

Genotypic Variation for Root Development, Water Extraction and Yield Components in Groundnut Under Low Phosphorus and Drought Stresses

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Abstract: [Context] Unpredictable water deficit (drought) and low soil phosphorus (LP) are major interacting constraints to groundnut growth and grain yield in Sahelian zones of West Africa. Combining breeding efforts for drought tolerance and P efficiency could lead to improve tolerance and grains yield in these zones. [Objectives] This study assessed six groundnut genotypes under lysimetric system to better understand the relative importance of P deficiency, water stress, and their interaction; investigate the water extraction pattern of genotypes under these constraints and identify tolerance related traits to accelerate development of more resilient varieties. [Methods] Thus, in experiment 1 (Exp.1) roots traits were investigated at 50% flowering, pod filling stage (60 days after sowing) and maturity stage (90 days after sowing) under high phosphorus (HP) and LP treatments. In experiment 2 (Exp.2), two water regimes (WW=well water, and WS = water stress) were imposed to HP and LP plants and parameters like total transpired water (TTW), transpiration efficiency (TE), water extraction (Wex), pods and haulm weights were investigated. [Results] Roots traits showed significant decrease due to LP stress, pod and haulm weights correlated significantly to roots length density (RLD) and roots dry matter (RDM). Genotypes 12CS-116 and ICGV 12991 revealed tolerant to LP stress while RLD and RDM revealed LP tolerance related traits in groundnut. Interacting effect of LP and drought stress (LPWS) was higher than separate effect of LP and WS. Under LPWS, Wex, TTW, TE, pod and haulm yields decreased significantly. This study suggests that RLD and RDM contributed to Wex in 12CS-116 and ICG 12991 under LPWS. 55-437 and JL-24 with highest TTW showed drought tolerance strategy while drought avoidance strategy could explain 12CS-116, 12CS-79, ICG 12991 and ICGV 97183 response to WS. Pod weight showed tight correlation ($R^2=0.7$) to TE only under LPWS suggesting that TE explains a large part of pod yield variation under LPWS conditions. TE revealed WS and LPWS tolerance related trait. The genotypic variation observed on Wex and TTW under LPWS suggests different patterns of water extraction and use among the groundnut genotypes.

Keywords: Water Extraction, Roots Traits, Drought, Low Phosphorus, Stress, Groundnut, Yield

1. Introduction

In Sahelian zones of the semi-arid tropics, groundnut (*Arachis hypogaea* L.) is widely cultivated in rainfed areas.

Drought stress has adverse influence on water relations, photosynthesis, mineral nutrition, metabolism, growth and yield of groundnut [1]. Intermittent drought, occurring almost each year in most of groundnut production Sahelian areas, leads to pods and haulm yields loss up to 55% [2].

When drought is combined with heat stress, the pods yield decrease reached up to 72% [3]. Drought stress significantly reduced total dry matter (41%), transpiration (33%) and chlorophyll content (40%) across genotypes but significantly increased transpiration efficiency (20.5%) and Chlorophyll density (22%) in peanut [4]. These authors observed significant genotypic variation for transpiration efficiency and chlorophyll parameters. Mid-season and terminal drought are major constraints of peanut production as they reduced pod yield, can increase the incidence of aflatoxin contamination while an early-season drought stress is not detrimental to peanut yield and it sometimes actually increases yield of peanut [5, 6, 7]. Drought at pod filling reduces growth, yield and seed quality of peanut (*Arachis hypogaea* L.) and great root system can reduce yield loss under water stress [8]. [9] reported that rooting depth and root branch density are important root architectural traits that directly influence the acquisition of water and nutrients in the soil strata. Drought stress reduced also the uptakes of N, P, K and Ca in peanut [10]. Useful traits, including rooting system and water uptake, to improve groundnut adaptation and productivity under drought are still needed.

The rainfed areas of Sahel are also characterized by low soil fertility which is additional major constraint of groundnut productivity. Among soil fertility factors and on the mostly acid sandy Sahelian soils, phosphorus (P) is the most limiting nutrient for crop production [11]. [12] reported that the acid Sahelian soils are low concentrated in plant available phosphorus (Bray-P typically 2 – 4 mg kg⁻¹) which affects growth and yield parameters. An early season deficiency of phosphorus leads to early irreversible restriction in crop development that can drastically reduce crop populations [13]. Phosphorus (P) deficiency is the most frequent nutrient stress for growth and development of grain legumes [14]. Although legumes can fix their own N, they often need other nutrients particularly phosphorus for good seed formation [15]. The requirement of P in nodulating legumes is higher compared to non-nodulating crops as it plays a significant role in nodule formation and fixation of atmospheric nitrogen. Other authors reported negative effects of P deficiency on the capacity to fix N, roots and leaves growth in legumes [16]. In Common bean, P deficient plants showed 50% lower net photosynthesis at ambient CO₂ concentration reflecting lower carboxylation efficiency [17]. In soybean (*Glycine max*), it was shown that P nutrient improved root traits to enhance tolerance of water deficit during reproductive growth, with less yield reduction at high applied P [18]. In groundnut, it was observed that under LP conditions, tolerant genotypes exhibited increased performance in various root traits and accumulated more root and shoot biomass and P [19, 20]. It was reported also that phosphorus deficiency reduced flower production, size of pods and adversely affect the formation of root nodules in groundnut [21]. [22] investigated the genotypic variation for roots traits in groundnut germplasm under phosphorus stress conditions and observed that ICGV 86590, ICGV 14475 and

ICVG 92188 were found tolerant by producing more lateral roots, root volume and root weight.

