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Research Article

Uncovering adaptive mechanisms to water deficit in low soil phosphorus tolerant common bean genotypes

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Abstract - Water-Deficit and low soil phosphorus (P) are major constraints for common bean (*Phaseolus vulgaris* L.) cultivation in sub-Saharan Africa (SSA). Tolerant varieties offer cost-effective alternatives to irrigation and fertilizers. This study examines how low soil P-tolerant common bean genotypes adapt to Water-Deficit through leaf morphology, physiology, and root development in greenhouse and field conditions. AFR703-1, AFR708, and K131 were arranged in a completely randomized design under Well-Watered and Water-Deficit conditions, with P applied at 0, 6, and 16 mg P kg^{-1} soil. In the field, identical genotypes were arranged in a randomized complete block design with P applied at 0, 12, and 32 kg P ha^{-1} under Well-Watered and Water-Deficit Environments. AFR708 showed a significant ($P < 0.001$) reduction in RWC (26%) under Water-Deficit without P mitigated by higher P levels, while AFR703-1 and K131 showed no significant difference ($P > 0.05$) under similar conditions. AFR703-1 and K131 exhibited significantly ($P < 0.05$) lower specific leaf area in Water-Deficit than Well-Watered conditions, contrasting with AFR708. Similarly, LMR in the studied genotypes decreased ($P < 0.001$) and with rising P under Water-Deficit, with diverse trends in Well-Watered conditions. AFR703-1 and K131 recorded higher NAR in Water-Deficit than Well-Watered conditions, contrary to AFR708. AFR genotypes decreased significantly ($P < 0.001$) showed enhanced root development in Water-

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Deficit, including increased adventitious, tap, and lateral roots, higher total biomass, and finer root length compared to Well-Watered conditions, despite lower grain yields, notably in Nakasongola site. Overall, AFR703-1 holds promise as a breeding parent for enhancing Water-Deficit resilience and P tolerance in common bean production, despite yield reduction under stress conditions.

Keywords: *Phaseolus vulgaris* L., relative water content, specific leaf area, net assimilation rate, Uganda.

1. Introduction

Common bean (*Phaseolus vulgaris* L.) plays a central role in addressing malnutrition and gender inequality in impoverished households across sub-Saharan Africa (SSA), Southeast Asia, and Latin America. It serves as a vital dietary source of proteins, carbohydrates, essential minerals, and vitamins for both rural and urban populations. In SSA, common beans are estimated to provide over 50% of the dietary protein requirements for many households (Namugwanya et al., 2014). Annual per capita consumption is notably higher where access to animal protein is limited. For instance, in Eastern Africa, the per capita intake can reach 50 to 60 kg annually in countries such as Rwanda, Kenya, and Uganda, significantly surpassing the 4 kg and 17 kg per year reported in Colombia and Brazil (Beebe et al., 2013).

Beyond their nutritional value, common beans are an important commercial crop that significantly enhances the incomes of many rural farmers in SSA, particularly benefiting women. Their affordability and long shelf life make them accessible to financially constrained households. As a "woman's crop", common beans empower women economically, challenge traditional gender roles, and promote greater decision-making within families (Beebe et al., 2013). The cultivation and trade of common beans create vital economic opportunities that alleviate poverty and improve livelihoods. In Uganda, beans significantly contribute to the livelihoods of poor households, accounting for up to 9% of their annual income, and playing a vital role in poverty reduction. Nationally, beans account for approximately 6.1% of the agricultural GDP (Sibiko et al., 2013), emphasizing their valuable contribution to food security and national economic development, thus, demonstrating the critical role of common beans in both local and national contexts.

