	Rank LP	HPMPH	LPMPH	Genotype	μHPTC	μLPTC	Rank HP	Rank LP	HPMPH	LPMPH
37	120.0§	94.5§	6	1	3.7ns	24.1ns	115	121.4§	83.5ns	1	82	11.7ns	7.8ns
21	119.6§	93.8§	9	2	33.7‡	28.6ns	47	121.2§	90.1ns	2	12	17.0ns	16.2ns
45	116.5§	93.8§	22	3	25.1ns	42.0ns	53	120.7§	93.5‡	3	4	64.6‡	69.6‡
53	120.7§	93.5§	3	4	64.6‡	69.6‡	2	120.6§	90.6ns	4	11	19.1ns	19.5ns
38	110.7ns	93.0§	73	5	29.2‡	38.0ns	41	120.0§	87.4ns	5	36	91.9‡	91.5‡
89	116.9§	92.4§	18	6	36.1‡	47.5ns	37	120.0§	94.5‡	6	1	3.7ns	24.1ns
84	115.2§	91.6ns	35	7	49.7‡	60.6‡	30	119.9§	86.6ns	7	45	59.1‡	43.5ns
135	115.0§	91.6ns	38	8	38.7‡	41.4ns	114	119.7§	90.6ns	8	10	17.6ns	23.4ns
129	108.3ns	90.8ns	95	9	4.0ns	25.0ns	21	119.6§	93.8‡	9	2	33.7‡	28.6ns
114	119.7§	90.6ns	8	10	17.6ns	23.4ns	28	119.5§	87.4ns	10	37	58.5‡	63.8‡
2	120.6§	90.6ns	4	11	19.1ns	19.5ns	122	118.7§	87.5ns	11	35	26.0‡	18.7ns
47	121.2§	90.1ns	2	12	17.0ns	16.2ns	71	117.8§	87.0ns	12	42	31.4‡	14.3ns
3	117.8§	90.0ns	13	13	2.4ns	7.9ns	3	117.8§	90.0ns	13	13	2.4ns	7.9ns
123	114.8§	89.7ns	39	14	28.0‡	48.5ns	121	117.7§	85.2ns	14	53	61.4‡	54.2ns
76	111.4ns	89.6ns	65	15	82.5‡	98.1‡	102	117.5§	80.9ns	15	108	58.9‡	34.8ns
μ-select	116.6	91.7		Mean		39,4	μ-select	119.5	88.6	Mean		37.1	
μ-pop	109.1	77.2					μ-pop	109.1	77.2				
S	7.5	14.5					S	10.4	11.4				

† μ-pop, the grand mean; μ-select, the mean at 10% selection intensity.

‡ Significantly different from μ-pop or from midparental value at $P < 0.05$.

§ Significantly different from μ-pop or from midparental value at $P < 0.001$.

observed significant G × P interaction (Table 3). Selection differential (S) at 10% selection intensity was higher under HP for inbred lines (Supplemental Table S2), whereas it was higher under LP for testcrosses (Table 4). The response was better in direct selection in the target environment than in indirect selection for both sets of experiments (inbred and testcross). Since our main interest would be the response gained for testcrosses, we observed S = 14.5 and S = 10.4 under LP and HP, respectively, for testcrosses. The REIS for LP tolerance under HP conditions was 95.2% for inbred lines and 72% for testcrosses.

Performance as Lines per se vs. Testcrosses

The heterotic performance of the testcrosses under LP over their midparental values was mostly positive, ranging from 1.9 to 98.1% except for one genotype, ICML-IS 11033 × ICML-IS 11183, which had a negative midparent heterosis of −5%. The mean MPH under LP was 43.5%. Under HP, all MPH estimates were positive except for four genotypes which had negative heterosis. The MPH ranged from −11.3 to 91.9% with a mean of 39.2% (data not shown). The MPH for the 10% best testcrosses ranged from 7.9 to 98.1% under LP with a mean of 39.4%, whereas under HP the range was between 2.4 to 91.9% with a mean of 37.1% (Table 4). Across P levels, MPH was also mainly positive and ranged from 3.6% to 124.9% with one exception, ICML-IS 11033 × ICML-IS 11103, which had negative heterosis of −1.6%. The correlation between testcross performance and MPH was nonsignificant for both HP and LP. The phenotypic correlation between inbred lines performance and testcross performance was positive and significant under both HP and LP ($r = 0.31$ and $r = 0.32$ respectively; $P < 0.001$) (Table 5 lower triangle; Fig. 1c, d), whereas genetic correlations (r_g) were moderate between the inbred lines and testcrosses (Table 5 upper triangle). The genetic correlation was highest ($r_g = 0.49$) between inbred lines and testcrosses under LP (LP inbred vs. LP testcross), with a relative efficiency for indirect selection

Table 5. Phenotypic (lower triangle) and genetic (upper triangle) correlations among midparent heterosis under high phosphorus (HPMPH), midparent heterosis under low phosphorus (LPMPH), inbred lines performance under high phosphorus (HPIBL), inbred lines performance under low phosphorus (LPIBL), testcross performance under high phosphorus (HPTC), and testcross performance under low phosphorus (LPTC) conditions.