In the West African Sahel, unpredictable rainfall deficit and low soil phosphorus (P) are major interacting constraints to crops growth and grain yield. Several research works were conducted on drought tolerance in groundnut [2, 3, 23-29]. Previous works have shown that phosphorus nutrient is an important factor improving the tolerance ability to water stress [30, 31]. Peanut genotypes that have higher root length density in deeper soil layers have enhanced drought tolerance, which can result in a higher pod yield and harvest index under pre-flowering drought conditions [32]. In common bean, [33] reported that shallow-rooted genotypes grow relatively better under P stress, deep-rooted genotypes grow better under water stress, while genotypes with a dimorphic root system permitting vigorous rooting throughout the soil profile grow best in the combined stress treatment. However, even known that in West African Sahel, drought affects groundnut cultivated on low P soil, as far as we know, research has not been done on the interaction between low P and water stress particularly on roots and canopy response, water and phosphorus use. Improvement of peanut to extract water from the whole soil profile might increase drought tolerance [34]. To do so, investigation on the genotypic variation in the pattern of water extraction in soil profile is required. We hypothesize that in groundnut, combining breeding efforts for drought tolerance and P efficiency could lead to improve tolerance and grains yield in Sahelian zones. Therefore, this work aims to (i) better understand the relative importance of P deficiency, water stress, and their interaction, (ii) identify measured traits related to better performance of genotypes under these constraints to accelerate development of more resilient varieties to drought and low phosphorus stress, and (iii) investigate water extraction pattern of genotypes under low P and drought stress.

2. Material and Methods

This study was conducted at the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Sahelian Centre (ISC) in Sadoré (45 km south of Niamey, Niger, 13°N, 2°E) from June to November 2014 (rainy and off-season). The experiments used six genotypes JL-24, ICGV 97183, 55-437, 12CS-116, 12CS-79 and ICG 12991 selected based on their response to drought stress under field conditions. ICG 12991, ICGV 97183 and 55-437 were considered as tolerant; 12CS-116 and 12CS-79 were intermediate while JL 24 was sensitive [2, 7]. These six genotypes were evaluated in two different experiments in lysimetric system. The characteristics of the soil were 5.8 pH H₂O (1:2.5), 3.6 mg Bray-P kg⁻¹ soil, 0.1% organic matter (C) and 81 mg total N kg⁻¹. The 6 entries were evaluated in high phosphorus (HP) and low phosphorus (low P) treatments trials planted side by side using 3×2 α-lattice design with five replications in each P treatment. The temperature and relative humidity of the air were collected

from a temperature and relative humidity recorder (Gemini Tinytag Ultra 2 TGU-4500 Data logger Ltd, Chichester, UK) located in the crop canopy.

2.1. Experimental Conditions

The lysimetric system was well described in our previous works [35, 28]. All lysimetre tubes (PVC cylinders) were placed upright in 1 m deep trench, over which the weighing mechanism could be moved to select individual cylinders for weighing. The tops of the cylinders were equipped with metal collars and chains to allow the lysimetre tubes to be lifted and weighed. The lysimeter tubes weighting procedure involved a crane balance (S-type load cell with a 200 kg load capacity; Mettler-Toledo, Geneva, Switzerland) connected to a block chained pulley to lift the tubes. The soil used to fill the lysimetre tubes was collected from the farm of ICRISAT Sadoré station. Top soil (0-20cm) and deep soil (20-100cm) from the farm were collected separately. To mimic the field conditions, the lysimetre tubes (25 cm diameter, 130cm height) were filled with deep soil (100 cm height) followed by top soil (20 cm height). The upper 10 cm of the tubes was left empty to allow the application of a layer of anti-evaporation beads and for watering.

2.1.1. Experiment 1 (Exp.1)

Three seeds were sown by hand; seedlings were thinned to one plant per tube at 14 days after sowing (DAS). The experimental design was a 3×2 α -lattice design with 5 replications in each P treatment. LP and HP treatments were at either side of the trench in which all the tubes were placed in order to avoid HP plants shading the LP plants. The soil was kept at 90% of field capacity until harvest. The 6 genotypes randomized within each of the five replications. To investigate roots traits under low varying P conditions, 5 plants of each variety and per phosphorus treatment were uprooted at 50% flowering time, 60 days after sowing (pod filling stage) and at maturity date for extracting roots as described by [36]. During the experiment (end June to mid-September), mean temperatures (Min and Max) were 24 and 33°C respectively while the Min and Max mean relative humidity were respectively 53.5 and 98.5%.

