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Agronomic performance of pearl millet genotypes under variable phosphorus, water, and environmental regimes

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Abstract

Water and P deficiency can significantly limit pearl millet [*Pennisetum glaucum* (L.) R. Br.] productivity and response to N application in the arid and semi-arid regions of Africa. The objectives of this research were to quantify the responses of improved pearl millet genotypes and a landrace to contrasting rainfall gradient and P deficient soil conditions across different locations in Niger. The study was conducted at four locations: (a) Tara, (b) the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT) research station at Sadoré, (c) Maradi, and (d) Araourayé, Niger, during 2015 and 2016 rainy seasons. Results of the study indicated that the effect of P fertilizer application on shoot weight, panicle weight, grain yield, and harvest index was different by environment (year × location). As high as 113% straw yield, 72% panicle weight, and 100% grain yield advantage was obtained with P application over low P in favorable environments. Across all genotypes and in both P treatments, irrigation had a consistent effect on the agronomic performance. On average, there was significantly greater straw yield (629 vs. 492 g m^{-2}), panicle weight (472 vs. 229 g m^{-2}), grain yield (257 vs. 122 g m^{-2}), and harvest index (0.25 vs. 0.15) in the irrigated site compared with rainfed sites. Among the tested genotypes, Mil de Siaka showed relatively consistent performance in irrigated, water deficit, and P deficient conditions, emerging as an ideal candidate for inclusion into pearl millet breeding programs, aimed toward developing multi-stress tolerant pearl millet varieties.

1 | INTRODUCTION

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is a hardy cereal, grown mostly in marginal environments in the arid and semi-arid tropical regions of Asia and Africa. It is primarily cultivated under rainfed conditions, wherein drought and drought-induced heat stress are major constraints (Nelson et al., 2009). Pearl millet is one of the major food crops and source of income for approximately 120 million people in semi-arid areas of West and Central Africa (WCA) (ICRISAT-WCA, 2017; Li et al., 2010). The cropped area of pearl millet in WCA is 16.8 million ha, of which about 7 million ha are in Niger (CGIAR, 2012, Kousik, Thakur, & Subbarao, 2011). In Niger, pearl millet is mostly grown in Sahelo-Sudanian to Sahelian zones, which are characterized by a strong North–South annual rainfall gradient, with an average of 1 mm

Abbreviations: HI, harvest index; HSD, Tukey's honest significant difference; LP, low phosphorus; NP, normal phosphorus; RH, relative humidity; Tmax, average daily maximum temperature; Tmin, average daily minimum temperature; VPD, vapor pressure deficit; WCA, West and Central Africa.

decrease for every kilometer from South to North (Akponikpe, 2008). This gradient in rainfall leads to drought stress, which reduces crop productivity. In addition, the beginning date of the rainy season is quite variable across pearl millet-growing locations, both within and between years (Salack et al., 2016). Due to these conditions, grain yield of pearl millet in Niger is very low (0.5–0.7 Mg ha^{-1}), and hence unable to meet the increasing demand. Although, 85% of the farming households in Niger cultivate pearl millet, productivity is a persistent challenge to meet the demand driven by 17 million people (Ministere de l'Agriculture, 2012). Characterizing various pearl millet genotypes under diverse environments and identifying environmentally stable and productive genotypes, is one of the major research needs.

In addition to drought, low soil fertility, especially low soil P, is another major constraint to pearl millet productivity in many parts of WCA. About 80% of the sub-Saharan African soils are deficient in P, which is a critical nutrient for normal plant growth and without which addition of other inputs and technologies is shown to be less effective (Bationo, Kihara, Waswa, Ouattara, & Vanlauwe, 2005; Verde & Matusso, 2014). Phosphorus deficiency can significantly limit crop productivity and response to N application (Bationo & Mokwunye, 1991). In the sandy Sahelian soils, total P can be as low as 40 mg P kg^{-1} and available P <2 mg P kg^{-1} (Bationo et al., 2005). Specifically, in Niger, the available P in millet-producing soils ranges between 1.7 and 8.5 mg kg^{-1} (Manu, Bationo, & Geiger, 1991), whereas 25–35 mg kg^{-1} is considered adequate for normal growth of pearl millet (Siddo, Salou, & Ide, 2013). External application of a small amount of P fertilizer (equivalent to 125–500 g P ha^{-1}) was shown to enhance pearl millet seedling establishment and early seedling growth (Valluru, Vadez, Hash, & Karanam, 2010). In addition, microdosing of fertilizer has recorded yield gains in West Africa (Buerkert & Hiernaux, 1998; Hayashi, Abdoulaye, Gerard, & Bationo, 2008; Pender, Abdoulaye, Ndjeunga, Gerard, & Kato, 2008). Although external application of fertilizer is recommended, high cost, limited supply and poor infrastructure for marketing have resulted in limited use of mineral fertilizers by smallholder farmers in WCA. Hence, breeding for high-yielding millet under low P and water-deficit conditions is practically relevant and an important contribution to improve and sustain pearl millet production in West Africa.

The variability in environmental conditions particularly temperature and precipitation is predicted to increase in the future (IPCC, 2014). Increasing pearl millet productivity in this context remains a stiff challenge to crop scientists and farmers. This requires systematic characterization including selection of genotypes and soil and water management practices to minimize or tolerate environmental constraints and soil nutritional limitations. Water-deficit stress is often associated with high evaporative demand (vapor pressure deficit, VPD), leading to increased crop or tissue heat stress

Core Ideas

- A 100% grain yield advantage was obtained with P application in favorable environments.
- Across genotypes and P treatments, irrigation had a consistent positive effect.
- Mil de Siaka was a consistently good performer in irrigated, water, and P deficit conditions.

(Brisson et al., 2010; Schoppach et al., 2016). In West Africa, significant yield loss (5–90%) on pearl millet and other crops is caused by striga (*Striga aspera* and *S. hermonthica*; Kountche et al., 2013; Obilana & Ramaiah, 1988). Evaluating a diverse set of genotypes for response to water deficit, heat stress, resistance to striga, and VPD in multi-locations is essential for identifying genotypes that have greater plasticity and maintain yield stability in a range of environmental conditions. The objectives of this research were to quantify the responses of improved pearl millet genotypes and a landrace to contrasting rainfall gradient and P deficient soil conditions across different locations in Niger. Specific objectives were to investigate: (a) plasticity and yield stability of pearl millet genotypes in a range of environmental conditions, (b) P deficiency and water-deficit stress interaction on growth and productivity of pearl millet genotypes across locations, and (c) identify robust pearl millet genotypes with improved adaptation to climatic variability and low P conditions.

2 | MATERIALS AND METHODS

2.1 | Study locations

The field studies were conducted in four locations: (a) Tara, (b) the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT) research station at Sadoré, (c) Maradi, and (d) Araourayé, Niger, during 2015 and 2016 rainy seasons. The four locations were chosen based on an increasing rainfall gradient from North to South. Tara is located in Sahelo-Sudanian zone in the South, Sadoré in the Southwest region of the Sahelian zone, Maradi is located in the northern part of the Sahelian zone and Araourayé is also located in the northern part of the Sahelian zone. The average maximum and minimum temperature, relative humidity, VPD, and cumulative sum of rainfall before flowering and after flowering are presented in Table 1.