	HPMPH	LPMPH	HPIBL	LPIBL	HPTC	LPTC
HPMPH						
LPMPH	0.83***					
HPIBL	−0.94***	−0.89***		0.92	0.45	0.41
LPIBL	−0.83***	−0.92***	0.70***		0.46	0.49
HPTC	−0.03ns	−0.16ns	0.31***	0.31***		0.69
LPTC	−0.17ns	0.05ns	0.27***	0.32***	0.41***	

*** Significant at the 0.001 probability level.

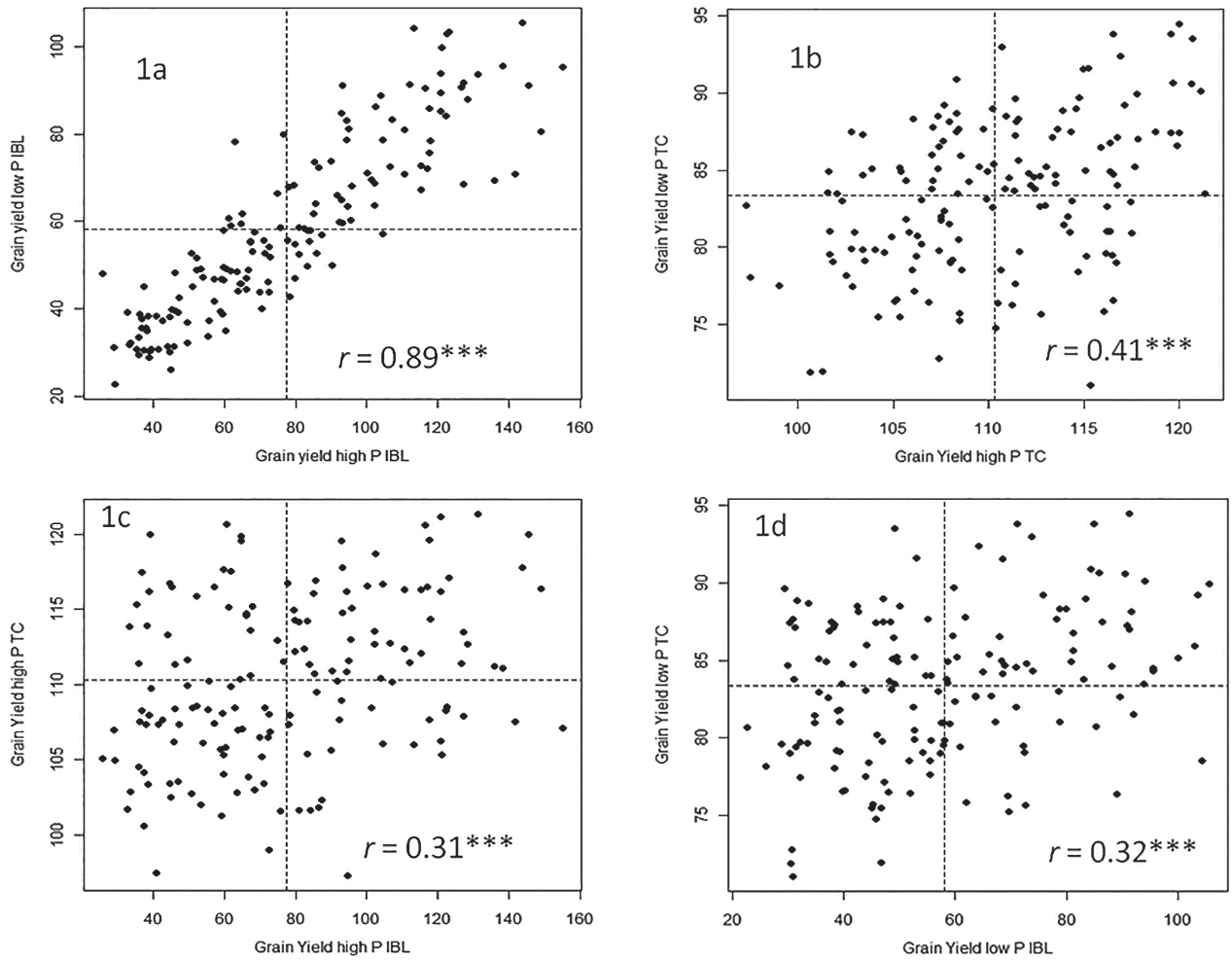

Figure 1. Relationships between grain yield best linear unbiased predictors under low phosphorus (LP) and high phosphorus (HP) conditions for (a) inbred line trial (IBL), (b) testcross trial (TC), and the association between IBL and TC under (c) HP and (d) LP.