2.1.2. Experiment 2 (Exp. 2)

The experimental conditions (soil, seeds sowing, design, genotypes, etc.) were the same as in experiment 1 except that (i) two plants were left per tube after thinning and (ii) in addition to P treatments, 2 water treatments (WW or full irrigation until harvest and WS or drought stress imposed from flowering to maturity times) were applied. This aimed to investigate the separate and combined effects of low P and WS on the 6 genotypes. The Min and Max mean temperatures were 24.7 and 33°C, and the Min and Max mean relative humidity were 24 and 90% during the cropping period (end August to November).

2.2. Phosphorus and Water Treatments

Two phosphorus treatments (HP and LP) were imposed in Exp.1 and Exp.2. The HP treatment consisted of applying 7.5 g DAP tube⁻¹ (equivalent to 100 kg ha⁻¹) in a circle 2–3 cm around the seedling area after emergence. The LP lysimetre tubes (LP treatment) did not receive any P application but were supplied with urea (3.45 g applied in two doses) to compensate for DAP nitrogen input into HP tubes. DAP (18% N, 46% P₂O₅ and 0% K₂O) and urea (46% N, 0% P₂O₅, % K₂O) were used in these experiments because they are the common fertilizers used by Sahelian farmers. Water treatment WW was a full irrigation (90% of field capacity) until harvest for both Exp.1 and Exp.2. WS treatment imposed in Exp.2 was an intermittent drought consisting of cycles of drying (irrigation interruption) and re-watering (1000mL of water per tube) when the majority of WS plants showed clear wilting symptoms [2]. Given the diameter of the lysimetre tubes, this was equivalent to 16mm of water when extrapolated to a field conditions. Prior to impose WS, the lysimetre tubes were water saturated, drained during 2 days to reach field capacity and the soil surface was covered with a 2cm thick layer of polyethylene beads to minimize soil evaporation [37].

2.3. Measurements

Phenology (flowering and maturity times), yield and its components were measured in both Exp.1 and Exp.2. The leaf area and roots traits (volume, length, length density, dry matter) were specially investigated in Exp.1 while water extraction and transpiration efficiency (TE) were measured only in Exp.2.

2.3.1. Roots Traits Measurement: Volume, Length Density and Dry Matter

To explore roots traits and assess genotypic variation among the 6 varieties under HP and LP treatments, for each genotype, roots of 5 plants of each P treatment were extracted at 50% flowering time (21 – 24 DAS), 60 DAS and at maturity date (84 - 90 DAS). Before extracting the roots, shoot and pods were harvested and separated. The roots extraction consisted of gently washing the soil from both ends of the cylinders after removing the end cap. Total root depth was measured by stretching the entire root system. Then, the root system was divided into 15cm portions which were digitized with a scanner and analyzed using WinRhizo software (Regent Instruments INC, Quebec, Canada) to determine the roots volume (RV), roots length (RL) and roots length density (RLD). After RV, RL and RLD measurement, samples were bagged, dried and weighed for roots dry matter determination (RDM). Pod and haulm yield were determined after harvest.

2.3.2. Transpiration Measurement, Water extraction (Wex) and Transpiration Efficiency (TE) Determination

In Exp.2, two plants were left per tube after thinning. The day before water stress imposition, one of 2 plants of each tube was harvested, dried at 70°C for 2 days and

initial biomass (IDM) was determined. During water stress period, transpiration was measured via a gravimetric procedure by weighing cylinders regularly (twice per week). As there was no evaporation nor draining, the difference of consecutive lysimetre weights, plus water added after the previous weighing, was equivalent to the transpiration [38]. The total transpired water (TTW) of WW and WS plants was determined as cumulative transpiration from water stress imposition (25 DAS) to 85 DAS. At maturity, plant of each cylinder was harvested, dried at 70°C for 2 days for determining the final dry matter (FDM). The transpiration efficiency (TE) was calculated as: $TE = (FDM - \text{mean IDM}) / TTW$. Initial tubes weight (beginning of weighing) and final tubes weight (end of experiment) were used to determine the water extracted of HP and LP plants under WW and WS conditions. Water extraction (Wex) was then calculated as: $Wex = \text{initial tube weight} - \text{final tube weight}$. Pod and haulm yield were determined after harvest.

3. Statistical Analyses

GENSTAT 14th edition (VSN International Ltd, Hemel Hempstead, UK) was used to perform statistical analyses. A one-way and two-way analysis of variance (ANOVA) were performed to assess the effect of genotype (G), phosphorus treatment (Trt), water regime (RH) and the GxTrt, GxRH and/or GxTrtxRH interactions for the different traits measured. Microsoft office Excel 2016 Software (Microsoft Corp., Redmond, WA, USA) was used for linear regression by plotting different traits to determine the R^2 and regression equation. A t-test was performed, differences between the mean values of treatments were evaluated at $P = 0.05$

Table 1. Roots length (cm) under high (HP) and low phosphorus (LP) treatments at flowering, pod filling (60 DAS) and maturity times in 6 groundnut genotypes. DAS = days after sowing, G = genotype, Trt = phosphorus treatment.