Despite its importance, common bean production is restricted by nutrient deficiencies, especially phosphorus (P) and nitrogen (N). The deficiency of P is particularly critical due to the high P fixation capacity of highly weathered tropical soils, which are rich in sesquioxides. These soils are acidic, leading to increased solubility of iron (Fe^{3+}) and aluminum (Al^{3+}), which precipitate the available forms of P, making them less accessible to plants (Balemi & Negisho, 2012). Phosphorus deficiency significantly impacts nitrogen nutrition in bean production, especially for resource-constrained farmers dependent on biological nitrogen fixation. Adequate P is essential for nodulation and efficient nitrogen fixation, crucial for maximizing bean yields. Nonetheless, many low-income households lack access to affordable inorganic P fertilizers (Benson et al., 2012; Okoboi & Barungi, 2012). Exploring low-cost strategies using adaptable materials to address low P levels is essential, particularly for female-led bean farmers with limited resources.

Breeding programs in tropical and subtropical regions have made significant advances in developing beans with low P tolerance, addressing P stress and N deficiency through biological nitrogen fixation

(Sulieman & Tran, 2015; Lazali & Drevon, 2021). Genetic and metabolic studies have elucidated the mechanisms behind low P tolerance, providing a scientific basis for these advancements (Beebe et al., 2013). Despite these advancements, practical application remains limited. Additionally, research often overlooks the impact of extreme climate events, such as soil water deficits, on these common beans.

Although common beans have evolved adaptive mechanisms to cope with P scarcity (Balemi & Negisho, 2012; Paz-Ares et al., 2021), shifting rainfall patterns create a significant research gap. Seasonal water shortages push the limits of low soil P-tolerant common beans, raising questions about their resilience against soil water deficit. Climate change exacerbates this challenge, as unpredictable rainfall patterns worsen P deficiency during water deficit, undermining the benefits of low soil P-tolerant bean genotypes (Cavalieri, 2011). With over 60% of global common bean yield losses attributed to water deficit environments (Soureshjani et al., 2019), it is clear that P availability and water deficit are intimately linked. This interplay highlights the urgent need for integrated nutrient and water management strategies to boost crop resilience.

Adapting to P deficiency and water deficit involves complex physiological, morphological, and biochemical adjustments. While improved root architecture and P uptake efficiency can alleviate some effects of low P and water deficit, the ability of a plant to survive under water stress also hinges on factors such as relative water content, net assimilation rate, and leaf morphology (Poorter et al., 2012). Low soil P-tolerant beans can optimize carbon gain through increased net assimilation and reduce water loss with adaptive leaf morphology. Understanding how these beans integrate P efficiency with water deficit tolerance is essential for enhancing crop resilience. This study hypothesizes that common bean varieties with low P tolerance use adaptive leaf and root mechanisms to mitigate the challenges posed by simultaneous P scarcity and water deficits, providing insights for refining breeding programs and selecting optimal parental lines.

2. Materials and methods

2.1 Description of study sites

This study comprised both field and greenhouse experiments. The field portion was conducted at two sites: one in Mukono district at the Mukono Zonal Agricultural Research and Development Institute (MuZARDI), representing a Well-Watered Environment, and the other in Nakasongola district at the Wabinyonyi site, representing a Water-Deficit Environment. This investigation spanned two rainy seasons in 2014, allowing for the analysis of differing rainfall conditions between the two districts. Mukono received optimal rainfall, while Nakasongola faced rainfall limitations, challenging the soil water requirements for a bean plant. The greenhouse experiment was also carried out at MuZARDI in 2020.

The Mukono site, situated in central Uganda at latitude 0.3333° N (0^0 20′ 0″ N) and longitude 32.7667° E (32^0 46′ 0″ E), sits at an altitude of 1189 meters above sea level (masl). Its climate is marked by a bimodal rainfall cycle, featuring a prolonged wet season from March to June and a shorter one from August to November. With annual rainfall averaging around 1200 mm, the temperature variations at the Mukono site typically range from 20 to 28°C. Meanwhile, the site received optimal rainfall during the study period, it was codenamed as a Well-Watered Environment (WWE). The soil composition at MuZARDI is predominantly red tropical soils (Ferralsols), which are known for their low levels of available P, posing a constraint for common bean production (GOU, 2004).