for testcross performance from inbred lines performance (REIS) of 56.1%. The REIS under HP was 50%. The lowest genetic correlation was observed if the inbred lines selected under HP were used to predict testcross performance under LP (r_g = 0.41 and REIS 47.4%).

DISCUSSION

Appropriate P Treatment Levels for Testing

The current study revealed a general reduction in mean grain yield as well as plant height and delay in flowering under LP vs. HP conditions. Similar trends have been reported in other crops under LP conditions: Leiser et al. (2012) in sorghum [*Sorghum bicolor* (L.) Moench], Parentoni et al. (2010) in maize (*Zea mays* L.), Beebe et al. (2007) in common bean (*Phaseolus vulgaris* L.). Banziger et al. (1997) and Parentoni et al. (2010) observed that significant yield reductions (43 and 50%, respectively) began to appear at genetic correlations close to 30% (r_g = 0.30) in low N and low P studies in maize. The two studies, however, used more pairwise trials to study this relationship (14 and 15 pairwise trials respectively). The genetic correlations in our pairwise trials remained consistently high (i.e., > 0.8). Furthermore, we had fewer pairwise trials for assessing the relationship between RYR and r_{gs} (six pairs for inbred lines and five pairs for testcrosses) because we had to drop some trials due to unavoidable environmental constraints such as extreme drought and/or too much rainfall leading to too many missing values. Nevertheless, the high genetic correlation between LP and HP trials coupled with the highly significant negative correlation between RYR and genetic correlation implied that our HP and LP trials were not sufficiently differentiated and this seems to agree with the additive main effects and multiplicative interaction (AMMI) biplot in Supplemental Fig. S1 as evidenced by a small angle between HP and LP trials per location. Furthermore, on the basis of the current results, yields should be reduced by about 48 and 55% in testcrosses and inbred lines, respectively, to be able to screen for LP tolerance rather than yield potential. This implies that our RYR averaging 24% for inbred lines and 29.2% for testcrosses were too low. This therefore discounts our general hypothesis that P is the major factor creating grain yield differences between LP and HP. We attribute this insufficient differentiation between HP and

LP to a lack of P response, which could be as a result of several factors. The very low initial Bray-P values ranging from 3.0 to 7.7 mg P Kg^{-1} soil, compounded by the low pH values (pH ranging from 4.6 to 6.6) (Table 1) in some locations might have caused high P fixation of the applied P fertilizer, thus making it plant unavailable. The positive correlation between GY and soil pH (r = 0.79 and r = 0.56; P <0.001) for inbred lines and testcrosses, respectively, imply that GY reduction was related to the pH and herewith to P availability and possibly Al-toxicity (though these were not tested in the current study), thus confounding the effect of adaptation to low P soil conditions. In addition, late application of the phosphate fertilizers after sowing—due to erratic rainfall, especially during the rainy season of 2011—could also have contributed to the lack of a strong P-response, as indicated by Valluru et al. (2010). Furthermore, poor soil fertility has been shown to often occur with drought in farmers' fields and separating the effects of drought stress from those of LP stress could pose a challenge since drought affects both HP and LP trials and could mask the effect of P application (Ho et al., 2005). Our experiments were rain fed and evaluated during the rainy season in the target region and thus exposed to the same random drought stress found in the farmers' conditions. Our observation of significant association between RYR and number of days with rain during flowering of r = 0.89 under HP, r = 0.85; P <0.001 under LP in inbred lines, and r = 0.51 and r = 0.75; P <0.001under HP and LP, respectively, in testcrosses imply that other factors besides P-bioavailability were in play and did mask the effect of P supply in the current study and this could explain the reduced RYR between LP and HP as observed. This is evidenced by the small (compared with the genotypic variance component) though significant P effect in our study despite application of enough P to the HP treatment and underlines the need to control the soil environment to avoid P complexing.