	Flowering (50%)		60DAS		Maturity	
	HP	LP	HP	LP	HP	LP
55-437	2478a	2204a	12560a	8966b	12468a	9147a
ICGV 97183	2244a	1727a	14217a	12204ab	10882a	10749a
JL-24	2282a	2218a	13645a	11193ab	12780a	8051a
12CS-116	3310a	2892a	14333a	8054b	17493a	12766a
12CS-79	2993a	2069a	12589a	12282ab	13700a	10968a
ICG 12991	2950a	2292a	16917a	14419a	16956a	11878a
Mean	2710	2234	14044	11186	14047	10593
G (F prob)	0.314 ^{ns}	0.388 ^{ns}	0.816 ^{ns}	0.04*	0.497 ^{ns}	0.353 ^{ns}
Trt (F prob)	0.041*		0.029*		0.020*	
GxTrt (F prob)	0.943 ^{ns}		0.836 ^{ns}		0.915 ^{ns}	

* = significant at 5% level. ns = no significant at 5% level. Means with the same letter are not significantly different within the same treatment

Table 2. Roots length density (RLD) under high (HP) and low phosphorus (LP) treatments at flowering, pod filling (60 DAS) and maturity times in 6 groundnut genotypes. DAS = days after sowing, G = genotype, Trt = phosphorus treatment.

	Flowering (50%)		60DAS		Maturity	
	HP	LP	HP	LP	HP	LP
55-437	0.049a	0.044a	0.25a	0.17b	0.25a	0.18a
ICGV 97183	0.045a	0.034a	0.28a	0.24ab	0.21a	0.21a
JL-24	0.046a	0.044a	0.27a	0.22ab	0.25a	0.16a
12CS-116	0.066a	0.058a	0.28a	0.26b	0.35a	0.25a
12CS-79	0.06a	0.041a	0.25a	0.24ab	0.27a	0.22a

4. Results

4.1. Low Phosphorus Stress Effect on Agromorphological Traits Under Lysimetre Conditions

Roots traits investigated in Exp.1 revealed any significant LP effect or genotypic variation on roots diameter. However, a significant genotypic variation was observed at 60 DAS for roots volume (RV) and indicated that ICGV 97183 and ICG 12991 showed the highest RV. LP stress also decreased significantly the roots length (RL) (Table 1) and roots length density (RLD) (Table 2). At flowering, pod filling and maturity times, the roots length decrease was 18, 20 and 24% respectively while RLD decreased respectively up to 17, 21 and 25%. Under LP conditions, ICG 12991 revealed the highest RLD at 60DAS. Significant genotypic variation was observed at flowering, pod filling and maturity times for root dry matter (RDM) and revealed the highest values on 12CS-116 and ICG 12991 (Table 3). Phosphorus treatment effect on RDM was significant only at maturity time and showed 27% decrease due to LP. At harvest, ANOVA revealed that LP stress decreased significantly haulm weight (33%) and pods weight (27%). 12CS-116 and 12CS-79 showed higher pods weight than ICGV 97183, ICG 12991, 55-437 and JL-24 under LP stress. The highest haulm weight was observed on 12CS-79, 55-437, 12CS-116 and ICG 12991. As LP decreased the RL, RLD, RDM, pod and haulm weight, linear regressions were performed to determine any relationship between productivity and roots traits. Thus, at flowering time, pod filling stage and maturity date, the regression between decrease in pod and haulm weights and decrease, in RL, RLD and RDM showed significant relationship between RLD and pod, and haulm weight only at pod filling (60 DAS) stage (Figure 1).

	Flowering (50%)		60DAS		Maturity	
	HP	LP	HP	LP	HP	LP
ICG 12991	0.059a	0.045a	0.33a	0.28a	0.34a	0.23a
Mean	0.054	0.045	0.28	0.22	0.28	0.21
G (F prob)	0.324 ^{ns}	0.454 ^{ns}	0.716 ^{ns}	0.03*	0.487 ^{ns}	0.233 ^{ns}
Trt (F prob)	0.041*		0.016*		0.011*	
GxTrt (Fprob)	0.909 ^{ns}		0.799 ^{ns}		0.772 ^{ns}	

* = significant at 5% level. ns = no significant at 5% level. Means with the same letter are not significantly different within the same treatment

Table 3. Roots dried matter (RDM) under high (HP) and low phosphorus (LP) treatments at flowering, pod filling and maturity times in 6 groundnut genotypes. DAS = days after sowing, G = genotype, Trt = phosphorus treatment.

	Flowering (50%)		60DAS		Maturity	
	HP	LP	HP	LP	HP	LP
55-437	0.34ab	0.43a	4.22ab	3.5b	4.92b	3.06a
ICGV 97183	0.33b	0.31a	3.49b	3.89ab	4.17b	4.07a
JL-24	0.34b	0.40a	3.19b	3.54b	4.24b	3.39a
12CS-116	0.54a	0.50a	4.82ab	4.63ab	7.20a	4.75a
12CS-79	0.44ab	0.39a	4.13ab	3.94ab	5.55ab	3.71a
ICG 12991	0.46ab	0.41a	6.01a	5.72a	6.56ab	4.90a
Mean	0.4	0.4	4.31	4.21	5.44	3.98
G (F prob)	0.034*		0.025*		0.044 *	
Trt (F prob)	0.594		0.767		0.004*	
GxTrt (Fprob)	0.943		0.454		0.742	

* = significant at 5% level. ns = no significant at 5% level. Means with the same letter are not significantly different within the same treatment

