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Root Architectural Development and Yield Sensitivity of Phosphorus Tolerant Common Bean under Low Soil Phosphorus and Drought

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Authors' contributions

This study was carried out in collaboration amongst all authors. Author NM conducted this study as part of her Ph.D. studies, she designed, implemented the experiment and analysed data. Author JST co-designed and supervised the study implementation. Authors EO and TAB provided technical input in the implementation of the research. All authors participated in the development of the manuscript and approved it for publication.

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ABSTRACT

Aims: The study assessed the effect of limited soil phosphorus and drought on yield sensitivity and root architectural development of low phosphorus tolerant common bean *(Phaseolus vulgaris* L.) materials

Study Design: This was a randomised complete block design in which 2*3*5 factorial treatment combinations of drought, P levels and genotypes, respectively.

Place and Duration of Study: The study was carried out in Central Uganda; Nakasongola representing a drought-stress and Mukono Zonal Agricultural Research and Development Institute

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(MUZARDI) representing non-drought-stress for two rainy seasons (March-June and August - December 2014).

Methodology: In each study site, four low phosphorus tolerant genotypes (AFR703-1, AFR708, JESCA, and MCM2001 using K131 as a local check) were planted in plots treated with 0, 60 and 160 kg P ha^{-1} in the form of Triple Super Phosphate.

Results: The P-treatments neither had significant influences on grain yield nor root response; and no significant interactions with drought and genotypes. Yield did not significantly vary by drought treatments, but by genotypes (P<0.001), with AFR708 registering the highest yield of 1122 kg ha^{-1}. Drought-stress induced significant root development, namely adventitious roots, tap and lateral root lengths, and total root lengths, in some genotypes. Genotype AFR703-1 and AFR708 had an edge over the local check; they produced multiple root systems.

Conclusion: Under drought stress, the AFR gene pool was superior in root development, namely number of adventitious and lateral roots, and taproot and lateral root length. In contrast, grain yield of these materials was suppressed by drought stress.

Keywords: Phaseolus vulgaris; drought-stress; multiple root systems; climate changes.

1. INTRODUCTION

Plant-available phosphorus in the soil, together with drought are key abiotic factors severely constraining common bean production, especially in resource-constrained Sub-Saharan African farming systems [1-4]. The two constraints frequently co-exist in soils of the tropics and impact on bean production by well over 60% [1,5-8]. The supply of plant-available P declines along with decreasing soil moisture [9,10], thus the changing climate from wetter to drier conditions aggravates the situation.

Root architecture is a significant component in the performance of common beans grown under low soil P levels and drought conditions. Depending on their architecture, root systems govern the ability of a plant to access nutrients and moisture in a wide range of the soil [11]. Moreover, P is a sparingly mobile nutrient that resides largely in the topsoil layers. Consequently, root systems that dwell more in topsoil explore it and take advantage of P acquisition [12-14]. Conversely, soil moisture is often more abundant in the deeper soil horizons, especially during dry periods; thus, the deeper the root system the more the plant will access moisture [3,11,15].

Based on architectural root traits, selection of genotypes has resulted in improved root systems that perform well either under low soil P availability or drought conditions. Studies show that some plants have abundant diverging patterns of root systems in both top and sub-soil layers, which enhance efficient absorption of P and soil moisture. Suriyagoda, Ryan [7] reported that roots of some Australian native perennial legumes explored extensively, the top and lower layers of soils deficient in both plant-available P and moisture, respectively. A study carried out by Morino, Obrador [6] on Mediterranean shrubs, also revealed that some plant species had sufficient root systems in different soil layers, enabling them to utilise both P and moisture. Thus, improved low P tolerant and drought resistant genotypes have been investigated, but implementation of the results is yet to be promoted [4]. Besides, the response of architectural root traits to the combined effects of low levels of P and moisture deficit in soils has received less attention in common bean because the architectural root traits have been explored independent of the two abiotic constraints. It is not clear whether the yield sensitivity of the P-tolerant genotypes can be stimulated or compromised by the combined effects of low P and drought. It also remains to be investigated the changes in root architecture of these genotypes in response to the combined effects.