Nakasongola District, nestled within Uganda's Cattle Corridor, stands out as one of the country's driest regions.

Extending between latitudes 0° 57′ 44.89″ and 1° 40′ 42.76″ North and longitudes 31° 58′ 03.77» to 32° 48′ 00.29″ East, the area covers an altitude range from 129 to 1524 meters above sea level. Despite its geographical diversity, the district receives a modest annual rainfall of 915 to 1021 mm. It experiences an extended arid period lasting over five months, especially from June to August, during which evaporation exceeds rainfall by a factor of six (6) (GOU, 2004). Nakasongola is affected by extreme spatial and temporal rainfall fluctuations, often experiencing severe droughts. The lowest temperature ranges between 15.0 and 20.9°C; while the highest temperature peaks from 25.4 to 33.7°C (GOU, 2004). This site was designated as a Water-Deficit Environment (WDE), mirroring the dry conditions with limited rainfall during the study period. This emphasizes its classification within the semi-arid spectrum of Uganda's agricultural landscape. The dominant soil of the site consists of pale-yellow fine-grained sands (Gleyic Arenosols/Entisols) with reported low levels of available P for common bean production (Mfitumukiza et al., 2020).

2.2 Greenhouse experiment

The treatments included two low soil P tolerant common bean genotypes, AFR703-1 and AFR708 (hereafter referred to as AFR), and a check variety, K131. These were tested under two water conditions (Water-Deficit and Well-Watered) and three P levels (0, 6, and 16 mg P kg^{-1} of soil). Triple super phosphate (TSP) was used as the source of P. Treatments were arranged in a completely randomized design, with fifteen replications, and the study was repeated twice. Ten litre pots made of polyvinyl chloride (PVC), were filled with soil collected from MUZARDI fields after air-drying for seven days.

Bean seeds were sourced from the International Center for Tropical Agriculture (CIAT) Common Bean Breeding Program in Kawanda, Uganda. Seeds were Coated with the effective Rhizobium Tropici CIAT899 strain (Mak-Bio-N-Fixer), sourced from the Biological N_2 Fixation Laboratory at the College of Agriculture and Environmental Sciences, Makerere University-Uganda. To ensure optimal growth conditions, each pot received one carefully inoculated seed per genotype, planted at a depth of approximately 5 cm. Phosphorous fertilizer, in the form of TSP; was applied to the respective pots before initiating any water treatments.

All plants were initially grown under Well-Watered (WW) treatment for 22 days, after which Water-Deficit (WD) was induced in half of the pots, with exclusively distilled water utilized throughout the study. This approach ensured consistency in experimental conditions by eliminating impurities and confounding variables. It allowed for a controlled environment to accurately assess the effects of water deficit and phosphorus deficiency on plant growth. A day before imposing Water-Deficit condition, two plants (pots) per treatment combination were harvested to measure initial plant biomass. The remaining pots were soaked with water overnight. The next day, polyethylene sheets were placed over the soil in all pots to prevent water loss through evaporation. Pots under WW condition were gradually reduced to soil moisture levels 200 g, lower than the original weight, to prevent anaerobic conditions; a protocol consistently maintained throughout the study. Pots subjected to Water-Deficit were allowed to dry down, and received water only when the net loss of soil water exceeded 60 g day^{-1}, with any excess added (Devi et al., 2009). Soil water levels were monitored daily by weighing all pots.

Plant parameters measured included (i) relative water content (RWC), (ii) Net Assimilation Rate (NAR), (iii) Specific Leaf Area (SLA), (iv) Leaf Mass Ratio (LMR), and (v) Relative Growth Rate (RGR). The RWC of plant leaves was assessed on two randomly selected plants per treatment combinations, at three phytomer positions, namely at basal, medium, and apical, on fully expanded leaves, this was done at 13 and 23 days after initiating the Water-Deficit treatment (days of Water-Deficit -DWD), representing 35 and 45 DAP. Leaf discs were excised and their fresh weight was measured. Then, the discs were immersed in distilled water to record their turgid weight. The discs were dried using an adsorbent paper, before determining their dry weight. The RWC (%) was calculated according to Rosales et al. (2012).