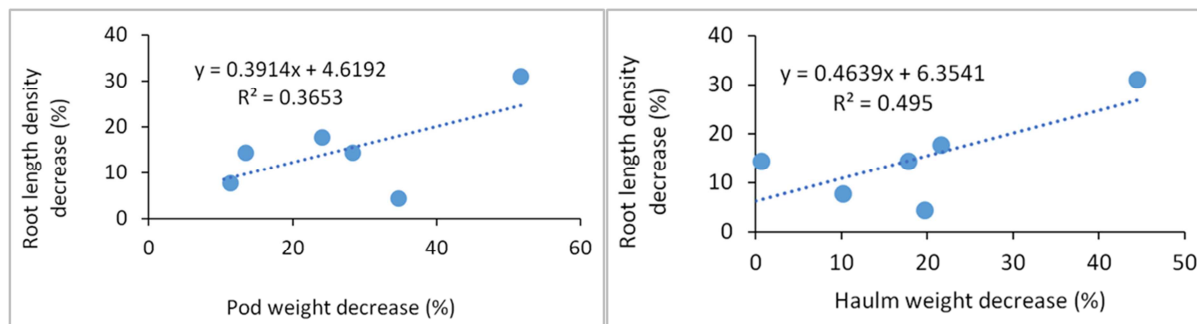


Figure 1. Relationship between decrease (%) in pod and haulm weights, and in root length density (RLD) due to LP at pod filling stage.

4.2. Genotypic Variation in Response to Combined Low Phosphorus and Water Stress (LPWS) Under Lysimetre Conditions

4.2.1. Water Extraction

Water extraction (Wex) measurement during Exp. 2 showed that LP plants extracted less water (4.4 kg plant⁻¹) than HP plants (5.2 kg plant⁻¹). Wex decrease was 6% due to LP and 46% due to WS. Under LPWW conditions, 12CS-116 and ICG 12991 showed high Wex. When LP stress was combined to WS, significant ($P = 0.001$) genotype (G), P treatment (Trt) and water regime (Wr) interaction (GxTrtxWr) was observed. Thus, under HP treatment, 12CS-79, 55-437 and ICG 12991 showed the highest Wex while under LP treatment the highest Wex was observed on 12CS-116, 12CS-79 and ICG 12991. LPWS plants extracted 51% less water than HPWW plants. Under LPWS 12CS-79, 12CS-116 and ICG 12991 extracted more water than 55-437, ICGV 97183 and JL-24. The TTW (sum of transpiration during WS period) data showed significant decrease under WS (67%) and LP (8%) conditions. The significant ($P = 0.004$) genotype and water treatment interaction (GxTrt)

observed indicated that under WW conditions, 12CS-79, 12CS-116, 55-437 and ICG 12991 transpired much water than ICGV 97183 and JL-24 whereas under WS conditions, 55-437 and JL-24 showed the highest TTW. Under both HP and LP treatments, 12CS-116, 12CS-79, 55-437 and ICG 12991 revealed higher transpired water than JL-24 and ICGV 97183. When LP plants were subjected to WS (LPWS), TTW decrease was up to 69%, the highest TTW was observed on 55-437 and JL-24.

4.2.2. Transpiration Efficiency

The transpiration efficiency (TE) significantly increased (11%) under WS while it decreased due to LP stress (8%). ICGV 12991 revealed the highest TE (2.29 mg g⁻¹) under WS conditions whereas under LP conditions, ICGV 12991, ICGV 97183 and JL24 had the highest TE (2.03 mg g⁻¹, 2.08 mg g⁻¹ and 2.083 mg g⁻¹ respectively). Correlation between TE under HP and TE under LP revealed significant ($r^2 = 0.81$) only under WS (Figure 2a, b). Relationship between TTW under HP and LP showed high correlations under both WW and WS conditions (Figure 2c, d). TE was also significantly correlated ($R^2 = 0.7$) to pod weight only under WS conditions (Figure 3e,

f, g, h). The regression between TTW and pod weight revealed also high correlations under HPWW, LPWW, LPWS and

HPWS treatments (Figure 3a, b, c, d).

