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Genetic variability studies for quantitative traits in pearl millet (*Pennisetum glaucum* L.) mapping population and maintainer lines under different phosphorus fertilizer rates in Sudano Sahelian Agro-Ecology of Nigeria

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Low soil Phosphorus is considered to be one of the major limiting factors to pearl millet production in sub-Saharan Africa (SSA). This study seeks to establish the extent of genetic variability in the pearl millet mapping population and maintainers under varying levels of phosphorus. A set of twenty-four pearl millet mapping population and maintainer lines were evaluated at the International Institute of Tropical Agriculture (IITA) Minjibir experimental station under two levels of Phosphorus application to determine the genotype responses and to identify major traits involved in Phosphorus tolerance. The experiment was laid out in an alpha lattice with three replications. Analysis of variance revealed significant differences for all 11 characters studied. The study identified phosphorus-tolerant lines, P1449-2, PT732B-P2, ICMB 89111, ICMB 90111, and susceptible lines; H77/833-2 P5 (NT), Tift 186, and H77/833-2 (reselected), which could be utilized in developing QTLs to aid in marker-assisted breeding. Phosphorus fertilizer application resulted in significantly higher grain and grain yield components. Phosphorus application significantly increased heritability and genetic advance values in most of the yield and yield components. High heritability (60.12) coupled with high genetic advance (317.56) was found for head weight, followed by grain weight with high heritability (44.45) and high genetic advance (99.46), indicating that most likely the heritability is due to additive gene effects, and selection based on these characters would be effective for further pearl millet mapping population improvement program.

Key words: Pearl millet, phosphorus, heritability, genetic advance, quantitative trait loci, marker-assisted selection.

INTRODUCTION

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is one of the important cereal crops of hot and dry areas of arid and semi-arid climatic conditions. It grows on poor sandy soils and in drought-prone areas. It is nutritionally better than many cereals as it is a good source of protein, having higher digestibility (12.1%), fats (5.0%), carbohydrates

(69.4%), and minerals (2.3%) (Samtiya et al., 2023). West Africa is one of the most food-insecure regions of the world. Rapid human population growth and stagnating crop yields greatly contribute to this fact (Felix, 2019). Phosphorus fertilizer use in WA is among the lowest in the world due to inaccessibility and high prices, often unaffordable to resource-poor subsistence farmers. Phosphorus is the second most limiting nutrient in crop production after nitrogen (Jagmandeep et al., 2017). Hinsinger (2001) reported that crop production is reduced due to Phosphorus deficiency on an estimated 5.7 billion ha of land. It plays a vital role in increasing crop yield because it improves crop quality and provides resistance against diseases. It also plays a key role in the formation of energy-rich phosphate bonds like adenosine triphosphate (ATP), phospholipids, and a major part of the nucleus of the cells, where it is involved in the organization of the cell and the transfer of hereditary characteristics (Shivuam et al., 2020).

Genetic variability studies in crops provide basic information regarding the genetic properties of the population studied, based on which breeding programs are designed for further improvements (Singh et al., 2013). These studies are also helpful in understanding the nature and extent of variability that can be attributed to different causes, the sensitivity of crops to environmental influences, the heritability of the characters, and the genetic advance that can be realized in practical breeding. Hence, to have a comprehensive understanding of any genetic material, it is necessary to have an analytical assessment of its yield and yield components. Since heritability is also influenced by environment, the information on heritability alone may not help in pinpointing characters enforcing selection. Nevertheless, the heritability estimates in conjunction with the predicted genetic advance will be more reliable (Muhammad et al., 2015).

While tremendous progress has been made through breeding to improve pearl millet for resistance to insect pests/diseases and enhanced food and forage quality characteristics, slow progress has been made to improve this crop for tolerance to low soil phosphorus through exploring the genetic variability present in the pearl millet mapping population under different phosphorus levels (Felix, 2019). With pearl millet production moving into more marginal and less fertile soils, coupled with the high cost of chemical fertilizers and a growing concern about environmental pollution, interest in identifying genetic variation among pearl millet cultivars and breeding for nutrient use efficiency, particularly phosphorus, has recently increased (Hash et al., 2002). Genetic variability for phosphorus use efficiency has been confirmed for crops such as rice, maize, white clover, etc. (VandeWiel et al., 2016; Wissuwa et al., 2016). Breeding for crops that may produce higher yields under phosphorus-limited conditions appears to make an important contribution to an environmentally friendly and economically feasible strategy in order to improve pearl millet yield in sub-Saharan Africa (SSA) under subsistence farmers' conditions (Dorcus et al., 2016). The overall goal of the present article is to explore the prospects of using pearl millet genetic diversity to contribute toward solving the phosphorus deficiency issue in SSA. Phosphorus is a complex trait, and breeding for phosphorus tolerance in pearl millet would likely benefit a lot from marker-assisted selection (MAS). Therefore, the first step before embarking on this selection method would be to determine the extent of genetic variability, traits' inter-relationships, heritability, and genetic advance, followed by the identification of pearl millet lines that vary in phosphorus tolerance levels. The highly heterozygous nature of cross-pollinated pearl millet and the limited availability of diverse and representative inbred material led us to assess the possibility of finding contrasting lines for phosphorus tolerance among parental lines of existing pearl millet mapping populations. Finding phenotypic contrast in any of these parental pairs would open the possibility of mapping phosphorus tolerance quantitative trait loci (QTLs) where parental lines showed an important contrast in their yield response to a phosphorus-deficient environment (Sunita et al., 2017). The emergence of novel molecular approaches such as genome editing, genomic selection, marker-assisted breeding, and high-throughput phenomics has reformed the scope of crop breeding, enhancing much more productive utilization of artificial and naturally created variations and phenotyping (Xu et al., 2020). In pearl millet, MAS has been utilized for the development of lines tolerant to drought stress, thus improving the overall genetic gain (Rani et al., 2021). Use of genomics for developing pearl millet lines tolerant to low Phosphorus has not been fully exploited. An attempt has been made in this study to assess the genetic variability, inter-relationship of traits, heritability, and genetic advance in mapping population pearl millet under different phosphorus levels with a view to selecting genotypes with contrasting yield and yield contributing variables. This information is needed before progressing further for the identification of phosphorus tolerance QTLs to aid in marker-assisted breeding. The objective of this study was

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to screen some pearl millet mapping population under zero phosphorus and phosphorus fertilizer application levels to (1) select the most contrasting parental lines, (2) assess the relative contribution of phosphorus levels to grain yield and its yield components, and (3) to identify the major traits involved in phosphorus tolerance as a genomic resource for QTLs and MAS.