The soils in these locations are sandy, characterized with low P, low pH, low inherent soil fertility and organic matter content, leading to very low water holding capacity (Batiano et al., 2005; Manu et al., 1991). Prior to sowing, soil samples from 0 to 40 cm deep at Sadoré-ICRISAT and Maradi

TABLE 1 Site characteristics, average maximum and minimum temperature (Tmax and Tmin, respectively; ˚C), relative humidity (RH; %), vapor pressure deficit (VPD; kPa) and cumulative rainfall (mm) before and after flowering. Numbers in parenthesis with rainfall amount indicate the amount of irrigation

Location	Before flowering		After flowering	
	2015	2016	2015	2016
Tara (11˚55′ N, 3˚19′E, 240 masl; 500–800 mm mean annual precipitation)				
Tmax, ˚C	33.6	31.6	36.6	36.2
Tmin, ˚C	24.0	23.4	23.2	24.3
RH, %	74.8	81.3	35.5	62 .9
VPD, kPa	0.8	0.7	2.6	1.6
Rainfall, mm	279.4	426.4	0.0	58.2
Sadore-ICRISAT (13˚14′ N, 2˚17 E, 240 masl; 500–600 mm mean annual precipitation)				
Tmax, ˚C	34.0	32.8	37.2	37.2
Tmin, ˚C	23.9	23.4	22.2	23.3
RH, %	74.3	78.1	45.7	59.7
VPD, kPa	1.0	0.8	2.2	1.7
Rainfal, mm	279.4	290.1	17.5 (150)	46.1 (200)
Maradi (13˚27′ N, 7˚06′ E, 385 masl; 400–500 mm mean annual precipitation)				
Tmax, ˚C	34.2	33.9	38.2	37.1
Tmin, ˚C	23.6	23.9	22.6	21.2
RH, %	68.7	66.3	34.0	25.9
VPD, kPa	1.2	1.3	2.8	3.0
Rainfall, mm	261.1	307.4	0.0	0.0
Araourayé (13˚51′ N, 7˚28′ E, 385 masl; 350–400 mm mean annual precipitation)				
Tmax, ˚C	33.8	33.3	37.8	38.0
Tmin, ˚C	23.3	23.0	20.9	20.9
RH, %	67.7	69.7	46.3	45.5
VPD, kPa	1.2	1.1	2.2	2.2
Rainfall, mm	248.0	215.0	17.0	0.0

were collected using a manual auger and analyzed for available P following Bray 1 procedure (van Reeuwijk, 1993), total N using Kjeldahl method (Houba, Van der Lee, & Novozamsky, 1995), and other physical characteristics (Table 2). Soil characteristics for Tara and Araourayé are taken from previous studies (Fechter, Allison, Sivakumar, Ploeg, & Bley, 1991; Issaka, 2001, Siddo et al., 2013), where similar soil test procedures were used (Table 2).

2.2 | Experimental design and treatments

Experimental design was an alpha lattice with two factors, fertilizer and genotypes, and four replications. The two P fertilizer levels as the main plot (low phosphorus, LP; and normal phosphorus, NP) were identical in all sites. For LP treatment no external P was added but for the NP treatment, P was applied as diammonium phosphate (DAP) (18% N–46% P_2O_5–0% K_2O_5) to meet the NP recommendation (170 kg P_2O_5 ha^{-1}). Urea meeting the same amount of N as in DAP was applied to LP treatment. Fertilizer application was conducted in two splits: 1 wk after sowing (100 kg P_2O_5 ha^{-1} and 39 kg N ha^{-1} for NP; only 39 kg N ha^{-1} for LP) and then 30 d after sowing (70 P_2O_5 ha^{-1} and 27 kg N ha^{-1} for NP; only 27 kg N ha^{-1} for LP). The second treatment factor was nine pearl millet genotypes including eight improved varieties (ICMV-IS 99001, ICMV-IS 89305, ICMV-IS 94206, Striga-Sadore, Striga-epis court, SOSAT-C88, ICRI-Tabi, Mil de Siaka) and one landrace (Ankoutess), considered as subplot treatments. These genotypes were selected based on previous evaluations in lysimeter and field conditions (Beggi, 2014).

At each location plot area was 4 m^2, including four rows of 2 m length. Row spacing was 0.5 m and each row had five hills. Between 5 and 10 seeds were sown by hand in each hill, in 3-cm deep holes in all four locations. Seeds were sown only after receiving at least 20 mm rainfall. Two weeks after sowing, plants were thinned to two plants per hill.

All except the Sadoré-ICRISAT experiment were maintained under rainfed conditions. The Sadoré-ICRISAT experiment was irrigated with a linear move system (Valmont Irrigation Inc.) and used as a non-stress control (see Table 1 for the amount of irrigation applied). At grain maturity, a 1-m^2 area was harvested in the central part of each plot (five hills, i.e., 10 plants). Shoot (leaf and stem) and panicles from this harvested area were sun dried for 4 wk before taking their air-dry weight. After panicle weight was measured, panicles were

TABLE 2 Soils characteristics at four experimental locations in Niger

Location	pH	Organic C	Soils characteristics				
			Sand	Silt	Clay	Extractable P	Total N
		%				mg kg^{1}	
Tara	8.2–8.8	0.02–0.03	81.8	8.6	9.6	1.3–4.2	130–270
Sadore-ICRISAT	5.9–6.8	0.09–0.22	90.7	6.2	3.2	9.0–11.0	109.4
Maradi	5.4–6.4	0.03–0.12	96.6	2.7	0.7	1.9–3.7	96.3
Araourayé	5.4–5.8	0.11–0.20	97.5	4.1	0.6	3.6–4.2	50-60

hand threshed, and total dry weight of seeds was recorded. All three agronomic measurements (straw yield, panicle weight, and grain yield) were expressed as g m^{-2}. Harvest index (HI) was calculated as ratio of grain mass to total biomass (shoot and panicle), using the following formula (Equation 1).

$$\text{HI} = \frac{\text{Grain mass}}{\text{Biomass}} = \frac{\text{Grain mass}}{\text{Straw yield} + \text{Panicle weight}} \quad (1)$$

2.3 | Data analysis

Analysis of the effect of year, location, genotypes, P treatments, and their interactions on response variables (straw yield, panicle weight, grain yield, and harvest index) was conducted in SAS (SAS Institute, 2012) using PROC MIXED procedure. In the analysis; year, location, P treatments (main plot), genotypes (subplot), and their interaction were considered as fixed effect while block (replication) was a random variable. The location × year interaction was considered to be the effect of environment. When factor effects are significant in the above type 3 test, a mean separation test (Tukey's Honest Significant Difference [HSD] test) was conducted.