It has been observed that common bean genotypes adapt with varying capacities to low levels of P and drought conditions. This may be explained by their different abilities to acquire P and moisture from the soil. Beebe, Rao [8] demonstrated that selection of common bean genotypes to overcome the impact of drought enhanced yield in P limited conditions. A study conducted by Ho, Rosas [11] on root architectural trade-offs for water and P acquisition reported that the shallow-rooted BAT 477 developed a deep root system that increased utilization of P in soils deficient of the nutrient and moisture. Thus, synergism within the root system might be central for adaptation in common bean genotypes to low levels of plant-available P and moisture in the soil. The objective of this study was to assess the effects of limited phosphorus and drought on yield sensitivity and root architectural development of low P-tolerant bean (*Phaseolus vulgaris* L.) materials. The study tested the hypothesis that some low P-tolerant bean genotypes have multiple root systems for both P and soil moisture acquisition.

2. MATERIALS AND METHODS

2.1 Description of Study Sites

A field experiment was carried out in Mukono and Nakasongola districts of central Uganda, during two rainy seasons (March-June and August-December 2014). Mukono District is located at 00º 15’ 00” N latitudes and 32º 30' 00" E. It is characterised by bimodal rainfall seasons with a mean annual rainfall of 1100-1600 mm. The district has a mean annual maximum temperature of 25 to 28ºC and minimum annual temperature of 15 to 18ºC [16]. This site represented the non-drought-stressed environment, herein referred to as non-drought-stress (NDS) treatment. Nakasongola District is located in the cattle corridor and is one of driest districts in Uganda. It lies between 1º 19' 60" N and 1º 19'58" N, and 32º 30' 00" E. The district receives 500 to 1000 mm of rainfall *annum*$^{-1}$ and experiences a five-month long dry period. The district is characterised by extreme spatial and temporal rainfall variability and experiences high frequent and severe droughts (Kisamba-Mugerwa, 2001 unpublished). This site represented the drought-stressed environment herein referred to as drought-stress (DS) treatment.

2.2 Soil Measurements

For pre-experimental characterisation at each site, soil samples were collected at a depth of 0-20 cm before the plots were prepared. The samples were air-dried and analysed for pH in water (1:1), total N, Bray-1-extractable-P and organic matter. Other properties included exchange cations (K+, Ca^{2+} and Na+). Total N was determined by Kjeldahl digestion process followed by colorimetric procedure and the rest were determined by procedures described by Page, Miller [17]. Laboratory data are presented in Table 1.

2.3 Field Experiment

Treatments included four low P-tolerant common bean (*Phaseolus vulgaris* L.) genotypes; AFR 708, AFR 703-1, JESCA and MCM 2001, tested against K131 as a local check. AFR 708, AFR 703-1, MCM 2001 and K131 are crosses of Mutikired/AFR308, Bean98/ZAA39//ZAA39, IVT831629/BAT1554 and IVT831607/RAB71, respectively. AFR 703-1 and AFR 708 are Andean materials. The rest of the genotypes are of Mesoamerican origin (Dr. Clare Mukankusi Clare, Regional Breeder, East and Central African Bean Network, Kampala Uganda, pers. comm.). The materials were obtained from Bean Research Program of the International Centre for Tropical Agriculture (CIAT) in Uganda. The genotypes were planted in plots treated with P levels of 0, 60 and 160 kg ha^{-1} in the form of Triple Super Phosphate (TSP) in each drought treatment. This was to assess possible drought effects on their tolerance under low P supply. The experiment was arranged in a factorial structural combination of drought treatment, P levels and low P-tolerant common bean genotypes. All treatments were in triplicates and were laid out in a randomised complete block design (RCBD). Plants were spaced at 60 cm between and 20 cm within rows, giving a plant density of 213,333.3 plant ha^{-1}. The experiment was repeated once; in blocks a few meters away from the first blocks in both districts.

Table 1. Physical and chemical properties of the experimental soil (0-20 cm)

Soil characteristics and its unit	Drought-stress (DS)	Non-drought-stress (NDS)	P-value
Soil pH (H_2O)	6.32	6.11	0.45
Organic matter (%)	2.22	2.44	
Total N (%)	0.16	0.14	0.340
Bray-1 P (mg kg^{-1})	8.4	7.1	0.120
Exchangeable bases (cmol. 100 g^{-1}):			
Na^+	0.25	0.52	0.060
K^+	0.32	0.28	0.277
Ca^{2+}	8.17	9.84	0.045
Soil textural class	Sandy loam,	Loam	

T-test performed and mean differences are based on null hypotheses of H_0: difference = 0

Seeds were inoculated with Rhizobium tropici CIAT899 strain, provided by the Biological N_2 fixation laboratory of the School of Agricultural and Environmental Sciences, Makerere University. Four inoculated seeds were sown manually; and seedlings were thinned to two plants per hill at 14 days after emergency (DAE). Weeding was done manually with hand hoes at 28 and 49 days after planting. Pests for common beans were controlled using Tafgor-40-EC (Dimethoate 40% inflammable) at 600 ml ha^{-1}.