MATERIALS AND METHODS

A set of twenty pearl millet mapping population parental lines (Table 1) and four elite B-lines/ maintainer lines (ICMB 89111, ICMB 90111, ICMB 92666, and ICMB 95333) were screened to determine their responses to different phosphorus fertilizer levels. These materials offer unique advantages in evaluating P efficiency because some cytoplasms may interact with nuclear genes to confer better adaptation to stresses. The materials were screened at the International Institute of Tropical Agriculture (IITA), Kano sub-station research farm at Minjibir (Latitude 12°13'N, Longitude 8°69'E, and altitude of 416 masl) with long-term average rainfall of 850 mm, which is unimodal with a peak in August. The maximum air temperature occurred between March and May. The soil is characterized by well-drained sandy loam (typic Ustipsamment) with high bulk density, low water retention, neutral-to-alkaline pH (H_20), low in Nitrogen, available Phosphorus, exchangeable Potassium, cation exchange capacity, and organic carbon (Table 2). Owing to the limited quantity of planting material, the size of the experimental plot was restricted to 2 rows of 5 m long and replicated three times. Plant spacing was 50 cm intra-row spacing, while inter-row spacing was 75 cm. Before planting, the experimental site was cleared of plant debris, harrowed, and thereafter ridged using a tractor. Treatments were P1 (zero phosphorus fertilizer application), while P2 was 30 kg phosphorus fertilizer per hectare, which approximates farmers' practice. The fertilizer was applied on the P2 plots after ridging and seed sown thereafter. The crop was later top dressed with 60 kg N/ha after manual weeding. The seeds were treated with Apron Star seed dressing chemical. Data were collected from the two rows of each plot. All the data were sampled following recommendations by the International Board for Plant Genetic Resources (IBPGR) and International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) descriptor for pearl millet (IBPGR and ICRISAT, 1993). Seeds used for this study were introduced from ICRISAT Corporate Headquarters, Patancheru, India while traits sampled were days to 50% flowering (bloom), downy mildew score (dm), grain weight (gwt), number of hills (hill), head weight (hwt), panicle number (pan no), panicle length (panl), plant height (pht), smut score (smut), stand count (stand co), number of tillers (tiller). The experiment was laid out in an alpha lattice with three replications. Analysis of an unbalanced design for the generation of predicted means was done on the data collected using GenStat VSN International (2015), Hemel Hempstead, UK. Pearson's correlation coefficients and cluster analysis (Dendogram) of the traits were obtained using SPSS version 16 (SPSS, Chicago, Illinois, USA). Broad sense heritability (h^2) was calculated from the accumulated Analysis of variance generated as explained by Fehr (1993):

$$h^2 = GV/PV \times 100\%$$

$$EV = MSR$$

$$GV = (MSG - MSR)/R$$

$$PV = EV + GV$$

where GV = genotypic variance, PV = phenotypic variance, EV = environmental variance, MSR = mean square error, MSG = mean square genotype, and R = number of replicates. Genetic advance (GA) was calculated according to Johanson et al. (1955) as follows;

$$GA = K (GV/\sqrt{PV})$$

where K = 2.06 at 5% selection intensity.

RESULTS AND DISCUSSION

Analysis of variance (ANOVA) for all the traits sampled was highly significant ($P < 0.05$) for the pearl millet mapping population and the maintainer lines, while the mean square for phosphorus was significant for all the traits except panicle length, plant height, smut damage score, and number of tillers. The interaction between pearl millet genotypes and phosphorus levels was not significant for any of the traits (Table 3).

The genetic materials used for this study did not maintain any consistent clustering pattern among the different phosphorus levels, indicating that phosphorus levels influenced the expression of these traits differently among the 24 pearl millet mapping populations. In both P1, P2 and P1 and P2 combined there were consistent clustering pattern for all the genotypes identified as tolerant lines (P1449-2 (14), PT732B-P2 (13), 1CMB 89111 (21) and ICMB89111 (21) and ICMB 90111 (22) and susceptible line (H77/833-2 P5 (NT)(8)), Tift 186 (19) and H77/833-2 re-selected (9). The tolerant lines (No 14, 13, 21, 22) clustered within the first group in the dendogram, while the susceptible lines (No 8, 9) were the closest in P1, P2, and P1 and P2 combined. (Figures 1 to 3). Table 4 shows that there was a wide variation for all the traits sampled under zero phosphorus application level. Genotype P1449-2 produced the highest gain in weight (kg), followed by PT732B-P_2, ICMB 89111, and ICMB 90111 in that order. Genotype P1449-2 is a stable source of dowry mildew selected at ICRISAT (Table 1). It also harbored a low dm (1.83) attack in this study. This genotype is found to be adapted to both low soil P and high dm endemic areas. Similarly, PT732B-P_2 had low downy mildew infestation. These two promising genotypes are late maturing and photo sensitive. A previous study reported by Simon et al. (2023) pointed out that pearl millet maturity date significantly influences P use efficiency and yield through genetically controlled traits related to root architecture, with late maturing genotypes expressing sustained and higher total P uptake owing to a deep and extensive rooting system. ICMB 59111 and ICMB 90111 were bred targeting low soil phosphorus environments by ICRISAT scientists. Some of the high-yielding genotypes are mutant materials known to contain

Table 1. Description of 20 inbred mapping population parental lines of pearl millet used for the study.