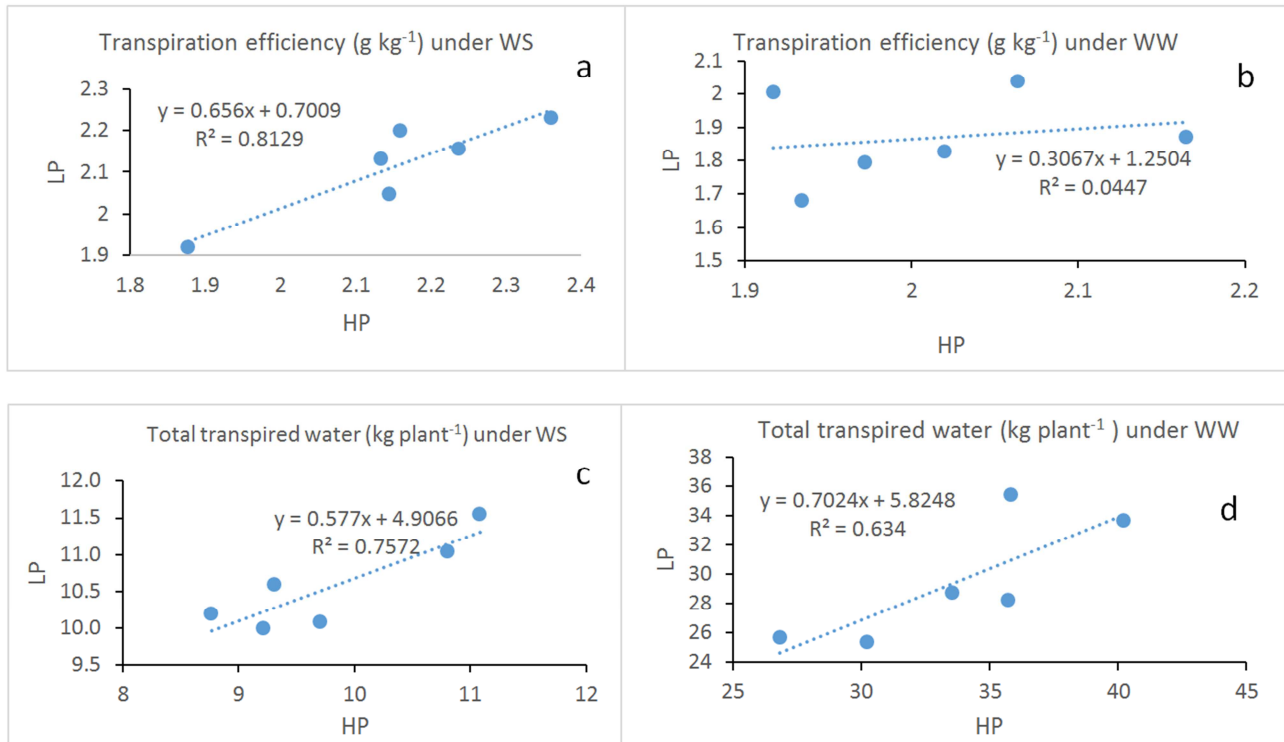
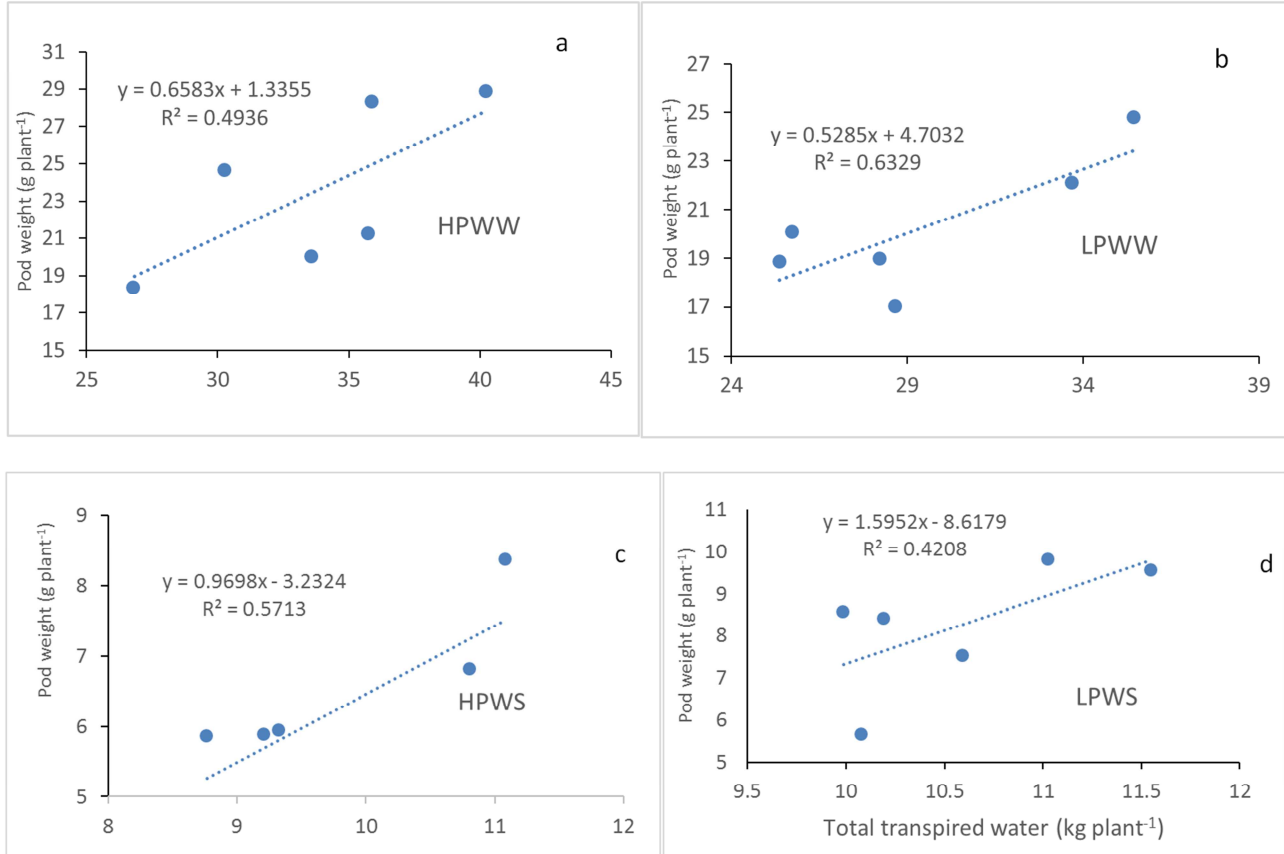


Figure 2. Relationship between transpiration efficiency (a) and (b), total transpired water (c) and (d), under low P (LP) and high P (HP); well watered (WW) and water stressed (WS) conditions.