2.4 Data Collection and Analysis

Climate data on the amount of rainfall, number of rainy days, minimum and maximum temperatures were collected from the sites using rain-gauges placed within the study sites. The climate data are presented in Table 2.

For root measurements, destructive sampling was used whereby five plants were carefully uprooted from the middle of each plot, using a random sampling procedure at mid-pod formation stage depending on the genotypes. The plants were bagged in polyethylene before being washed with tap water. They were then left to drip for a 20-30 minutes and placed flat on graph paper. The roots were separated into adventurous, basal and tap roots, and lateral roots on the tap root.

The number of roots, together with their root hairs were counted and root length were measured using a ruler, after which the roots were oven-dried at 80ºC for 48 hr and dry weight determined using a digital balance with a precision scale up to +0.001. Specific root length (SRL) was calculated as total length per unit of root dry weight. Root hairs were visually counted under a magnifying lens of X40 resolution. The root to shoot ratio was also determined as a proportion of root biomass to shoot biomass. Pod height was measured at physiological maturity on five sampled plants per plot, using a ruler. The number of pods per plant and seeds per pod were also determined by counting, respectively, pods and seeds on the same plants. Total grain yield was recorded by harvesting the plants in the entire plot, and the weight of the total grains measured using a digital electronic balance. The weight of 100 seeds was determined on seeds randomly collected from all plants harvested per plot.

2.5 Statistical Analysis

Normality for all the variables was tested by Shapiro-Wilk test [18]. All the root variables were normal (P=0.05). Data for the two seasons were tested for homogeneity using Bartlett's test [19] before the combined analysis. According to the Bartlett's test for homogeneity of variance, the adventitious roots, basal root hairs, length of tap root $plant^{-1}$ and total yield were homogeneous (P<0.001). However, the number of adventitious root hairs, basal roots, taps root hairs, lateral roots plant tap $root^{-1}$, length of lateral roots on the tap roots, total root length, stem biomass, shoot biomass, root biomass and root to shoot ratio, were not homogeneous across the two seasons at 5% level of significance. Therefore, to test mean differences, a combined analysis was carried out by a Generalised Linear Model (GLM) with a random statement using StataSe statistical package, 11^{th} edition. A simple correlation was used to establish the relationship between root characteristics and yield; and yield components of low P tolerant bean genotypes.

Table 2. Weather conditions during two rainy seasons of the study at the non-drought-stress (NDS) and drought-stress (DS) sites in Uganda

Season	Drought treatment	Total rainfall (mm $season^{-1}$)	Daily rainfall (mm day^{-1})	Number of rainy days	Daily mean min. temp. (°C)	Daily mean maxim temp. (°C)
March - June (A)	DS	241.0	2.38	29	18.4	30.1
March - June (B)	NDS	587.6	5.82	52	17.9	27.5
Mean Difference (A-B)		-346.6	-3.43 (p=0.007)	-23	0.53 (p=0.000)	3.08 (p=0.000)
August - December (C)	DS	256.1	2.54	28	18.0	29.8
August– December (D)	NDS	542.8	5.38	45	17.4	27.7
Mean Difference (C-D)		-286.7	-2.84 (p=0.014)	-17	0.60 (p=0.001)	2.32 (p=0.001)

T-test was performed and mean differences are based on null hypotheses of H_0: difference = 0. Values in parentheses are probability values

3. RESULTS

3.1 Yield and Biomass

The effect of P and its interactions with bean genotypes, drought or both were not significant (P>0.05) on grain yield and biomass production. Likewise, Drought treatments (DS and NDS) did not affect the grain yields significantly (Table 3), but grain yields from genotypes were significantly (*P*=0.05) different (Table 4).

The interaction between bean genotypes and drought on grain yield was also significant (*P*=0.05). The DS reduced grain yield of AFR 703-1 and AFR 708 by 31 and 42%, respectively, more than the check (Fig. 1); however, the grain yield of MCM 2001 was not reduced significantly.