Name	Pedigree/origin	Remarks	Registration/references
(LGD-1) –B-10	Partial backcross d_2 dwarf, e_1 early (donor = Tift756) derivative of a bold-seeded Iniadi landrace sample from Togo; bred at Tifton, GA, USA, reselected at ICRISAT, Patancheru	d_2 dwarf, e_1 photosensitive early flowering	Jagmandeep et al. (2017) and Johanson et al. (1995)
(ICMP85410)-P7	{[SC 14(M)-1] × [SD_2 × EB_2 (DI088)] -1}-64	d_2 dwarf, late flowering	Johanson et al. (1995) and Kumari (2013)
(Tift 23 DB)-P5	Partial backcross d_2 dwarf, derivative of forage seed parent maintainer line Tift $23B_1$; bred at Tifton, GA, USA	d_2 dwarf, many tillers	Johanson et al. (1995) and Lakshmana and Guggari (2001)
(IP 18292, WSIL)-P8	Genetic stock (Ws, D_2, Y, Gl) with complex pedigree developed at ICRISAT-Patancheru	d_2 dwarf, long panicle	Johanson et al. (1995) and Muhammad et al. (2015)
(ICMP 451)-P8	Downy mildew resistance restorer selection from ICMP 451 (LC3N 72-1-2-1-1)	Tall, long panicle bristles	Johanson et al. (1995) and Rani et al. (2021)
(81B)-P6	Downy mildew resistance outcross derivative of Tift 23 D_2 B_1 selected from a mutation breeding program at ICRISAT, Patancheru	d_2 dwarf	Johanson et al. (1995) and Rani et al. (2021)
(ICMP 451)-P6	Downy mildew resistance restorer selection from ICMP 451 (LCSN 72-1-2-1-1)	Tall, long panicle bristles	Johanson et al. (1995) and Rani et al. (2021)
(H77/833-2)-P5(NT)	Off-type segregant from H77/833-2	Short, many tillers, photoperiod-sensitive early flowering	Johanson et al. (1995)
(H77/833-2 selection	Elite pollinator line from Haryana Agricultural University, Hisar, India	Short, many tillers, photo-sensitive, early flowering, seedling heat stress tolerant	Johanson et al. (1995)
PRLT 2/89-33	Inbred line bred at ICRISAT, Patancheru, from the bold-seeded early composite (largely based on Iniadi landrace germplasm and derived breeding materials), with the pedigree BSEC 8501-13-2-2-3-2	Medium tall, early flowering, seedling heat stress sensitive, terminal stress tolerant	Johanson et al. (1995)
(W504)-1-1	Breeding line from the India Agricultural Research Institute, New Delhi, India	Tall, medium-late flowering	Samtiya et al. (2023)
(P 310-17)-B	A stable source of downy mildew resistance was selected at ICRISAT Patancheru from germplasm line 1P 6329 from Mali	Tall, late flowering	Muhammad et al. (2015) and Samtiya et al. (2023)

Table 1. Contd.

(PT 732B)-P2	“spontaneous” dwarf mutant in elite breeding line from Tamil Nadu Agricultural University, Coimbatore, India	d_2 dwarf, photoperiod-sensitive late flowering	Sathya et al. (2014) [18]
(P 1449-2)-P1	IP 21168; stable source of downy mildew resistance selected at ICRISAT Patancheru from germplasm line 1P 5853 from Senegal	Tall, photoperiod-sensitive late flowering	Muhammad et al. (2015)
(ICMB 841)-P3	Downy mildew-resistant outcross of MS 5141B; developed at ICRISAT Patancheru by pure line selection for disease resistance in a contaminated seed lot of MS 514B	Medium tall, medium-early flowering	Sathya et al. (2014) and Shivuam
(863B)-P2	Maintainer line developed at ICRISAT- Patancheru by selfing in a bold-seeded Iniadi landrace sampled from Togo	Medium tall, medium early flowering, drought-tolerant	Shivuam
Tift 238 DI)-P158	d_1 dwarf restorer of the A_1 cytoplasmic male sterility system bred at Tifton, GA, USA	Late flowering	Simon et al. (2023)
(IP 18293)-P152	d_2 dwarf, purple foliage genetic stock with complex pedigree developed at ICRISAT, Patancheru	-	Muhammad et al. (2015)
Tift 186	Forage pollinator bred at Tifton, GA, USA by selfing in a forage germplasm accession from South Africa	Tall, late flowering	Singh et al. (2013)
Tift 383	d_2 dwarf forage pollinator bred at Tifton, GA, USA from Tift 186 x d_2 dwarf (Tift 239 D_2B_2 x Tift 186)	Late flowering	Sumanth (2011)

Source: International Crops Research Institute for the semi-arid Tropics (ICRISAT), Patancheru, Hyderabad 502 324, India.

rare alleles least affected by leaf diseases and are better in enhancing photosynthetic capacity, such as stay green traits and other metabolic processes that help in mining phosphorus. Conversely, significantly low grain weight (kg) was observed for the following genotypes in descending order: H77/833-2 P5 (NT), Tift 186, and H77/833-2 (reselection). Poor performance of H77/833-2 P5 (NT) and off-type segregants may be due to their genetic instability. Moreover, off-type plants may compete unevenly for nutrients, leading to canopy heterogeneity, which can reduce overall photosynthetic efficiency, sink-source balance, and grain yield. As reported previously by Christopher et al. (2010), variations in plant types negatively influence grain yields and their components. H77/833-2 is a reselection basically bred for heat tolerance. In this experiment, it was grown under moisture sufficiency, and as expected, it performed poorly. Tift-186 was bred as a forage material with low grain yield attributes. Tift 383 produced significantly higher grain weight in the zero-phosphorus application level than in the phosphorus application level, suggesting that the material is adapted to low soil phosphorus and possesses the genetic ability to mine soil phosphorus.

Table 5 shows that the four best grain yielders under zero phosphorus application level equally top the list of high performing genotypes under phosphorus fertilizer application level, with P1449-2 being the best performer, followed by ICMB

Table 2. Meteorological and soil physical and chemical information of the experimental site, Minjibir, Kano, Nigeria.