The second analysis was on the effect of water deficit (i.e., rainfed vs. irrigated) on straw yield, panicle weight, grain yield, and harvest index. We grouped the three sites (Araourayé, Maradi, and Tara) under rainfed and one site (Sadoré) under irrigated condition. In order to test, if response variables (straw yield, panicle weight, grain yield, and harvest index) were affected by water deficit and its interactions with P fertilizer application, a test was run in SAS PROC MIXED procedure with response variables modeled against fixed variable (year, water deficit, P fertilizer, genotype, and their interactions) and block (replication) in a random statement. Mean separation tests for fixed variables that showed significant differences, in all the above analyses, at $P < .05$ were conducted using Tukey's HSD test. Furthermore, a simple correlation analysis was conducted among response variables straw yield, panicle weight, and grain yield using SAS PROC CORR procedure.

3 | RESULTS

3.1 | Straw yield

For straw yield, the three-way interactions of location × year × P and location × year × genotype were significant (Table 3). The year × location component of these interactions represent effect of environment. Therefore, our results indicate significance of environment to responses of main plot (P) and subplot (genotypic) treatments.

In 2015, there was no significant straw yield difference between the LP and NP at Araourayé and Maradi, but

TABLE 3 Main effect of location, year, treatments with type 3 test of fixed effects (environment, year, P treatments, genotypes, and their interactions) on response variables (straw yield, panicle weight, grain yield, and harvest index) of pearl millet grown at four diverse water availability and disease locations in Niger. The main effect values are the lsmeans of four replicates and either 2 yr, two P rates, and nine genotypes for main effect of location; four locations, two P rates, and nine genotypes for main effect of year; four locations, 2 yr, and nine genotypes for main effect of P; and four locations, 2 yr, two P rates for main effect of genotype

Fixed effect	Straw yield	Panicle weight	Grain yield	Harvest index
	g m^{-2}			
Location				
Tara	456b[a]	285b	159b	0.19c
Sadoré-ICRISAT	629a	468a	258a	0.25a
Maradi	413b	104c	41c	0.07d
Araourayé	454b	289b	182b	0.21b
HSD	81	50	31	0.02
Year				
2015	453b	274b	136b	0.17b
2016	523a	309a	181a	0.19a
HSD	45	35	21	0.02
P fertilizer rate				
0	419b	255b	146b	0.19a
170	557a	326a	173a	0.17b
HSD	44	34	21	0.02
Genotypes				
Ankoutess	444	290	156ab	0.19ab
ICMV-IS 89305	466	290	160ab	0.18ab
ICMV-IS 94206	498	272	155ab	0.16b
ICMV-IS 99001	491	291	147b	0.16ab
ICRI-Tabi	468	292	165ab	0.18ab
Mil de Siaka	525	331	189a	0.19a
SOSAT-C88	464	266	143b	0.17ab
Striga-Sadore	508	285	153ab	0.17ab
Striga-epis court	529	300	167ab	0.17ab
HSD	ns	ns	42	0.03
Type 3 test of fixed effects				
Location (L)	<.0001	<.0001	<.0001	<.0001
Year (Y)	<.0001	0.0005	<.0001	<.0001
Y × L	<.0001	<.0001	<.0001	<.0001
P treatment (P)	<.0001	<.0001	0.0003	0.0006
L × P	<.0001	0.0037	0.0057	<.0001
Y × P	0.3318	0.2675	<.0001	<.0001
Y × L × P	**<.0001**[b]	**<.0001**	**<.0001**	**0.0127**
Genotype (G)	0.2878	0.2153	0.0233	0.0095
L × G	0.0091	0.1272	0.0013	0.0327
Y × G	0.4219	0.6671	0.2213	0.3657

(Continues)

TABLE 3 (Continued)

Fixed effect	Straw yield	Panicle weight	Grain yield	Harvest index
Y × L × G	**0.0017**	0.6968	**0.0232**	**0.0089**
P × G	0.5864	0.3415	0.4108	0.1699
L × P × G	0.1168	0.4253	0.1798	0.1925
Y × P × G	0.8284	0.8660	0.1971	**0.0003**
Y × L × P × G	0.0639	0.6212	0.6402	0.1057

Note. HSD is minimum difference between two treatments used to declare they are significantly different using Tukey's Honest Significant Difference Test. ns is nonsignificant.
[a]Within location, year, or treatments and under each response variable, means that share the same letter or those that have no letter are not significantly different.
[b]Values in bold are significant fixed effect variables discussed in results and discussion.

there was 113 and 47% straw yield advantage with NP over LP at Sadoré-ICRISAT and Tara, respectively (Table 4). Both Araourayé and Maradi having greater post-flowering temperature accompanied with significantly lower rainfall in 2015 (Table 1) compared to other locations explains the limited response to P fertilizer in these locations. In 2016, there was no significant yield difference between LP and NP at Maradi or Sadoré-ICRISAT, but NP had 34 and 84% yield advantage with NP compared to LP at Araourayé and Tara, respectively (Table 4). Lack of response to P fertilizer at Maradi in both years was perhaps related to a lack of rainfall after flowering (Table 1). At Sadoré-ICRISAT, rainfall amount and distribution (Table 1) was better in 2016 and straw yield at zero level of P application performed equal to P-fertilized plots, and both recorded greater straw yield compared with other locations (Table 4). Lack of response to P application at Sadoré-ICRISAT was attributed to inherent high-extractable P in the soil (Table 2).

A significant genotypic difference in straw yield was recorded in 2015 and 2016 for Maradi and in 2016 at Sadoré-ICRISAT (Table 3, Figure 1). In 2015 at Maradi, genotype ICMV-IS 99001 had greater yield than ICMV-IS 94206, ICRI-Tabi, and SOSAT-C88. There were no significant differences among genotypes at any other location in 2015. In 2016, ICMV-IS 94206 yielded greater than SOSAT-C88 at Sadoré-ICRISAT and genotype Striga-Sadore yielded significantly greater straw yield than SOSAT-C88 at Maradi (Figure 1). There was no significant difference between genotypes in either year at Araourayé or Tara.

3.2 | Panicle weight

When panicle weight was modeled against environment, P, and genotype, and their interaction; the three-way interactions between environment and P (location × year × P) was significant (Tables 3 and 4).