There is Genetic Variation for Grain Yield under Low P

Significant genetic variation for grain yield under LP conditions is a prerequisite for any breeding program targeting LP environments. The results of the current study indicate the presence of significant genetic variation in West African pearl millet for grain yield under LP conditions. The high broad-sense heritability estimates, especially in the inbred lines (>0.7) under LP conditions, merit the possibility of efficient genotypic selection for low-input production systems. The relatively lower broad-sense heritability observed in the testcrosses (>0.5) can be attributed to the fact that all inbred lines were crossed to one tester, thus reducing genetic variation and therefore the very limiting soil conditions could have hindered expression of differences more in testcrosses compared with parental inbred lines. The lower broad-sense heritability in the LP treatment compared with HP treatment for both testcross and inbred lines can be attributed to a relatively higher extent of error (aVD) under LP with same genetic variation between HP and LP in the testcross trial and a lower genetic variation under LP with similar extent of error level between HP and LP in the inbred line trial. Lower heritability under LP due to increased error as observed in our testcross trial has also been reported in other low phosphorus tolerance studies: Atlin and Frey (1989) in oats (*Avena sativa* L.), Ding et al. (2012) in rape (*Brassica napus* L.), and Leiser et al. (2012) in sorghum. Banziger et al. (1997) and Li et al. (2011) also reported reduced heritability in maize under low N due to reduced genetic variance rather than increased error as observed in our inbred lines trial. Furthermore, the significant G × P interaction is indicative of differential response of genotypes to LP. The current test genotypes can therefore be used in breeding for high grain yield under LP. However, the significance of G × E, especially the two-way interactions (G × L and G × Y) as observed in both inbred and testcross trials underlines the need to evaluate the test materials in multienvironments to be able to identify superior materials for grain yield under LP. This therefore indicates the need to further delineate the locations into zones to take care of G × L and perform more testing for yield stability to take care of G × Y. For instance, G × Y was more important in the current study than G × L since we only evaluated the test genotypes in 2 yr (2011 and 2012). Our environments were more variable in RS 2011 than in RS 2012 and there appears to be a negative correlation of genotypic performance between the two years (Supplemental Fig. S1). It was noted that 2011 was a major drought year within the region, especially during flowering time, whereas 2012 was relatively wet (Haeseler, 2012).

Reduced Genetic Variation for Grain Yield under Low P in Testcrosses

We observed that testcrosses had relatively reduced genetic variance compared with inbred lines. This is in accordance with the quantitative genetic theory where the genetic coefficient of variation is expected to be about four times more in inbred lines than that of testcrosses (Miedaner et al., 2014; Smith, 1986). The reduced genetic variation is attributable to the fact that all inbred lines were crossed to one tester. This would imply that our tester was generally well performing, thus masking a high frequency of unfavorable alleles in the testcrosses (Smith, 1986). Since we did not have prior information about the response to low phosphorus conditions of the tester used in the current study, the tester was included in the inbred line trials as an internal check. We observed that the tester was moderately good, with a mean of 86.1 g m^{-2} under HP against 61.8 g m^{-2} HP trial mean and a mean of 61.1 g m^{-2} under LP against 54.0 g m^{-2} LP trial mean. Most of the studies focussing on comparison between lines per se

performance and testcross performance in maize under stress have always used elite inbred lines with prior information on performance and heterotic grouping (Betrán et al., 2003; Kebede et al., 2013; Parentoni et al., 2010). Furthermore, most of them have included more than one tester. The tester used in the current study was selected mainly on the basis of sufficient seed availability; it was one of the inbred line panels under study whose heterotic grouping is unknown. Stich et al. (2010), using simple sequence repeat markers, did not find any definite structure within the West and Central African pearl millet inbred lines. The same results have been confirmed (unpublished data, 2014) on the structure of the pearl millet inbred line panel currently under study based on diversity array technology (DarT) markers. So it was not possible to take heterotic groups into account when developing the present testcrosses.

Testcross Superiority and Potential for Hybrid Breeding

We observed higher means under both HP and LP for testcrosses compared with inbred line. Furthermore, we observed significant and desirable MPH for grain yield in most of the testcrosses. The significant positive correlation between inbred lines performance and testcross performance and a nonsignificant correlation between testcross mean performance and MPH could indicate that additive and dominant gene effects act independently in the testcross populations reported (Xin et al., 2011). However, we cannot conclude on the mode of gene action on the basis of the current data because only one tester was used. The higher means observed for testcrosses compared with inbred lines as well as positive heterosis indicate potential for hybrid breeding in West and Central African pearl millet. Single-cross hybrids in pearl millet would maximize heterozygozity and allow for the maximum exploitaition of heterosis (Velu et al., 2011). However, single-cross hybrids would also be very vulnerable due to genetic uniformity. Genetically more heterogeneous hybrid types would be preferable in this regard. For any pearl millet hybrid breeding program in West and Central Africa, more information on the combining ability of the breeding material is very important. Betrán et al. (2003) observed that GCA was more important in maize under drought than specific combining ability (SCA) and that SCA became more important under low nitrogen conditions. Velu et al. (2011) showed that GCA was more important in breeding for iron and zinc content in pearl millet. Since only one tester was used in this study coupled with the lack of prior information on its performance under LP, we recommend the inclusion of more testers with different responses to LP in further LP tolerance studies to be able to distinguish GCA and SCA of the inbred lines and determine if a weak or strong tester should be used for further studies.