Variable	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sept	Oct	Nov	Dec	Total
Total rainfall (mm)	0	0	0	0	0	148.2	223.9	222.7	192.6	54	0	0	841.4
Number of rainy days	0	0	0	0	0	5	7	9	7	3	0	0	31
Max air temp (°C)	26.2	31.8	35.7	36.4	36.5	34.2	33.2	31.5	31.0	31.6	30	31.9	-
Min air temp (°C)	21.8	14.8	20.8	22.3	22.8	23.7	22.6	22.8	22.5	22.3	16.6	13.1	-

pH (H_20): 6.0-7.0; organic carbon: Low 2-6 g/Kg; total nitrogen: low, <1 g/kg; Available phosphorus: Low to moderate 5 to 15 mg/kg; Exchangeable Potassium: low (0.1 to 0.5 cmol(+)/kg); Cation Exchange Capacity (CEC): Low (10 to 20 cmol/kg); Soil class: sandy loam.
Source: Hakeem et al. (2024).

Table 3. Analysis of variance (ANOVA) for growth and reproductive characters in twenty-four mapping populations and maintainer lines of pearl millet.

Traits	No MPP	MSMPP	MSP	MS (MPP×P)	MSR
bloom	24	599.652**	119.174**	8.536^{ns}	7.366
dm	24	10.224**	3.063*	0.584^{ns}	0.616
gwt	24	45423**	34696*	4782^{ns}	8686
hill	24	87.14**	277.778**	10.444^{ns}	8.996
hwt	24	219534**	536030**	29675^{ns}	31898
pan no	24	2836**	7846.5**	477.4^{ns}	429.6
panl	24	153.4**	60.68ns	27.99^{ns}	28.6
pht	24	6716.2**	118.8ns	313.9^{ns}	609.4
smut	24	1.111**	0.31ns	0.409^{ns}	0.463
Standco	24	48.763**	215.111**	6.546^{ns}	8.955
tiller	24	32.851**	13.646	3.273^{ns}	4.776

*Significant at 5% probability level, **significant at 1% probability level, ns: non-significant. No MPP: Number of mapping population pearl millet, MSMPP: mean square for mapping population pearl millet, MSP: mean square for phosphorus, MS (MPP x P): mean square for mapping population pearl millet by phosphorus interaction, MSR: mean square for error. Bloom (days to 50% flowering), dm (downy mildew score, gwt (grain weight), pan no (panicle number), panl (panicle length), pht (plant height), smut (smut score), stand co (stand count), and tiller (number of tillers).

89111, PT 732B-P_2, and ICMB 90111. These four genotypes were therefore considered stable under the two phosphorus environments. It is interesting to note that H77/833-2 P5(NT), Tift 186, and H77/833-2 (reselected) performed significantly lower than the rest genotypes in zero phosphorus level, also performed poorly under phosphorus fertilizer application, showing that they were probably not responsive to phosphorus fertilizer application. Genotype 863B-P_2 produced very poor grain weight in zero phosphorus application, but significantly higher grain weight under phosphorus fertilizer application, meaning that the genotype was responsive and sensitive to phosphorus fertilizer application.

Mean performance for grain yield of 24 mapping population pearl millet for zero and phosphorus fertilizer application combined (Table 6) indicated that genotype P1449-2 also produced significantly higher grain weight than the rest genotypes, followed by PT732B-P2 and ICMB 89111.

The effect of zero phosphorus and phosphorus fertilizer application on various pearl millet traits is shown in Table 7. The result showed that phosphorus fertilizer application resulted in significantly higher grain weight, hill count, head weight, panicle number, stand count, and number of tillers when compared with zero phosphorus application, while it significantly reduced days to flowering (bloom), downy mildew, and smut scores. Higher phosphorus levels, therefore, increased grain weight, hill count, head weight, panicle number, stand count, and number of tillers. This result is similar to the findings of Vangala et al. (2022).

Correlation coefficient of the traits of the 24-mapping population of pearl millet on zero phosphorus level is shown in Table 8. Grain weight strongly and positively correlated with hill count (0.553), head weight (0.938),

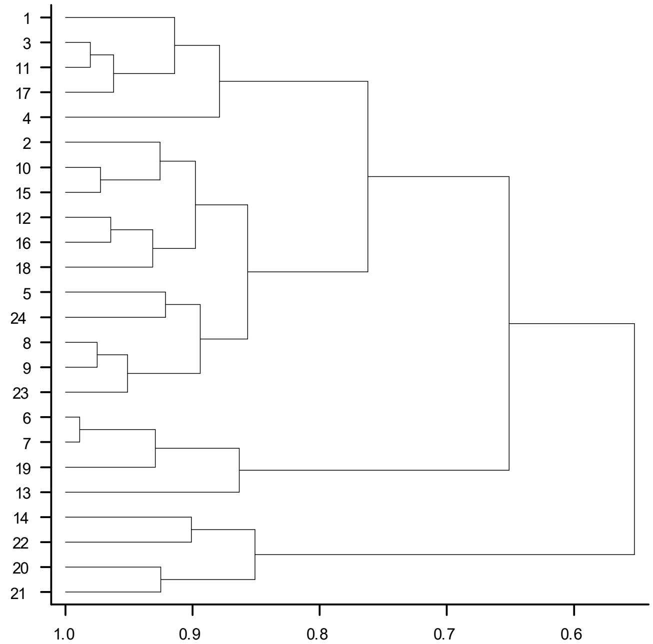

Figure 1. Cluster for all the traits of the 24-mapping population of pearl millet on P1.

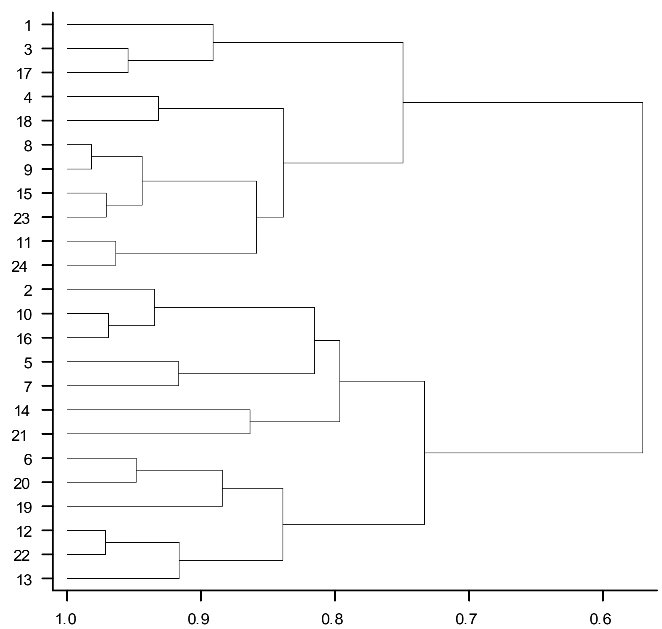

Figure 2. Cluster for all the traits of the 24-mapping population pearl millet on P2.