TABLE 4 Straw yield, panicle weight, grain yield, and harvest index of pearl millet grown at four locations over 2 yr [environment (location × year)] at two levels of phosphorus fertilizer in Niger during 2015 and 2016. The location and P values are the lsmeans of 2 yr, four replicates, and nine genotypes

	2015			2016		
	P fertilizer levels, kg ha^{-1}					
Location	0	170	HSD	0	170	HSD
	Straw yield, g m^{-2}					
Tara	215b[a]	317a	55	455b	835a	103
Sadoré-ICRISAT	431b	917a	189	582	586	ns
Maradi	376	478	ns	415	379	ns
Araourayé	475	407	ns	398b	536a	60
	Panicle weight, g m^{-2}					
Tara	142b	210a	28	397b	574a	61
Sadoré-ICRISAT	271b	479a	96	381	362	ns
Maradi	114	138	ns	178	170	ns
Araourayé	218a	155b	63	258b	444a	74
	Grain yield, g m^{-2}					
Tara	54	45	ns	191	319	39
Sadoré-ICRISAT	243	276	ns	266	246	ns
Maradi	47	52	ns	30	34	ns
Araourayé	227a	143b	40	120	239	47
	Harvest index					
Tara	0.16a	0.09b	0.04	0.24	0.24	ns
Sadoré-ICRISAT	0.29a	0.18b	0.05	0.27a	0.25b	0.02
Maradi	0.09	0.08	ns	0.05	0.06	ns
Araourayé	0.24a	0.21b	0.03	0.16b	0.24a	0.03

Note. HSD is minimum difference between two treatments used to declare they are significantly different using Tukey's Honest Significant Difference Test. ns is nonsignificant.
[a]Within locations and each year under each response variable, means that share the same letter or those that have no letter are not significantly different ($p = .05$).

Panicle weight response to application of P fertilizer was different across environments (Table 4). In 2015, there was no significant panicle weight difference between LP and NP at Maradi, but there was significant panicle weight increase (44–48%) with P application at Sadoré-ICRISAT and Tara. On the other hand, panicle weight was significantly lower (20%) with P application at Araourayé in 2015. In 2016, there was no significant panicle weight difference between the LP and NP application at Maradi and Sadoré-ICRISAT; but 72 and 53% advantage in panicle weight for P application was recorded over LP at Araourayé and Tara, respectively (Table 4).

3.3 | Grain yield

Similar to straw yield, environment by P (location × year × P) and environment by genotype (year × location × genotype) interactions were significant for grain yield (Table 3).

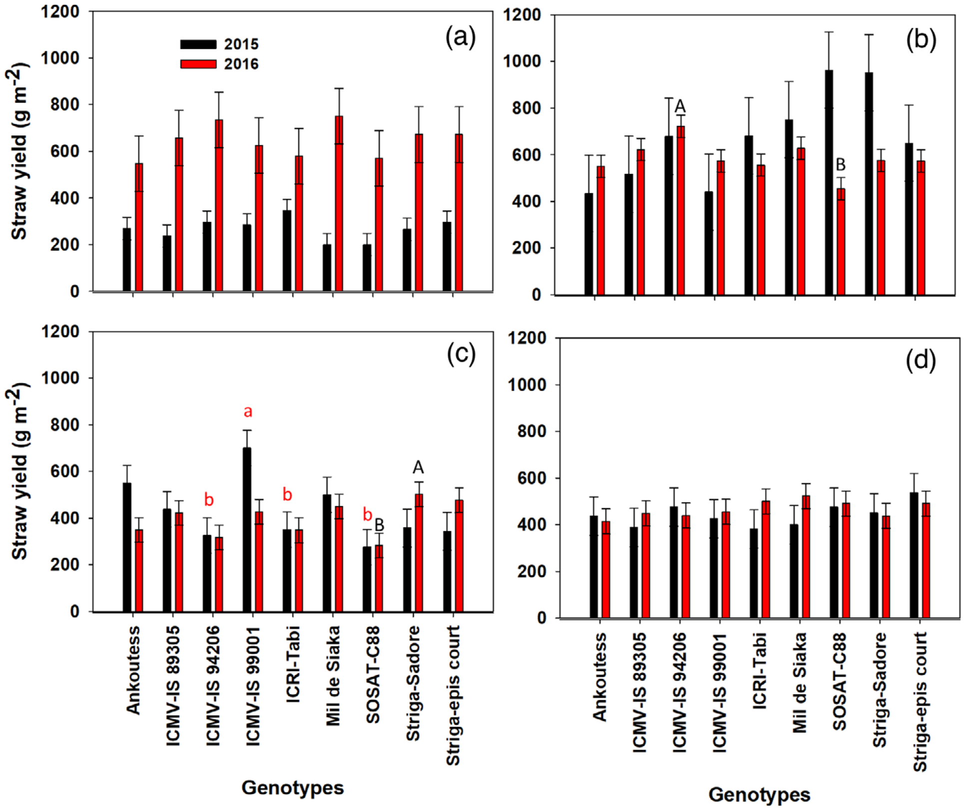

FIGURE 1 Straw yield at (a) Tara, (b) Sadoré-ICRISAT, (c) Maradi, and (d) Araourayé sites in Niger with nine genotypes in 2015 and 2016. The G × L × Y values are the lsmeans of four replicates and two P rates for each location. Error bars are standard errors. Bars with no letter or similar small letters in 2015 or similar capital letters in 2016 are not significantly different. Here comparison of genotypes is made within years and location; for across years and location comparison, HSD value is 441 g m^{-2}

For the location × year × P interaction, in 2015, there was no significant grain yield difference between LP and NP application at Tara, Sadoré-ICRISAT, and Maradi, but a decline in yield with P fertilizer application was observed at Araourayé (Table 4). In 2016, there was no significant yield difference between LP and NP at Sadoré-ICRISAT and Maradi, but there was 67 and 100% yield advantage with NP compared with LP at Tara and Araourayé, respectively.

The location × year × genotype interaction had a significant genotypic difference in grain yield in 2015 at Sadoré-ICRISAT (Figure 2). In 2015 at Sadore-ICRISAT site, genotype Mil de Siaka, ICRI-Tabi, and Striga-Sadore yielded significantly greater than the remaining genotypes (Figure 2a). There was no significant difference among other genotypes in 2015. In 2016 there was no significant grain yield difference between genotypes at any of the four locations (Figure 2b).

3.4 | Harvest index

The three-way interactions between environment and P (year × location × P), environment and genotype (year × location × genotype), and year, P, and genotype (year × P × genotype) were significant (Table 3).

In 2015, harvest index (HI) for NP decreased by 44, 38, and 13% compared with LP in Tara, Sadoré-ICRISAT, and Araourayé, respectively (Table 4). In 2016 at Sadoré-ICRISAT, HI was greater in the LP treatment compared with the NP. In same year, 2016, at Araourayé, HI was greater by 50% in NP compared with LP.

In 2015, there was no significant genotype response in HI for LP; however, there was a significant genotype difference in HI with NP in 2015. Genotype ICMV-IS 89305, ICRI-Tabi, and Mil de Siaka had significantly greater HI compared with ICMV-IS 99001 (Figure 3).

In 2016, there was greater HI from SOSAT-C88 compared with Striga-epis court at Sadoré-ICRISAT (Figure 4).