Selection on the Basis of Line per se Performance not Advisable

The ability to predict hybrid performance under stress from the mean performance of the parental lines is of importance as it would reduce the need for hybrid evaluation. This ability to predict depends on correlations between line and testcross performance. We observed significant but low positive correlations between inbred line and testcross performance with higher correlations under LP conditions. Higher correlation coefficients between line per se and testcross performance were also reported for increasing drought and N stress (Betrán et al., 2003; Kebede et al., 2013; Presterl et al., 2002). Ward, (1994) suggested that the increasing correlation between parental lines and testcrosses in extreme environments was due to the increasing average environmental contribution to the phenotype under stress. Despite the higher correlations between the inbred line and testcross performance under LP, the low values for REIS using inbred lines of only 56% do not suggest indirect selection for testcross performance under LP on the basis of inbred line performance. This therefore indicates the need to carry out TC trials to be able to estimate hybrid performance under low P conditions. However, it remains to be established if using more testers would give a better correlation between inbred line and testcross performance.

Selection Strategy for Grain Yield under Low P

Developing phosphorus-efficient crops is not only an affordable option to the resource-poor farmers owing to the rising fertilizer prices but also contributes to global food security by the efficient use of a limited resource (Cordell et al., 2009; Gregory and George, 2011; Murrel and Fixen, 2006; Parentoni et al., 2010). Whether selection for grain yield should be performed under low P conditions or if indirect selection under fertilized conditions might be more efficient in finding high-yielding varieties is a pertinent question to be considered before setting up a breeding program targeting low-P conditions as prevalent in West Africa. Since our target variety type would be hybrids, information on direct or indirect selection of testcrosses is of highest interest. The moderate heritability for grain yield under LP coupled with lower REIS (72%) for testcrosses shows that direct testcross selection under LP is more effective than indirect selection under HP conditions. On the basis of our data, we propose the following selection strategy for pearl millet hybrid breeding targeting P-limited environments: (i) develop lines under modest P fertilization (enough P to obtain reasonable yields but no overfertilization to avoid selection for HP adaptation), (ii) continue with definition of heterotic groups on the basis of combining ability patterns, (iii) testing for GCA should start in early stages of the hybrid

breeding program, and (iv) consider testing under LP and HP if resources allow to also identify genotypes for intensified conditions and to see whether genotypes with wide adaptation across LP and HP conditions can be found.

CONCLUSIONS

This study investigated pearl millet breeding strategies targeting adaptation to low-phosphorus soils in West Africa. Problems were encountered in achieving good differentiation between low and high phosphorus test environments due to other environmental constraints such as drought and soil acidity limiting the response to phosphorus application. Nevertheless, important conclusions can be drawn: there is significant genetic variation in current West African pearl millet inbred lines and testcrosses for grain yield performance under highly stress-prone, low phosphorus environments. Improving productivity in this type of environments by selection should therefore be possible. Direct selection in the stress environment is expected to be more efficient than indirect selection under well-fertilized conditions and is therefore recommended. Significant heterosis underlines the potential usefulness of hybrid varieties. Testcross hybrid performance could not be sufficiently predicted by inbred line performance; early testcross performance evaluation in the target environment would therefore be required in a hybrid breeding program. Ultimately, varieties adapted to low-phosphorus soils should be integrated with specific measures to render the pearl millet production systems in West Africa more productive and sustainable, such as nutrient cycling, intercropping or rotations with legumes, better crop–tree–livestock integration, and modest applications of locally available rock phosphate. Breeding activities targeting low-phosphorus environments integrated with systems-oriented research should help enhance pearl millet productivity and thereby contribute to the food security of millions of smallholder farmers in the West African Sahel.

Supplemental Information Available

This manuscript includes two supplemental tables (selection of inbred lines under HP and LP and single environment BLUPs under LP for the inbred lines common between RS2011 and RS2012) and one supplemental figure (AMMI biplot-relationships between environments).

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