and panicle number (0.442). Similarly, Muhammad et al. (2015 reported that grain weight correlated positively with head weight and panicle number in pearl millet. Grain weight negatively correlated with days to 50% following (-0.03) and downy mildew (-0.243). Correlation coefficient of the traits of the 24-mapping population of pearl millet

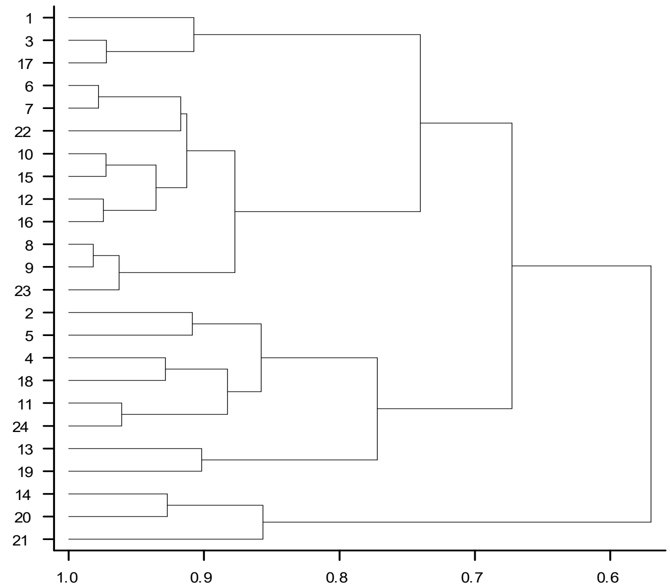

Figure 3. Cluster for all the traits of the 24-mapping population pearl millet on P1 and P2 combined.

Table 4. Performance of the 24-mapping population pearl millet on P1.

Geno	bloom	dm	gwt	hill	hwt	pan no	panl	pht	smut	stand co	tiller
LGD	40.33	3.33	15.70	1.33	47.80	7.04	17.83	128.30	2.00	3.67	6.10
ICMP 85410-P7	65.33	1.00	49.18	11.33	223.70	44.46	28.50	78.60	2.33	12.33	5.53
Tift 23DB-P5	60.00	5.00	27.41	3.33	71.80	12.78	15.93	78.50	2.00	8.33	2.96
Tift 23DB-P5	64.67	1.67	20.74	3.33	51.60	7.12	30.77	83.20	2.33	6.33	2.53
81B-P6	64.00	3.00	70.48	8.00	215.40	43.46	19.97	97.50	3.33	9.00	8.86
ICMP 451-P8	65.33	1.67	14.38	7.67	139.30	39.46	21.10	150.60	1.00	8.67	7.13
ICMP 451-P6	63.67	1.67	31.58	7.67	199.50	59.79	23.07	158.40	1.00	8.33	7.16
H 77/833-2-P5(NT)	52.67	2.67	8.91	8.00	62.00	23.79	12.87	96.00	1.67	10.33	5.86
H 77/833-2 reselection	60.67	4.00	7.21	8.00	88.40	31.79	12.17	102.00	2.33	8.33	5.76
PRLT 2/89-33	56.00	2.00	124.54	11.33	285.90	28.12	16.57	109.40	1.33	12.33	4.96
W 504-1-1	60.33	5.00	37.98	7.00	100.80	13.79	21.87	106.70	2.00	9.33	3.83
P 310-17-B	65.33	1.67	58.48	10.00	261.40	19.46	18.93	162.60	2.00	10.00	6.06
PT 732B-P2	63.67	1.33	262.34	6.00	553.70	29.79	31.97	207.30	1.33	6.33	8.06
P 1449-2	62.33	1.33	348.08	15.00	729.50	37.46	29.40	142.30	2.67	14.00	5.16
841B-P3	53.33	1.33	77.08	10.67	228.90	30.46	19.43	100.40	2.33	10.67	6.06
863B-P2	62.00	2.00	28.21	6.00	118.00	12.46	19.43	120.40	2.00	6.67	3.86
Tift 238D1	63.00	5.00	40.36	0.33	64.40	9.78	23.53	73.30	2.67	7.33	2.63
IP 18293	91.00	1.67	33.14	8.67	97.40	12.46	22.30	99.30	1.67	12.33	5.41
Tift 186	89.00	1.00	8.18	3.67	174.60	25.12	21.73	183.30	1.00	5.33	6.36
Tift 383	66.33	1.33	182.21	9.67	623.60	71.46	30.90	150.20	2.33	11.67	10.20
ICMB 89111	60.67	2.33	243.98	10.33	458.00	62.12	18.20	101.90	2.33	11.33	13.53
ICMB 90111	63.67	3.67	223.18	14.33	431.50	46.79	16.97	152.50	2.67	14.00	5.33
ICMB 92666	55.00	3.33	11.01	10.67	154.50	45.79	16.20	106.60	1.67	13.00	8.86
ICMB 95333	60.67	3.67	94.04	9.67	261.30	21.79	29.53	139.60	2.33	11.67	5.10
LSD (5%)	4.94	1.27	164.50	4.82	312.60	28.58	6.56	47.32	1.04	4.55	3.72

Bloom (days to 50% flowering), dm (downy mildew score, gwt (grain weight), pan no (panicle number), panl (panicle length), pht (plant height), smut (smut score), stand co (stand count), and tiller (number of tillers).

Table 5. Performance of the 24-mapping population pearl millet on P2.