3.5 | Water deficit vs. irrigated conditions

All four response variables significantly increased with irrigation (Table 5). The four-way interaction, year × irrigation × P × genotype, was only significant for straw yield. Significant irrigation × genotype and year × irrigation × P fertilizer

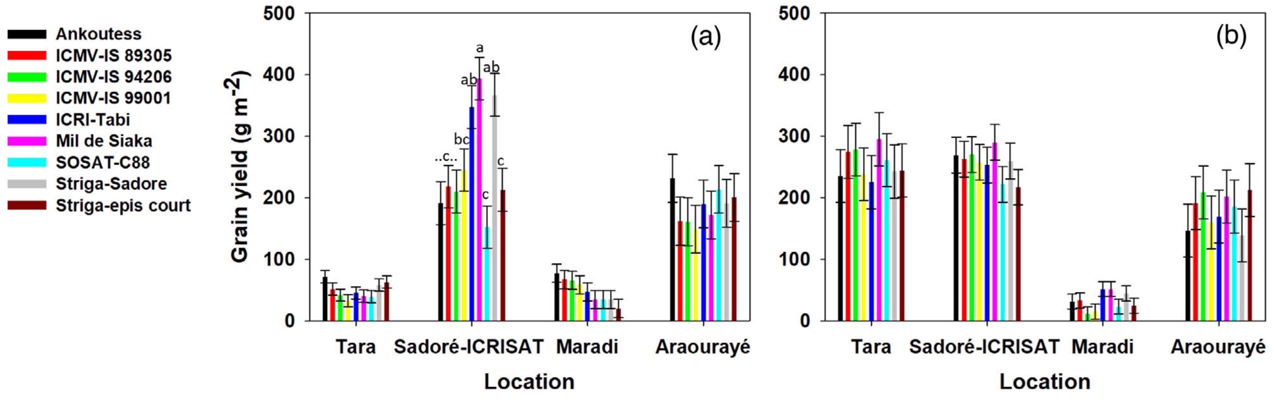

FIGURE 2 Grain yield at Tara, Sadoré-ICRISAT, Maradi, and Araourayé sites in Niger with nine genotypes in (a) 2015 and (b) 2016. The G × Y × L values here are the lsmeans of four replicates and two P rates for each year. Error bars are standard errors. Bars with no letter or share similar letters are not significantly different within a site and year. Here comparison of genotypes were made within years and location; for across years and location genotype comparison, HSD value is 158 g m^{-2}

interactions were obtained for all traits except HI (Table 5). We have restricted our presentation to the three-way interactions (irrigation × P × genotype), irrigation × P, irrigation × year, and irrigation × genotype interactions (Table 6, Figures 5 and 6).

There was a significant straw yield difference between average rainfed and irrigated site for ICMV-IS 94206, ICRI-Tabi, Mil de Siaka, SOSAT-C88, and Striga- Sadore genotypes (Table 6, Figure 6). A 48–85% straw yield benefit was obtained from irrigation among these genotypes compared with their rainfed yield. Panicle weights of all nine genotypes were significantly greater (77–143%) with irrigation. Grain yield also significantly increased in all genotypes, from 51 to 157%, in the irrigated site than their average rainfed grain yield. Except for two genotypes, SOSAT-C88 and Striga-epis court, HI was significantly greater and ranged between 42 and 109% with irrigation.

All four response variables, that is, straw yield, panicle weight, grain yield, and HI, significantly increased with irrigation in both the LP and NP application treatments. The interaction of water deficit and P fertilizer was only significant for straw yield and HI (Table 5). In the LP treatment straw yield, panicle weight, grain yield, and HI were greater by 30, 119, 137, and 84% with irrigation than rainfed (Table 6). With P application treatment straw yield, panicle weight, grain yield, HI increased by 53, 93, 88, and 42%, respectively, in irrigated compared with their rainfed values (Table 6).

Averaged across both water and P treatments, there was a significant gain in all the response variables with irrigation over rainfed system. Overall, straw yield increased by 43%, panicle weight by 106% greater, grain yield by 111%, and HI by 63% in the irrigated site than average yield of rainfed sites (Table 5).

4 | DISCUSSION

4.1 | Terminal water deficit and yield loss in pearl millet

In all locations except in Sadoré-ICRISAT, the rainfall during terminal stages (flowering and post-flowering stages) was limited (Table 1). The post-flowering drought stress exposure in Maradi, Tara, and Araourayé induced straw yield, panicle weight, and grain yield loss compared with irrigated location at Sadoré-ICRISAT (Table 6, Figure 5). Terminal drought during flowering reduces pollen tube growth and fertilization, resulting in lower seed- set, while stress during grain filling leads to a decrease in grain weight. Previous studies (Winkel, Renno, & Payne, 1997; Yadav, Hash, Bidinger, Cavan, & Howarth, 2002) have recorded a grain yield loss of 65% for pearl millet under terminal drought stress in Niger. Similarly, averaged across all nine genotypes over 2 yr a 53% reduction in grain yield was observed under rainfed conditions (averaged across Maradi, Tara, and Araourayé) compared to irrigated Sadoré-ICRISAT location in our study (Table 6, Figure 5). As a consequence of terminal drought and heat stress, there was significant difference in environmental conditions resulting in variable grain yield across locations, combined with striga infestation in Maradi (Figure 2). However, due to differences in locations, irrigation may not be the only factor that can account for all the observed differences between the irrigated and rainfed sites. Soil type and weather among the sites were different, which could also influence crop growth and productivity. Several studies have reported the significant negative effect of drought combined with heat stress on groundnut (*Arachis hypogaea* L.), chickpea (*Cicer arietinum* L.), lentil [*Lens culinaris* (L.) Medikus], and other crops in WCA (Awasthi et al., 2014; Hamidou, Halilou, &

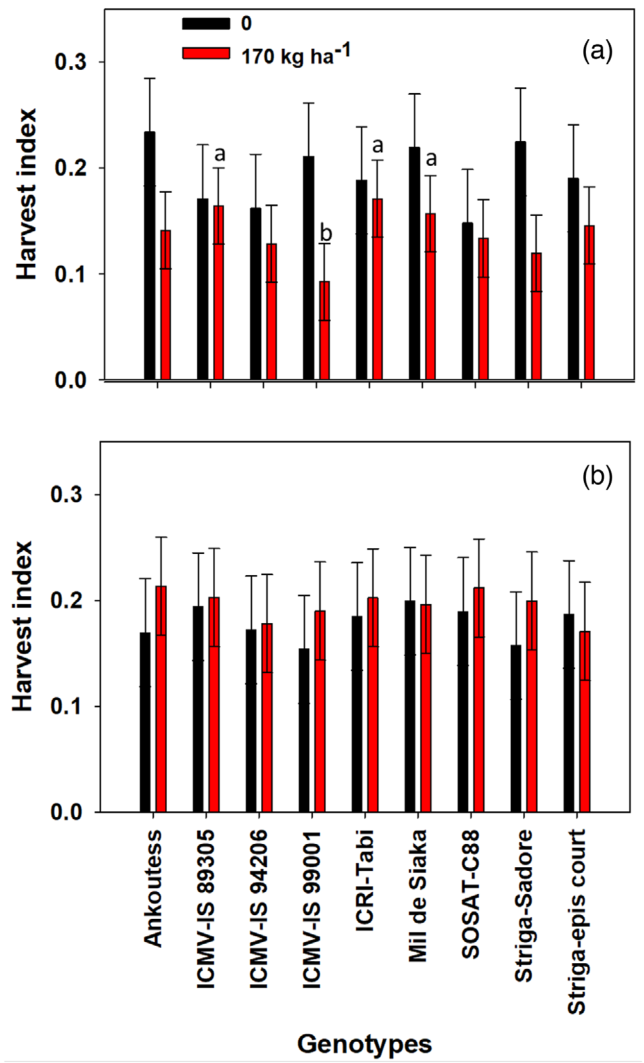

FIGURE 3 Harvest index average across four locations in Niger with nine genotypes in (a) 2015 and (b) 2016 with and without P fertilizer. The G × P × Y values are the lsmeans of four replicates and four locations for each year. Error bars are standard errors. Bars with no letter or share similar letters are not significantly different within a fertilizer treatment and a year. Here comparison of genotypes was made within years and P rate, for comparison across years and P rates the HSD value is 0.08