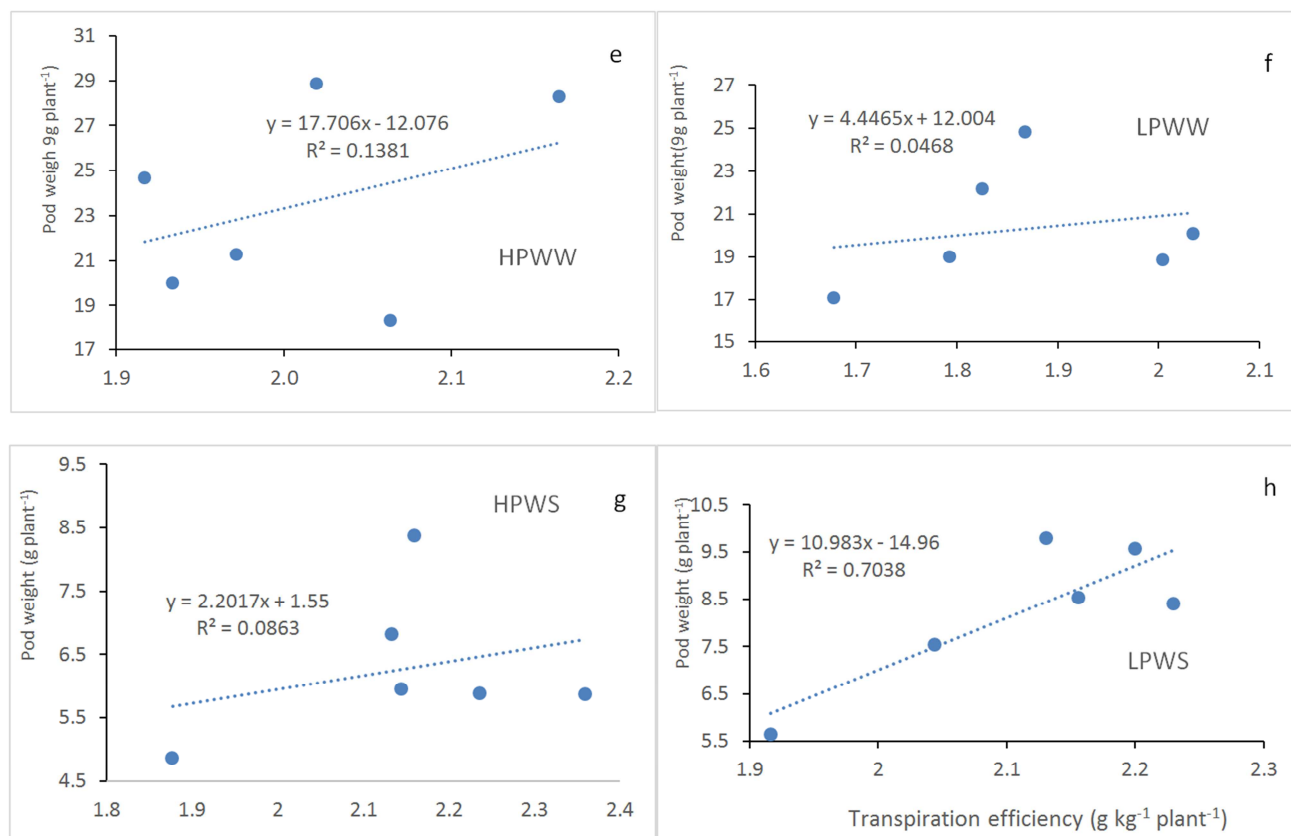


Figure 3. Total transpired water (a, b, c, d) and transpiration efficiency (e, f, g, h) relationship to pod weight under HP, LP and well watered (WW), water stressed (WS) conditions.

5. Discussions

5.1. Genotypic Performance Under Low Phosphorus Stress

Selection of varieties with desirable root morphological traits can be an effective way to expand their ability to acquire water and nutrients. It was reported that the ability of crops to absorb nutrients and water is closely associated with root morphological traits [39, 40]. In Exp.1, investigations on roots traits at 50% flowering, pod filling (60 DAS) and maturity (90 DAS) stages under LP conditions showed that LP stress decreased significantly the RL, RLD and RDM. However, a genotypic variation was observed which indicated that genotypes 12CS-116 and ICG 12991 revealed the highest RLD and RDM under LP conditions. In addition, correlation between productivity (pod and haulm) and roots traits under LP conditions showed that at pod filling stage (60 DAS), high pod and haulm weights were associated with high RLD. These findings showed that RLD and RDM contributed to the performance of 12CS-116 and ICGV 12991 under LP conditions. [20] Shen et al. (2001) found that under LP conditions, tolerant groundnut genotypes can extract phosphorus thanks to phosphorus solubilizing active substances from the root cell wall. This study findings suggest that 12CS-116 and ICGV 12991 revealed tolerant to LP stress and, RLD and RDM revealed LP tolerance related traits in groundnut.