Contrastingly, the differences in drought treatments neither affected accumulation of the below nor above-ground biomass of the bean plants (Table 3). However, genotype JESCA differed significantly in shoot biomass from the check, while JESCA and MCM 2001 produced lower root: shoot ratio than the check (Table 4).

The interactions between genotypes and drought treatment were significant on shoot and root biomass (Fig. 2). Genotype AFR 708 produced 29% more shoot biomass in the DS than the local check (Fig 2a). AFR 708 and MCM 2001produced 34 and 29%, respectively, more root biomass in the DS than the check (Fig. 2b); the biomass of AFR 703-1 and JESCA were not statistically affected by the interactions.

Table 3. Grain yield, root variables and biomass allocation in low P-tolerant bean genotypes under drought regimes

Root variables	NDS	DS	Difference
Grain yield (kg ha^{-1})	930	816	NS
Adventitious roots (numbers)	13.70	16.40	***
Adventitious root hair (numbers)	153	1181	**
Basal roots (numbers)	5.23	5.13	NS
Basal root hair (numbers)	320	202	**
Tap root hairs (numbers)	44.17	34.97	***
Tap root length (cm)	6.30	8.50	***
Lateral roots on tap root (numbers)	2.68	5.31	***
Length of Lateral roots on tap root (cm)	21.37	49.00	***
Total root length (cm)	173	186	NS
Specific root length (cm g^{-1})	304	300	NS
Shoot biomass (g plant^{-1})	5.07	4.60	NS
Root biomass (g plant^{-1})	0.62	0.69	NS
Root: shoot	0.14	0.15	NS

, **, *, indicate that treatment differences in the same row are significant at P= 0.05, 0.01 and 0.001, respectively; NS = non-significant*

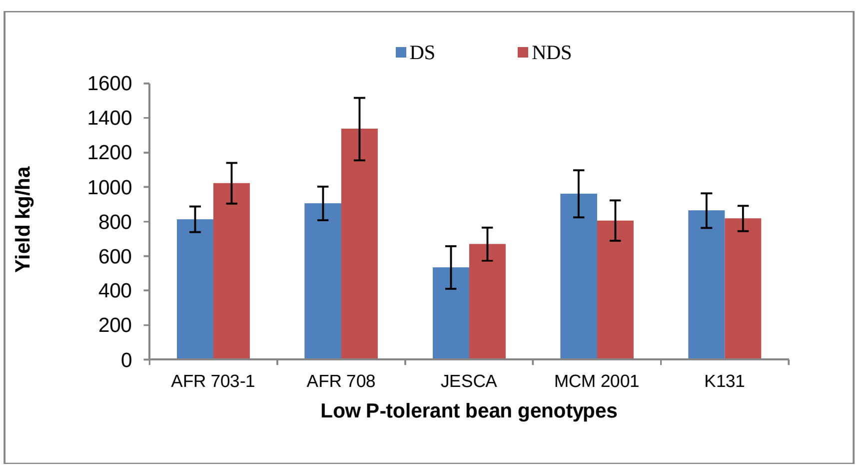


Fig. 1. Interactive effect of drought treatments and bean genotypes on grain yield. (Bars over the mean indicate standard error)

3.2 Root Architectural Responses to P-levels and Drought Treatments

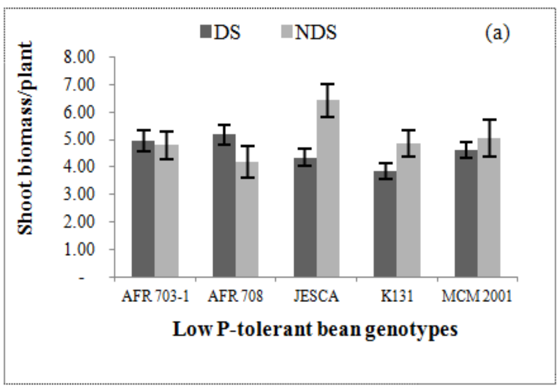
Application of P did not significantly affect bean root characteristics. Also, there were no significant interactions of P and drought treatments, genotypes or both (P>0.05). Common bean plants grown in the DS environment developed deeper taproots, longer and more lateral roots and more adventitious roots, than their counterparts growing in the NDS environment. In contrast, the plants had less root hairs in the DS than in NDS (Table 3). Genotypes significantly influenced the number of adventitious roots, tap root hairs, and tap root length, number of lateral roots and their lengths (Table 5). Genotypes AFR 703-1 and AFR 708 had more adventitious roots, adventurous root hairs, lateral roots on tap root plant, longer lateral roots, total root length and higher specific root length than the check. MCM 2001 had fewer tap root hair than the check, whereas the tap root length plant^{-1} was higher (P=0.05) in AFR 703-1 and lower (P=0.05) in MCM 2001 than the local check.