TABLE 5 Main effect of irrigation and a type 3 test of fixed effects (year, P treatments, genotypes, and their interaction) on response variables (straw yield, panicle weight, grain yield, and harvest index). Main effect of irrigation are the lsmeans of three locations for rainfed data and one location for irrigated location with 2 yr, four replicates, two P fertilizer rates, and nine genotypes

Fixed effect	Straw yield	Panicle weight	Grain yield	Harvest Index
	g m^2			
Irrigation				
Rainfed	441b[a]	229b	122b	0.15b
Irrigated	629a	472a	257a	0.25a
HSD	50	34	21	0.02
Type 3 test of fixed effects				
Year (Y)	0.4305	0.0569	0.0023	0.0091
IRR (I)	<.0001	<.0001	<.0001	<.0001
Y × I	<.0001	<.0001	0.0006	0.6663
P	<.0001	<.0001	0.0711	<.0001
Y × P	<.0001	0.066	0.1846	<.0001
I × P	**0.0015**[b]	0.3042	0.2377	**0.0001**
Y × I × P	**<.0001**	**<.0001**	**<.0001**	0.3805
Genotype (G)	0.0617	0.0449	0.0050	0.2610
Y × G	0.0200	0.3763	0.1550	0.3086
I × G	**0.0097**	**0.0522**	**0.0041**	0.1164
Y × I × G	0.0002	0.3364	0.0468	0.1995
P × G	0.0341	0.1117	0.3946	0.5910
Y × P × G	0.0664	0.5708	0.6546	0.0678
I × P × G	0.0064	0.3815	0.5101	0.6157
Y × I × P × G	**0.0048**	0.2385	0.8496	0.6616

Note. HSD is minimum difference between two treatments used to declare they are significantly different using Tukey's Honest.

[a]Within irrigation and under each response variable, means that share the same letter are not significantly different.

[b]Values in bold are significant fixed effect variables discussed in Results and Discussion.

Vadez, 2013; Sehgal et al., 2017; Sehgal et al., 2018). The rate and duration of seed filling was shown to affect the final seed weight, a primary component of total seed yield (Yang & Zhang, 2006). Occurrence of the combined drought and heat stress during seed filling reduces seed-filling duration and enhances assimilate remobilization rate from the source to sink, with the increased rate unable to overcome the loss in duration (Plaut, Butow, Blumenthal, & Wrigley, 2004). This was exacerbated by striga at Maradi (Table 3, Figure 2).

The reduction in grain yield could be mainly due to a reduction in growth of grain caused by reduction in assimilate supply and not by a reduction in the grain storage capacity (Bieler, Fussell, & Bidinger, 1993), which is supported by the reduced straw yield across all rainfed locations (Figure 5a, Table 5). There was a strong correlation ($r = +.88$) between panicle weight and grain yield. Therefore, the reduction in panicle weight under terminal drought (Figure 5b) can be considered to be a major factor leading to low grain yield in pearl millet. The reduction in grain yield under water deficit can also be linked to aboveground biomass, wherein lower straw yield would indicate a negative effect on assimilate production and supply to the developing grains, leading to reduced yield (Figure 5c). Similar response has been reported by (Yadav et al., 2002) with pearl millet under terminal drought recording 7.5–55.2% reduction in straw yield. In addition, terminal drought and heat stress has been shown to reduce the photosynthetic rate of plants both in growth chambers (Camejo et al., 2005; Prasad, Pisipati, Momcilovic, & Ristic, 2011) and

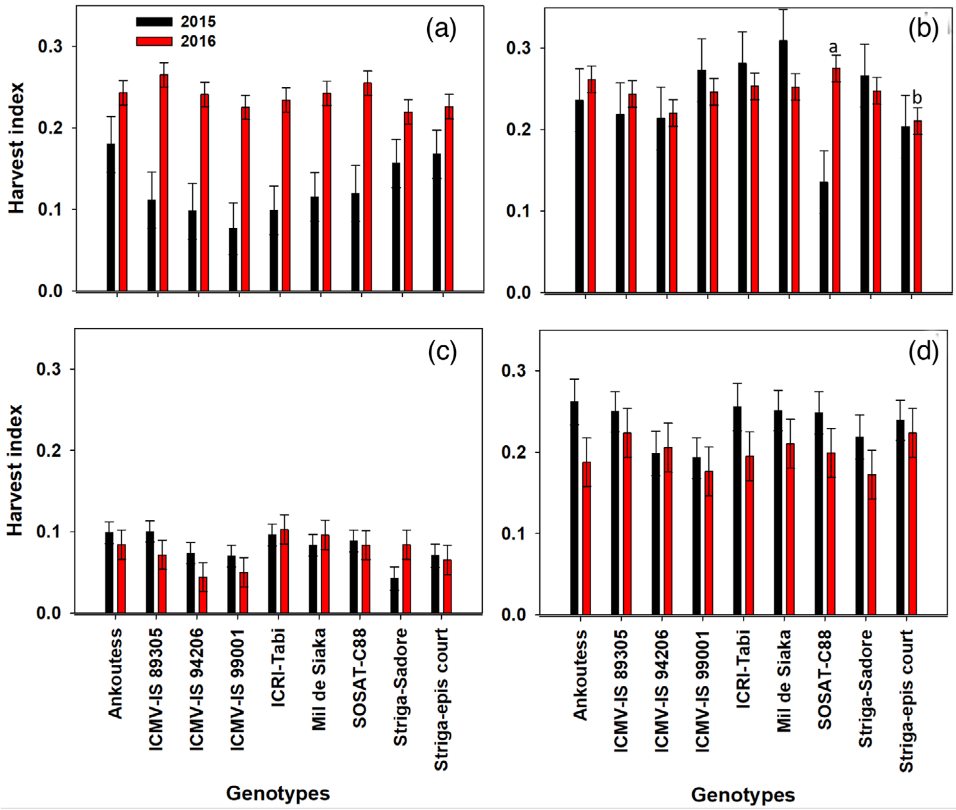

FIGURE 4 Harvest index at (a) Tara, (b) Sadoré-ICRISAT, (c) Mardi, and (d) Araourayé sites in Niger with nine genotypes in 2015 and 2016. The G × L × Y values are the lsmeans of four replicates and two P rates for each location. Error bars are standard errors. Bars with no letter or similar letters, within a year, are not significantly different. Here comparison of genotypes was made in each year by location; for comparison across environment (years and location) the HSD value is 0.13