Geno	bloom	dm	gwt	hill	hwt	pan no	Panl	Pht	smut	stand co	tiller
LGD	39.67	4.00	82.10	1.33	260.10	33.53	14.20	115.60	2.00	2.67	3.00
ICMP 85410-P7	64.67	1.00	138.10	14.33	445.00	58.18	31.60	72.80	1.67	14.33	6.30
Tift 23DB-P5	56.00	5.00	88.10	2.33	173.40	14.83	17.63	113.20	2.00	8.67	6.20
Tift 23DB-P5	62.33	2.33	15.80	9.33	59.90	7.85	32.80	81.30	2.33	7.67	4.43
81B-P6	62.67	2.67	17.50	11.00	200.40	58.18	24.93	100.20	2.67	11.67	11.30
ICMP 451-P8	62.67	2.00	127.00	11.33	451.10	78.51	23.27	150.90	1.33	11.33	7.43
ICMP 451-P6	63.33	2.00	113.20	14.33	491.40	101.85	23.67	150.70	2.67	14.00	5.63
H 77/833-2-P5(NT)	45.67	3.67	52.00	11.33	115.10	31.51	13.47	91.10	1.67	11.33	6.17
H 77/833-2 reselection	56.00	4.33	20.00	12.00	90.40	43.51	12.07	102.90	2.00	13.33	5.17
PRLT 2/89-33	52.67	1.67	155.40	14.67	403.80	42.18	16.77	75.20	1.33	14.67	6.07
W 504-1-1	58.67	5.00	86.60	13.00	204.50	21.85	23.37	112.00	2.00	13.33	5.43
P 310-17-B	63.33	3.67	130.40	9.67	309.90	23.85	19.60	158.70	2.00	11.00	5.97
PT 732B-P2	62.00	2.00	206.00	8.00	562.70	47.18	30.73	192.20	1.67	8.00	8.87
P 1449-2	62.33	1.33	346.70	15.67	821.00	40.85	31.43	145.50	2.33	15.67	7.30
841B-P3	59.33	2.67	119.60	13.00	384.40	45.51	20.20	119.30	2.00	14.00	7.50
863B-P2	60.33	1.00	226.40	11.33	503.40	33.85	19.83	114.90	1.33	11.67	5.97
Tift 238D1	61.33	5.00	0.70	2.33	12.30	2.71	25.27	84.60	2.33	10.33	2.60
IP 18293	88.67	2.00	21.90	6.67	64.90	12.51	27.97	93.20	1.67	12.33	4.87
Tift 186	86.00	1.00	46.10	6.00	785.80	81.83	20.07	179.40	1.53	9.33	7.97
Tift 383	63.67	1.00	149.50	15.67	704.80	91.51	30.73	152.20	1.67	16.00	8.20
ICMB 89111	57.33	2.67	283.50	16.33	586.40	108.18	18.77	102.00	2.33	17.00	13.87
ICMB 90111	60.33	3.67	192.80	11.67	437.40	65.18	19.20	157.90	1.67	12.33	7.20
ICMB 92666	54.33	3.33	26.70	13.00	204.50	70.85	17.07	115.70	1.67	13.00	8.83
ICMB 95333	62.00	4.67	144.20	14.33	484.30	27.85	30.53	104.00	2.33	16.33	5.73
LSD(5%)	3.98	1.33	143.80	4.96	284.70	32.66	3.65	32.68	1.21	5.30	3.58

Bloom (days to 50% flowering), dm (downy mildew score, gwt (grain weight), pan no (panicle number), panl (panicle length), pht (plant height), smut (smut score), stand co (stand count), and tiller (number of tillers).

on phosphorus fertilizer application is shown in Table 9. Grain weight correlated positively with hill count (0.494), head weight (0.749), and panicle number (0.326). It recorded a negative correlation with bloom (-0.104) and downy mildew (-0.376). Significantly high but negative correlation was observed between downy mildew and bloom (-0.429) in phosphorus fertilizer application level, while there was a non-significant but negative correlation between downy mildew and bloom (-0.349) in zero phosphorus application, revealing that downy mildew, a biological stress factor, reduced days to 50% flowering. There was significant but negative correlation between downy mildew and head weight (-0.406), downy mildew and panicle length (-0.410), downy mildew and plant height (-0.425) in zero phosphorus application while there was non-significant but negative correlation between downy mildew and panicle length (-0.378), downy mildew and plant height (-0.241) in phosphorus fertilizer application level indicating that phosphorus fertilizer application suppressed the expression of downy mildew. Also, the result showed that downy mildew negatively influenced some growth and yield components in pearl millet. Smut score significantly and negatively correlated with plant height (-0.451) in zero phosphorus, while it correlated negatively but not significantly with plant height (-0.155) under phosphorus fertilizer application.

Combined correlation effect of zero phosphorus and phosphorus application levels for the 24-mapping population pearl millet (Table 10) showed that grain weight is significantly influenced by head weight (0.857) while head weight was significantly and positively influenced by panicle number (0.604), and panicle length (0.423) indicating that grain weight can be improved indirectly through increasing panicle number and panicle length as secondary traits. This result is supported by Andhale et al. *(*2024 who found grain weight to correlate positively with panicle length and panicle number. It is important to note that downy mildew and smut count correlated negatively with most yield contributing variables in both phosphorus levels, although higher in zero phosphorus application, showing that the two biological threats were yield-limiting variables in pearl

Table 6. Mean performance of the 24-mapping population pearl millet in P1 and P2 combined.