The interactive effects between drought treatments and bean genotypes on root variables are presented in Fig. 3. There were significant interactions between drought treatments and

Table 4. Influence of low P-tolerant bean genotypes on biomass production and grain yield

Genotypes	*Biomass variables*			*Grain yield (kg ha^{-1})*
	Shoot (g plant $^{-1}$)	**Root (g plant^{-1})**	**Root: Shoot**	
AFR 703-1	4.889	0.692	0.147	918
AFR 708	4.682	0.672	0.158	1122*
JESCA	5.390*	0.672	0.123**	603*
K131 [a]	4.363	0.679	0.160	884
MCM 2001	4.832	0.625	0.140*	842

, **, * indicate that the effect of genotype in the same column are significantly different from the check at P = 0.05, 0.01 and0.001, [a] = local check genotype*



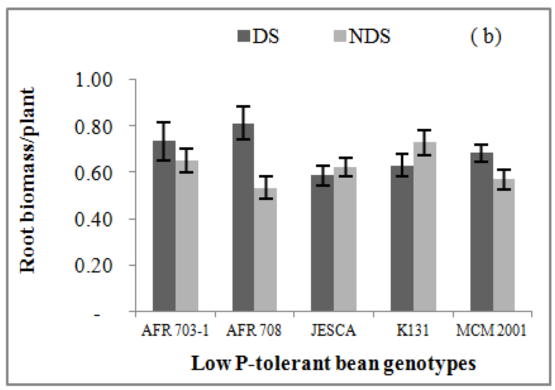


Fig. 2.The effect of drought treatments on (a) shoot biomass and (b) root biomass of the common bean genotypes. (Bars over means indicate standard error)

Table 5. Influence on root variables

Genotypes	**Root variables**							
	Adventitious roots #	**Adventitious root hair #**	**Tap root hairs #**	**Tap root length (cm)**	**Lateral roots on tap root #**	**Length of lateral**	**Total root length**	**SRL**
AFR 703-1	18.59 ***	1594*	39.29	8.659*	4.697*	45.14**	220.8***	364.6***
AFR 708	17.21 ***	1574*	39.32	7.912	4.963**	45.40**	206.6***	346.8**
JESCA	13.54	1286	39.64	6.838	3.092	25.47	161.8	286.3
K131 [a]	12.97	1186	43.32	7.371	3.699	30.51	161.4	259.9
MCM 2001	12.96	1141	36.26**	6.214*	3.535	29.41	148.3	253.4

**, ** and ***indicate significant different from a local check at P = 0.05, 0.01 and 0.001. SRL = Specific root length, # = numbers, [a]= local check genotype* genotypes on adventitious roots (P<0.001), number of lateral roots on the tap root and their lengths (P<0.001). The DS increased the number of adventitious roots (Fig. 3a), tap root lengths (Fig. 3b), number and lengths of lateral roots (Fig. 3c and d) in AFR 703-1 and AFR 708, compared to the local check. Drought stress significantly reduced the number of tap root hairs (P=0.05) in JESCA compared to the local check (Fig. 3e).

3.3 Correlations between Plant Parameters

The correlation between biomass with the grain yield; and yield components of low P-tolerant common bean genotype grown under drought and non-drought stressed conditions are shown in Table 6. Whereas shoot and root biomass were positively associated with grain yield under non-drought stress conditions, the tested biomass variables were not significantly associated with grain yield or yield component under the drought-stress.

The correlations between root variables and grain yield; and yield components were not significantly associated with the grain yield (Table 7). However, the adventitious roots, tap root length, lateral roots lengths, total root length and specific root length were positively associated with weight of 100 seeds under the drought-stress.