TABLE 6 Rainfed vs. irrigated straw yield, panicle weight, grain yield, and harvest index by pearl millet genotype (genotype × irrigation); and irrigation × P fertilizer rate interactions. Data are the lsmeans of three locations for rainfed data and one location for irrigated location with 2 yr, four replicates, and either two P fertilizer rates for G × I or nine genotypes for I × P

Genotypes	Straw yield			Panicle weight			Grain yield			Harvest index		
	Rainfed	Irrigated	HSD	Rainfed	Irrigated	HSD	Rainfed	Irrigated	HSD	Rainfed	Irrigated	HSD
	g m^{-2}											
Ankoutess	497	561	ns	250b[a]	473a	99	127b	230a	61	0.16b	0.25a	0.05
ICMV-IS 89305	432	570	ns	248b	480a	102	129b	240a	61	0.17b	0.24a	0.05
ICMV-IS 94206	431b	701a	139	240b	428a	108	119b	240a	70	0.14b	0.22a	0.05
ICMV-IS 99001	486	507	ns	227b	549a	114	111b	251a	61	0.13b	0.27a	0.05
ICRI-Tabi	418b	618a	101	256b	474a	87	117b	300a	56	0.15b	0.27a	0.04
Mil de Siaka	459b	677a	192	266b	590a	109	137b	342a	71	0.16b	0.29a	0.05
SOSAT-C88	382b	709a	157	237b	420a	112	124b	187a	62	0.16	0.21	0.05
Striga-Sadore	449b	764a	197	233b	567a	99	115b	313a	60	0.14b	0.26a	0.05
Striga-epis court	396	535	ns	191b	359a	102	126b	211a	64	0.16	0.21	0.05
P fertilizer rate												
0	389b	507a	52	192b	420a	41	108b	255a	25	0.15b	0.28a	0.02
170	492b	751a	80	278b	537a	52	139b	261a	32	0.15b	0.21a	0.02

Note. HSD is minimum difference between two treatments used to declare they are significantly different using Tukey's Honest Significant Difference Test. ns is non-significant.

[a]Within rows under each response variable, means that share the same letter or those that have no letter are not significantly different (p = .05).

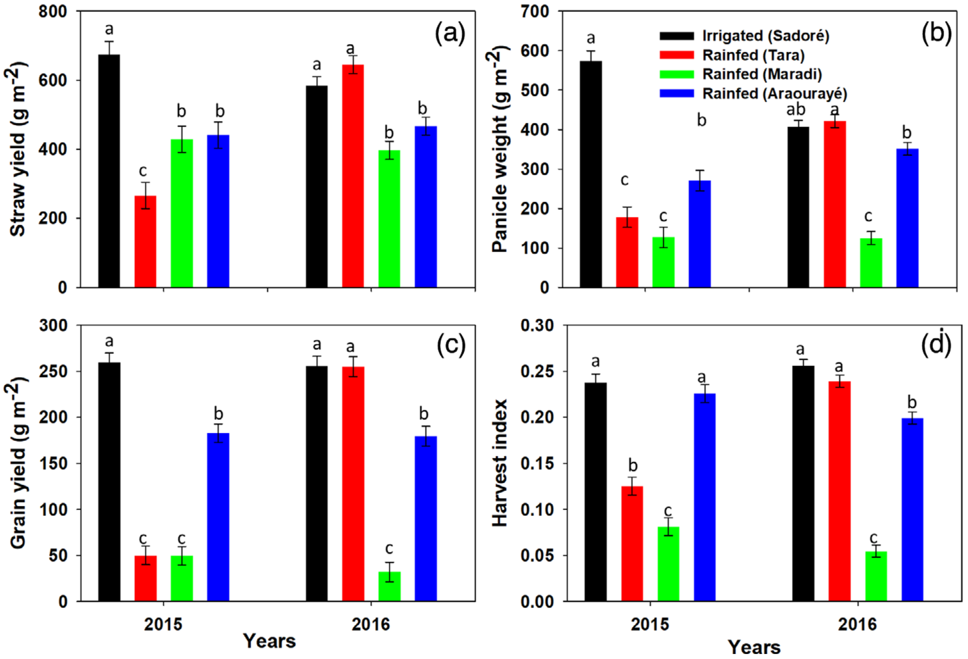

FIGURE 5 Comparison of (a) straw yield, (b) panicle weight, (c) grain yield, and (d) harvest index in irrigated (Sadoré-ICRISAT) and rainfed sites in 2015 and 2016 at Niger. Values (I × Y) are the lsmeans four replicates, two P fertilizer rates, and nine genotypes. Error bars are standard errors. Bars with similar letters, within a year, are not significantly different. Here comparison of irrigation and rainfed locations were made within years; for across years comparison of irrigation and rainfed locations, HSD values are 106, 69, 38, 0.03 for straw yield, panicle weight, grain yield, and harvest index, respectively

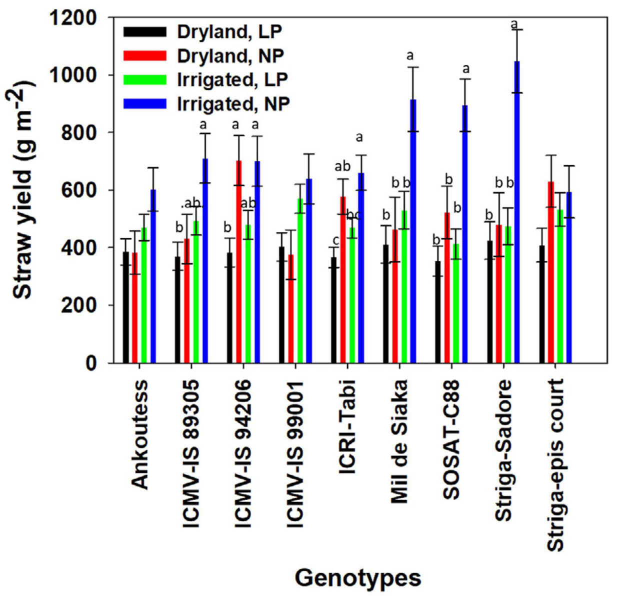

FIGURE 6 A genotype × P × irrigation interaction in straw yield average across years at Niger. Error bars are standard errors. The G × I × P values are the lsmeans of three locations for rainfed data and one location in Niger (Sadoré-ICRISAT) for irrigated location, 2 yr, and four replicates. Bars with similar letters or no letters, within a genotype, are not significantly different. Here comparison of irrigation and rainfed locations were made within genotype, for across genotype comparison of irrigation and rainfed locations, the HSD value is 288 g m^{-2}

under field conditions (Sehgal et al., 2017). In this study, there was a strong correlation ($r = +.63$) between straw and grain yield. Although, millet grain yield loss can also be associated to a reduction in panicle number (Yadav, Narwal, & Arya, 2012), this was not considered to have affected the findings presented.