Geno	bloom	Dm	gwt	Hill	hwt	Panno	panl	pht	Smut	stand co	tiller
LGD	40.00	3.67	57.69	1.33	156.70	19.74	16.02	122.00	2.00	3.17	4.54
ICMP 85410-P7	65.00	1.00	93.19	12.83	333.70	51.35	30.05	75.70	2.00	13.33	5.92
Tift 23DB-P5	58.00	5.00	43.82	2.83	97.90	11.17	16.78	95.80	2.00	8.50	4.59
Tift 23DB-P5	63.50	2.00	13.39	6.33	56.70	7.61	31.78	82.20	2.33	7.00	3.49
81B-P6	63.33	2.83	45.15	9.50	209.00	50.84	22.45	98.80	3.00	10.33	10.09
ICMP 451-P8	64.00	1.83	69.97	9.50	293.90	58.83	22.18	150.80	1.17	10.00	7.28
ICMP 451-P6	63.50	1.83	72.03	11.00	344.30	80.64	23.37	154.60	1.83	11.17	6.39
H 77/833-2-P5(NT)	49.17	3.17	30.54	9.67	89.20	27.73	13.17	93.50	1.67	10.83	6.02
H 77/833-2 reselection	58.33	4.17	14.00	10.00	90.40	37.70	12.12	102.40	2.17	10.83	5.46
PRLT 2/89-33	54.33	1.83	140.18	13.00	345.00	35.18	16.67	92.30	1.33	13.50	5.52
W 504-1-1	59.50	5.00	62.30	10.00	152.90	17.89	22.62	109.30	2.00	11.33	4.64
P 310-17-B	64.33	2.67	94.21	9.83	286.30	21.75	19.27	160.70	2.00	10.50	6.02
PT 732B-P2	62.83	1.67	235.35	7.00	559.10	38.49	31.35	199.70	1.50	7.17	8.47
P 1449-2	62.33	1.33	347.96	15.33	775.60	39.26	30.42	143.90	2.50	14.83	6.24
841B-P3	56.33	2.00	98.43	11.83	306.50	38.01	19.82	109.90	2.17	12.33	6.79
863B-P2	61.17	1.50	125.65	8.67	308.90	23.13	19.63	117.70	1.67	9.17	4.92
Tift 238D1	62.17	5.00	21.45	1.33	39.90	6.46	24.40	79.00	2.50	8.83	2.62
IP 18293	89.83	1.83	28.20	7.67	82.40	12.62	25.13	96.20	1.67	12.33	5.13
Tift 186	87.50	1.00	21.78	4.83	464.60	51.70	20.90	181.30	1.28	7.33	7.17
Tift 383	65.00	1.17	166.75	12.67	664.60	81.47	30.82	151.20	2.00	13.83	9.19
ICMB 89111	59.00	2.50	263.83	13.33	522.20	84.95	18.48	101.90	2.33	14.17	13.70
ICMB 90111	62.00	3.67	208.88	13.00	435.40	55.98	18.08	155.20	2.17	13.17	6.27
ICMB 92666	54.67	3.33	19.25	11.83	180.10	58.27	16.63	111.20	1.67	13.00	8.85
ICMB 95333	61.33	4.17	119.13	12.00	372.10	24.91	30.03	121.80	2.33	14.00	5.42
LSD(5%)	3.11	0.90	112.60	3.44	214.70	22.05	3.68	28.30	0.78	3.43	2.52

Bloom (days to 50% flowering), dm (downy mildew score, gwt (grain weight), pan no (panicle number), panl (panicle length), pht (plant height), smut (smut score), stand co (stand count), and tiller (number of tillers).

Table 7. Combined effects of different P-levels on the 24-mapping population of pearl millet.

P-levels	bloom	dm	gwt	hill	hwt	pan no	panl	pht	smut	stand co	tiller
P1	62.88	2.53	88.1	8	244.7	31.83	21.63	122	2.02	9.64	6.15
P2	61.06	2.82	120.3	10.78	371.8	48.83	22.72	120.2	1.93	12.08	6.76
Mean	61.97	2.67	104.2	9.39	308.25	40.33	22.18	121.1	1.97	10.86	6.45
LSD(5%)	0.9	0.26	32.04	0.99	61.07	6.27	1.06	8.17	0.23	0.99	0.73

Bloom (days to 50% flowering), dm (downy mildew score, gwt (grain weight), pan no (panicle number), panl (panicle length), pht (plant height), smut (smut score), stand co (stand count), and tiller (number of tillers).

millet, which could be moderated by improving the soil phosphorus status.

Estimates of heritability (broad sense) and genetic advance across the two phosphorus levels are shown in Table 11. Phosphorus fertilizer application generally enhanced the heritability of all the traits studied, meaning that the traits are stable across the environment, and rapid genetic gains and selection may be realizable. Zero phosphorus application reduced the level of heritability in both growth and yield variables. Heritability estimates ranged from 40.63 to 94.39 for phosphorus fertilizer application level, while for zero phosphorus application, they ranged from 35.08 to 91.65. The heritability under phosphorus fertilizer application was high for bloom (94.39), panicle length (88.5), downy mildew (72.07), plant height (70.95), panicle number (66.48), and head weight (60.12). It was, however, moderate for grain weight (44.45), stand count (40.63), and tiller number

Table 8. Correlation of the traits of the 24-mapping population of pearl millet on P1.

Traits	bloom	dm	gwt	hill	hwt	panno	panl	pht	smut	stand co	tiller
bloom	1										
dm	-0.349	1									
gwt	-0.03	-0.243	1								
hill	0.004	-0.319	0.553**	1							
hwt	0.055	-0.406*	0.938**	0.614**	1						
panno	0.018	-0.329	0.442*	0.580**	0.608**	1					
panl	0.282	-0.410*	0.397	0.007	0.472*	0.104	1				
pht	0.229	-0.425*	0.38	0.14	0.512*	0.254	0.301	1			
smut	-0.215	0.326	0.281	0.18	0.189	0.04	0.09	-0.451*	1		
Stand co	0.062	-0.084	0.447*	0.889**	0.476*	0.480*	0.003	-0.14	0.256	1	
tiller	-0.011	-0.325	0.369	0.334	0.481*	0.775**	-0.023	0.295	-0.038	0.211	1

Bloom (days to 50% flowering), dm (downy mildew score, gwt (grain weight), pan no (panicle number), panl (panicle length), pht (plant height), smut (smut score), stand co (stand count), and tiller (number of tillers).

Table 9. Correlation of the traits of the 24-mapping population of pearl millet on P2.