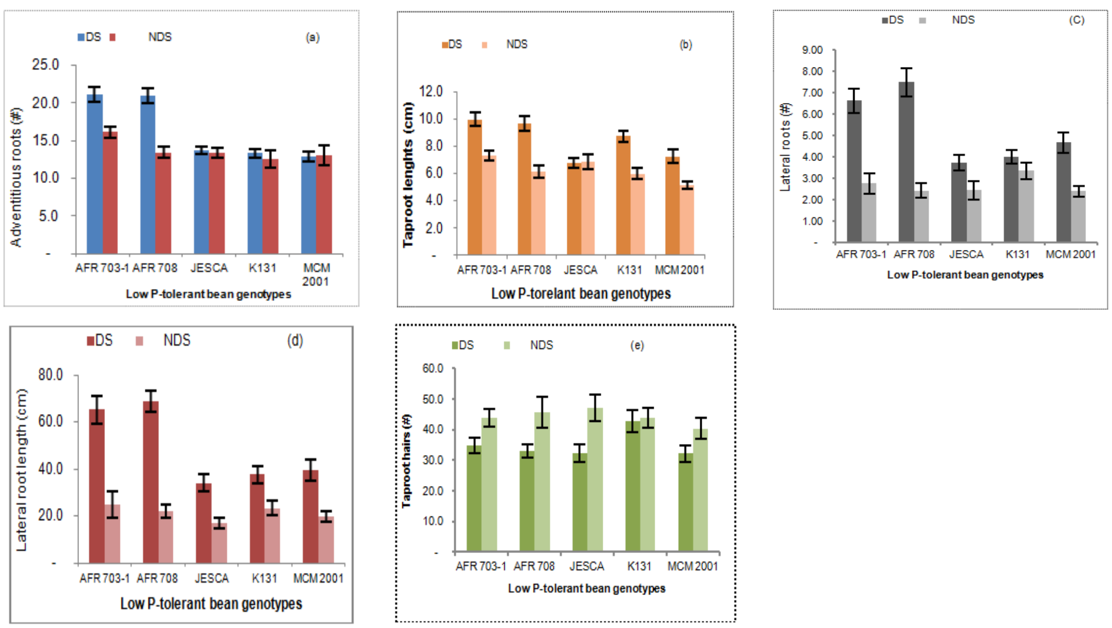


Fig. 3. Drought treatments and genotypes interactions on: (a) adventitious roots (#), (b) length of tap root and (c) Lateral roots (#), (d) length of lateral roots (cm), (e) tap root hairs. (Bars over the mean indicate standard error)

Table 6. Correlation coefficients (r) between biomass with grain yield; and yield components of bean genotypes grown under the drought treatments

Biomass components	Correlation under non-drought-stress (r)				Correlation under drought-stress (r)			
	Grain yield	Weight of 100 seeds	Pods plant^{-1}	Seeds pod^{-1}	Grain yield	Weight of 100 seeds	Pods plant^{-1}	Seeds pod^{-1}
Root biomass	0.40**	-0.17	0.48***	0.03	-0.13	0.19	-0.22	-0.03
Shoot biomass	0.36*	-0.14	0.47***	0.14	-0.14	0.21	-0.07	-0.03
Root: shoot	-0.29	0.06	-0.26	-0.20	0.03	0.03	-0.18	0.04

*The correlation is significant at *P= 0.05, **P =0.01, ***P<0.001*

Table 7. Correlation coefficients (r) between root variables and yield of bean genotypes grown under the drought treatments

Root variables	Correlation under non-drought (r)				Correlation under drought stressed (r)			
	Grain yield	Weight of 100 seeds	Pods plant^{-1}	Seeds pod^{-1}	Grain yield	Weight of 100 seeds	Pods plant^{-1}	Seeds pod^{-1}
Adventitious roots	-0.03	0.21	-0.13	0.14	0.06	0.72***	-0.02	0.06
Basal roots	0.16	0.22	-0.04	0.033	0.18	0.24	-0.36*	-0.35
Tap root length	0.11	0.18	0.13	0.04	-0.01	0.48***	-0.24	-0.22
Lateral root/tap root	0.07	-0.10	0.05	0.08	0.12	0.55***	0.05	0.05
Length of lateral roots	0.17	0.03	0.19	0.02	0.01	0.59***	-0.07	0.01
Total root length	0.20	0.28	0.10	-0.05	0.07	0.45***	0.04	0.11
Specific root length	-0.20	0.34***	-0.26*	-0.08	0.14	0.20	0.20	0.07