5.2. Low Phosphorus and Drought Stresses Interaction: Genotypic Performance for Water Extraction and Use

Results on water extraction (Wex) during Exp.2 showed that LP plants extracted 800g plant⁻¹ less water than HP plants. LP effects on plant growth resulting in biomass decrease could explain the water uptake reduction of LP plants compared to HP plants. WS decreased Wex up to 46% and 51% when WS associated to LP stress (LPWS). This indicates that when LP and drought stress interacted, their effect on Wex was higher than individual one. The significant GxTrtxWr interaction observed indicates that Wex varies according to P and water treatments. It also indicates difference in water requirement and use among the genotypes within water and P treatments. Under LPWW conditions, highest Wex was observed on 12CS-116 and ICG 12991 which showed high roots development (RLD, RDM). Previous works in groundnut reported that under LP conditions, tolerant genotypes exhibited increased performance in various root traits and accumulated more root and shoot biomass and P [19]. Analyzed data of Wex under WS revealed that genotypes 12CS-116, ICG 12991 and 12CS-79 extracted more water than 55-437, ICGV 97183 and JL-24. These findings suggest that RLD and RDM contributed to Wex in 12CS-116 and ICG 12991 under LP and WS (LPWS) although there is a lot of controversy around roots traits

contribution to Wex [41]. Indeed, authors [42, 43] demonstrated that drought tolerant genotypes had higher water extraction than sensitive genotypes under drought conditions. Water extraction under drought stress contributes to dehydration avoidance strategy although high water extraction ability leads to quick soil water depletion when the drought stress endured [44]. It was found that total water extracted from the soil profile did not relate directly to the pod yield [45]. In this study, transpiration was measured to investigate canopy contribution in LP and WS response. It was observed that TTW decreased up to 8% under LP, 67% under WS and 69% under LPWS conditions. Reduction of leaf area observed in LP plants (data not shown) could explain their TTW decrease. In chickpea, [21] found a positive correlation between leaf P concentration and transpiration rate of the young fully expanded leaves. Low transpiration under WS revealed stomatal closure to conserve water while high transpiration led to quick depletion of water in the reservoir [46]. Under LPWS, high TTW observed on 55-437 and JL-24 compared to 12CS-116, ICG 12991, ICGV 97183 and 12CS-79 suggests that 55-437 and JL-24 used drought tolerance strategy while the other genotypes used drought avoidance strategy. The significant and high correlation observed between TTW and pod weight in this study indicates that high TTW was an attribute of pod yield under both P and water treatments. This study findings support this idea as 55-437 and JL-24 with highest TTW showed high pod weight under LPWS conditions. Investigations on TE revealed a significant increase under WS, a decrease under LP stress while the combined effect of WS and LP stresses led to TE decrease. In peanut, [4] observed increased TE as well as increasing chlorophyll density due to thicker leaves under drought stress. The contrary effect of WS and LP stress on TE when they were imposed separately indicates that factors driving TE could be different. Authors reported that reducing stomatal conductance would lead to TE increase [47]. A TTW decrease was observed in this study, consequently, a stomatal conductance decrease to reduce transpiration under WS could explain the TE increase. [45] demonstrated also that TE difference among genotypes could have been driven mostly by the stomatal conductance regulation under high VPD. As for TE decrease under LP stress, photosynthetic activity could be the predominant factor influencing TE. Indeed, authors reported that phosphorus deficiency affecting the concentration of photosynthetic pigments or the leaves thickness could have reduced photosynthetic activities resulting in TE decrease [21, 45]. The TE decrease resulted from LPWS suggest that negative effect on photosynthetic activities predominated when LP and WS interacted. The findings of this study showed also that TE correlated tightly ($R^2 = 0.7$) to pod weight only under LPWS suggesting that TE explains a large part of pod yield variation under water and P stress conditions. Thus, LPWS tolerant genotype should show high TE.

6. Conclusion

Drought and low P stress affected growth and yield components in groundnut. This study showed that RLD and RDM were associated to high pod and haulm yield under LP and revealed tolerance related traits. Although LP stress led to less water extraction, the highest yielding genotypes extracted more water and showed the highest RLD and RDM 60 DAS. The decrease of Wex, TTW, pod and haulm yields was high when LP and WS (LPWS) were combined indicating that their negative effects increased when they interacted. TE increased under WS while it decreased under LP and LPWS conditions. These findings suggest different factors driving TE in groundnut response to LP and drought stress. The high correlation of TE and pod yield under LPWS suggests that TE was associated to LP and drought tolerance. Under LPWS conditions, different pattern of water extraction and use was observed among investigated genotypes. 12CS-116, 12CS-79 and ICGV 12991 revealed water savers or dehydration avoidant as they extracted much water and transpired less while 55-437 and JL 24 which showed high transpiration revealed wasteful water or drought tolerant.

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