Traits	bloom	dm	gwt	hill	hwt	panno	panl	pht	smut	stand co	tiller
bloom	1										
dm	-0.429*	1									
gwt	-0.104	-0.376	1								
hill	-0.046	-0.371	0.493*	1							
hwt	0.232	-0.627**	0.749**	0.442*	1						
panno	0.08	-0.475*	0.326	0.515**	0.624**	1					
panl	0.472*	-0.378	0.2	0.192	0.278	-0.067	1				
pht	0.26	-0.241	0.34	-0.028	0.613**	0.420*	0.079	1			
smut	-0.089	0.349	-0.077	0.027	-0.163	-0.045	0.232	-0.155	1		
Stand co	0.169	-0.206	0.407*	0.855**	0.358	0.396	0.2	-0.133	0.089	1	
Tiller	0.089	-0.324	0.4	0.478*	0.459*	0.676**	0.015	0.253	0.056	0.413*	1

Bloom (days to 50% flowering), dm (downy mildew score, gwt (grain weight), pan no (panicle number), panl (panicle length), pht (plant height), smut (smut score), stand co (stand count), and tiller (number of tillers).

(47.37). The heritability under zero phosphorus application was equally high for bloom (91.65) and downy mildew (71.52) but moderate for grain weight (38.65), smut score (35.08), stand count (40.94), panicle number (43.05), head weight (41.09), and tiller number (47.46). Sunita et al. (2017) found growth-related traits to exhibit moderate to high heritability, which is in line with this study's result.

Under phosphorus fertilizer application, genetic advance was high for head weight (317.56), grain weight (99.46), plant height (53.92), and panicle number (43.95), but lowest for downy mildew (2.26), tiller number (2.93), stand count (3.50), hill count (6.51), and panicle length (11.94). However, under zero phosphorus application, genetic advance was high for head weight (203.15), grain weight (98.57), and plant height (47.10), but lowest for smut score (0.57), downy mildew (2.14), tiller (3.02), stand count (3.04), hill count (5.07), and panicle length (8.78). Higher expression of genetic advance was observed for all traits in phosphorus fertilizer application level when compared with zero phosphorus application, indicating that phosphorus fertilizer application improved genetic advance in pearl millet. Therefore, genetic studies in pearl millet could be better done under improved phosphorus levels. In other words, selection of traits for genetic improvement in pearl millet may be done under phosphorus fertilizer application when the potential of the traits could be fully expressed.

Panse (1957) observed that a character that exhibited high heritability and genetic advance indicated a broad sense of additive gene action in its inheritance, and such a character could be improved by simple selection methods. Under phosphorus fertilizer application level, high heritability (60.12) coupled with high genetic

Table 10. Correlation of the traits of the 24-mapping population pearl millet on P1 and P2 combined.

Traits	bloom	dm	gwt	hill	hwt	panno	panl	pht	smut	stand co	tiller
bloom	1										
dm	-0.410*	1									
gwt	-0.085	-0.332	1								
hill	-0.026	-0.363	0.553**	1							
hwt	0.149	-.570**	0.857**	0.558**	1						
panno	0.055	-0.438*	0.374	0.571**	0.604**	1					
panl	0.387	-0.403	0.325	0.128	0.423*	0.024	1				
pht	0.25	-0.345	0.397	0.074	0.630**	0.374	0.187	1			
smut	-0.187	0.353	0.14	0.078	-0.04	-0.088	0.2	-0.369	1		
Stand co	0.121	-0.149	0.442*	0.878**	0.416*	0.438*	0.13	-0.135	0.163	1	
Tiller	0.039	-0.331	0.426*	0.466*	0.524**	0.790**	-0.024	0.274	0.054	0.359	1

Bloom (days to 50% flowering), dm (downy mildew score, gwt (grain weight), pan no (panicle number), panl (panicle length), pht (plant height), smut (smut score), stand co (stand count), and tiller (number of tillers).

Table 11. Heritability and Genetic advance for 24-mapping population pearl millet across two phosphorus levels.

Traits	Broad sense heritability		Genetic advance	
	P1	P2	P1	P2
bloom	91.65	94.39	19.65	19.86
dm	71.52	72.07	2.14	2.26
gwt	38.65	44.45	98.57	99.46
hill	55.81	63.36	5.07	6.51
hwt	41.09	60.12	203.15	317.56
pan no	43.05	66.48	19.79	43.95
panl	64.03	88.50	8.78	11.94
pht	53.91	70.95	47.10	53.92
smut	35.08	-	0.57	-
stand co	40.94	40.63	3.04	3.50
tiller	47.46	47.37	3.02	2.93

No values for ‘smut’ in P2 because of high residual error. Bloom (days to 50% flowering), dm (downy mildew score, gwt (grain weight), pan no (panicle number), panl (panicle length), pht (plant height), smut (smut score), stand co (stand count), and tiller (number of tillers).

advance (317.56) was found for head weight, followed by grain weight, indicating that most likely the heritability is due to additive gene effects and selection may be effective in improving the traits. This finding is in line with the results of Sumanth (2011) and Ashok (2012). High heritability (70.95) coupled with moderate genetic advance (53.92) was observed for plant height. Moderate heritability (66.48) coupled with moderate genetic advance (43.95) was observed for panicle number, while moderate heritability (63.36) coupled with low genetic advance (6.51) was observed for hill count, followed by stand count and tiller number. Similar results were observed for plant height, number of productive tillers, head weight, grain weight, and panicle number by Sumanth (2011), Ashok (2012), and Sathya et al. (2014).

High value of heritability coupled with high genetic advance were recorded for head weight and grain weight, indicating the important role of additive gene action for the expression of these traits. Therefore, selection based on these traits could bring about desired improvement in the yield of pearl millet. High heritability and low genetic advance were observed for the traits, days to 50% flowering (bloom), number of hills, panicle length, stand count, and tiller number, indicating that they were under the influence of non-additive gene action. Similar results were reported by Lakshmana and Guggari (2001).

Conclusion

Pearl millet production is affected mainly by several environmental factors, and phosphorus stress is one of the major constraints in the dry regions of Nigeria. Therefore, understanding the mechanism of responses to phosphorus stress using mapping population pearl millet is an important and basic part of crop improvement for enhanced genetic value. Thus, it is necessary to identify pearl millet genotypes that will produce better recombinants for efficiency in mobilizing phosphorus when crossed, especially within a phosphorus-deficient environment. Phosphorus-tolerant lines such as P1449-2, PT732B-P2, ICMB 89111, and ICMB 90111, and susceptible lines, H77/833-2 P5(NT), Tift 186, and H77/833-2 (re-selected) could be utilized in further genetic studies.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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