*The correlation is significant at *P= 0.05, **P =0.01, ***P<0.001*

4. DISCUSSION

The grain yield and root development of low P-tolerant genotypes used in the current study did not show significant differences (P>0.05) in relation to P application under different drought regimes. Similar findings were reported by Mourice and Tryphone [20], who observed that some low P-tolerant genotypes did not show significant response to increasing P levels in terms of yield. However, this was in disagreement with the study conducted by [12], which showed dominance in yield of P-efficient genotypes under low soil P levels compared to P-insufficient genotypes. Furthermore, the results revealed that low P-tolerant genotypes also have potential to perform equally well under combined different levels of plant-available P and moisture regimes. This is in agreement with [8], who reported that breeding for unfavourable condition did not hinder performance potential of the developed genotypes under favourable condition. This was further in disagreement with a study conducted by [13] that G19833; a low P tolerant genotype performed well in P deficient soils but poorly in P enriched soils. In the same study it was observed that AND696 performed well in P sufficient soil but poorly under low P soils. This suggests that the materials conserve their tolerance to low soil P supply in spite of their exposure to drought conditions.

Phosphorus levels did not influence the root variables that are associated to P acquisition and no significant interactions existed between P levels, drought treatments, or genotypes. However, that pattern was reversed in terms of root numbers and length for drought treatments (Table 3).The adventitious roots, tap root length, number of lateral roots as well as their lengths were significantly greater in the DS than in the NDS. Increased root length and rooting depth allow the crop to explore a larger soil volume and exploit the accessible soil moisture from deeper profiles, after the shallow roots have exhausted all the available moisture at the upper profiles [4]. Specifically, greater root length in the lower soil profile is a significant mechanism for drought resistance in common beans [11]. However, the grain yield in the present study did not significantly correlate with root variables under drought stress, possibly because the adaptations to unfavourable conditions by rooting mechanisms do not necessarily translate into yield [21]. Similar results were reported by Porch, Ramirez [22], who observed that BAT 477 with both shallow and deep rooted genotype did not yield better under interactive stressing conditions.

The low P-tolerant genotypes significantly differed in the number of adventitious, adventitious and basal root hairs; tap root length, number of lateral roots and their length, total and specific root length. Genotypes AFR 703-1 and AFR 708 registered considerably higher values in most of the root variables than the local check (Table 5). They equally possessed both shallow and deep root variables that provided them the capacity to exploit topsoil P and deep moisture resources, respectively. Similar results were reported by [11], that BAT 477 possessed both shallow and deep root systems. Suriyagoda, Ryan [7] too, reported that Cullen species developed both shallow and deep root systems when grown in low P soils under drought conditions. Our results have confirmed the hypothesis that some low P tolerant genotypes have multiple root systems for both P and soil moisture acquisition.

According to Suriyagoda, Ryan [7], root biomass is key for acquisition of soil resources that are limited in supply. Studies have revealed that root: shoot ratio rises with shrinking soil P levels [12,23] and moisture [9]. However, a higher allocation of biomass to roots and a lesser amount of shoots (root: shoot) in response to soil P deficiency and/or moisture deficit results into reduced plant growth, hence reduced grain yield production. This means that allocation of biomass to roots is done at the expense of the shoot biomass. However, in the present study AFR 708 which produced more root biomass in the DS than in the NDS did not do so at the expense of the shoot biomass. According to Ho, Rosas [11], common bean genotypes that are P tolerant and drought resistant produce higher root and shoot biomass and higher yields than the non-efficient genotypes. Therefore, since root and shoot biomass were positively associated with grain yield under NDS, they could be useful traits for exploitation in the selection of low P-tolerant bean genotypes under drought conditions.

5. CONCLUSION

Differences in phosphorus application rates had no effect on root architecture and grain yield of all genotypes. Genotypes AFR 703-1 and AFR 708 outperform the local check (K131) in terms of root development by the ability to develop the multiple root systems, especially under drought conditions. Overall, under drought stress, the AFR gene-pool proved superior in root development, namely number of adventitious and lateral roots, and taproot and lateral root length. In contrast, grain yield of these materials was suppressed by drought stress. The results have significant contributions for common bean breeding as far as improving performance of the crop under limited soil P and exploitation of moisture at different soil depths is concerned.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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