The link between grain development and the transfer of assimilates from the leaves, with the stems playing a buffering role, appears to be one of the main adaptations of pearl millet to terminal drought stress (Winkel & Do, 1992). Research has also showed that the tolerance of pearl millet genotypes to terminal drought is related to the availability of water during the grain-filling period. Sufficient soil moisture during the grain-filling period sustains photosynthesis supporting continued C supply to the grain during the critical period (Vadez, Kholova, Yadav, & Hash, 2013). Our results show that tolerance of pearl millet to drought after flowering has limits, that is, a season with rainless days after flowering results in significant yield reduction as observed in Maradi and Tara in 2015 (Table 1, Figure 2).

4.2 | Water deficit and P deficiency affect yield negatively

Phosphorus is an essential plant nutrient involved in cell growth and cell division and serves as a component of DNA and cellular energy transport (Gemenet et al., 2016). A shortage in soil P results in a decrease in plant growth, panicle weight, and grain yield in pearl millet. Straw and grain yield were greater in Sadoré-ICRISAT even with zero P application due to the inherent high levels of P compared to other locations (Tables 2 and 4). Millet yield reduction due to low P has been reported by several studies (Akponikpe, 2008; Bationo & Mokwunye, 1991; Gemenet et al., 2014; Gemenet et al., 2015; Manu et al., 1991). Application of P can increase shoot and grain yield in low P soils by not only supplying P but also by increasing uptake of other available nutrients such as N. Valluru et al. (2010) and Gemenet et al. (2014) have shown an increase in productivity and growth of pearl millet with an increase in P availability. In contrast, Serba and Obour (2017) did not find an effect of P application on millet straw yield in Kansas, perhaps due to sufficient available P in the soil. We have also reported no response to P application in few environments (Table 4). This could be the consequence of optimum level of P that already exist in the soil for locations like Sadoré-ICRISAT. Even though 25–35 mg P kg^{-1} was suggested for normal growth of pearl millet (Siddo et al., 2013), our results showed no grain yield response for 2 yr even with 9–11 mg P kg^{-1} in Sadoré-ICRISAT. In 2015, even though there was no grain yield response, straw yield responded positively to P application, suggesting normal growth of pearl millet described by Siddo et al. (2013) goes beyond millet response only through grain yield. In locations like Maradi, where rainfall was the main limiting factor, external application of P did not address the core problem, as availability of water might have limited uptake of P in both years.

Water deficit can be the primary reason for a lack of response to application of nutrients. Limited water availability in soil reduces nutrient uptake by roots and induces nutrient deficiency by decreasing diffusion of nutrient from soil to root (Alam, 1999; Assefa, Staggenborg, & Prasad, 2010; Viets, 1972). In this study, the effect of water deficit reduced response to applied P fertilizer, negatively influencing millet growth and productivity (Table 6). Similarly, Beggi, Hamidou, Buerkert, and Vadez (2015) and Payne, Lascano, Hossner, Wendt, and Onken (1991) have reported the effect of drought on P uptake and transpiration efficiency with Beggi et al. (2015) reporting a dramatic decrease (66%) of millet grain yield due to combined drought and P effect in a lysimeter system. The low yield observed during the two seasons in Maradi (Figure 2) was due to triple constraints (P deficiency, water-deficit stress, and striga infestation [the latter based on observed data at the affected site]). Kim, Akintunde, and Walker (1994) reported a huge damage of striga infestation on millet grain yield. Grain yield losses of up to 100% have been reported in susceptible cereal cultivars under high striga infestation particularly under drought conditions (Ejeta, 2007; Amusan, Rich, Menkir, Housley, & Ejeta, 2008). This suggests the need for incorporating improved P uptake and use efficiency and resistance to striga to attain better adaptation of newly developed pearl millet varieties under low P and drought environments.

4.3 | Genotypic diversity for water deficit and low P environments

Despite similar water-deficit levels experienced by all genotypes, ICMV-IS 99001 and Striga-Sadore consistently recorded greater straw yield in both years, at the most stressful environment in Maradi (Figure 1). This demonstrates the presence of genetic variation in response for water-deficit conditions that can be exploited in millet-breeding programs. Similarly, in 2015 at Sadore-ICRISAT, genotype Mil de Siaka, ICRI-Tabi, and Striga-Sadore yielded significantly greater grain yield than the remaining genotypes (Figure 2). The variation in grain yield at the irrigated site demonstrates that some genotypes might possess high levels of production efficiency under sufficiently watered and other more optimal conditions. Identifying genotypes that are stable across environments is needed as the aim is to develop varieties that are highly responsive to water availability but still maintain greater levels of productivity even under limited water availability. This phenomenon has been extensively tested and adopted in other breeding programs including rice (*Oryza sativa* L.) and maize (*Zea mays* L.) (Bankole et al., 2017; Shaibu et al., 2018).

The ability of a crop to be productive relatively similarly across different environments is measure of its stability. Often, genotypes are selected for one particular environment and fail to perform when conditions differ (Yan & Racjan, 2002). In this study, there were no significant genotypic differences within water deficit or irrigated treatments, but genotype Mil de Siaka showed consistent performance (Table 5, Figure 6) under irrigated, water deficit, and P deficit conditions and presents itself as an ideal donor to be considered in current pearl millet-breeding programs aimed toward developing multi-stress tolerance.

5 | CONCLUSION

The objectives of this research were to quantify the response to contrasting rainfall gradient and P deficient soil conditions of improved pearl millet genotypes and a landrace across different locations in Niger with contrasting rainfall gradient and P deficient soil conditions. The results of the study indicated a significant advantage of P application in environments with low soil P. All measured response variables increased significantly among tested genotypes, both with and without P application under irrigated conditions compared with rainfed sites. In extreme water-deficit condition, application of P fertilizer did not improve pearl millet productivity. Among genotypes tested, Mil de Siaka showed consistent performance in irrigated and water and P deficit conditions. Pearl millet varieties being developed require improved water-deficit stress tolerance, better P uptake and use efficiency and increased resistance to striga to enhance and sustain pearl millet productivity under future warmer and drier environments.

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AUTHOR CONTRIBUTIONS

Oumarou Halilou: Conceptualization; Data curation; Investigation; Methodology; Writing-original draft. Yared Assefa: Formal analysis; Writing-original draft. Hamidou Falalou: Conceptualization; Funding acquisition; Methodology; Project administration; Supervision. Harou Abdou: Data curation; Investigation; Methodology. Bacharou Achirou: Data curation; Investigation; Methodology. Sadissou Karami: Data curation; Investigation; Methodology. Krishna Jagadish: Conceptualization; Funding acquisition; Writing-original draft; Writing-review & editing.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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