For RGR (Relative Growth Rate) and its components, two plants were sampled at each stage of sampling, which occurred at 22, 35, and 45 days after planting (DAP). Leaf area was estimated by counting grid squares traced around fully expanded leaves (Dey et al., 2019). Biomass data, including total plant, leaf, stem, and root biomass, were determined after oven-drying at 80^{o}C for 48 hours. The determination of RGR, NAR, SLA, and LMR entailed utilizing different equations incorporating parameters such as dry weight, leaf area, and time according to Taulya et al. (2014) and Shibuya et al. (2016).

2.3 Field experiment

Treatments (bean genotypes and soil water treatment levels) were maintained in the greenhouse. The genotypes were grown in plots treated with different P levels: 0, 12, and 32 kg P ha^{-1}, codenamed as P0, P12, and P32 kg P ha^{-1} of Triple Super Phosphate (TSP) according to Lunze et al. (2007). Treatments were laid out in a randomized complete block design and replicated three times. The plot size measured 3 m by 3 m, with plants spaced 60 cm between rows and 20 cm within rows for optimal growth. Water-Deficit in the field was presumed to be the difference in soil water between the Well-Watered Environment (Mukono site) and Water-Deficit Environment (Nakasongola site).

The assessment of Water-Deficit relied on climate data, including rainfall, minimum and maximum temperatures, and evapotranspiration (ET0) calculated using the FAO Blaney-Criddle formula. The severity of Water-Deficit was gauged by a water Deficit Intensity Index (DII), with values between 26 and 50, indicating moderate stress and over 50; signifying severe stress (Sivakumar et al., 2011). Climate data monitoring encompassed rainfall quantity, the frequency of rainy days, and evapotranspiration. Rainfall measurements were obtained using rain gauges positioned within each study site. Supplementary rainfall and rainy-day data were sourced from regional agro-meteorological centres located at Mukono Zonal Agricultural Research Development Institute (MUZARDI) and Wabinyonyo for Mukono and Nakasongola Districts, respectively. The detailed results are presented in Namugwanya et al. (2018).

Soil sampling and analysis included collection of six sub-samples per block at a 0-20 cm depth, combined and quarter-sampled for approximately 500 g, following established Laboratory Methods of Soil and Plant Analysis (Estefan et al., 2013). At the mid-pod formation stage, root morphological traits were assessed by randomly selecting five plants. The roots were carefully separated, washed, and categorized into adventurous, basal, tap, and lateral roots on the tap root. The number of roots and their lengths were quantified using a 30-cm ruler, followed by oven-drying at 80 °C for 48 h to determine dry weight. The specific root length was computed as the total root length per unit of root dry weight (Kramer-Walter et al., 2016). Furthermore, the root-to-shoot ratio, which is the proportion of root biomass to shoot biomass, was analysed to provide valuable insights into the plant's below-ground architecture and resource allocation strategy.

2.4 Data analysis

Greenhouse and field data were analyzed separately. For greenhouse data, ANOVA was performed in Minitab 15 using a completely randomized design. Effects of water treatment, P, and genotypes were assessed, with LSD tests applied for mean separation at a 5% significance level. Multivariate analysis determined the contribution of measured plant traits to RGR within respective water levels, and model selection relied on AIC and BIC values (Hardin & Hilbe, 2018). The normal distribution of field variables was confirmed via the Shapiro-Wilk test, and non-homogeneity of variance was addressed through a combined analysis using a linear mixed-effects model (REML) in the Stata-SE Statistical Package (Field, 2009). Dunnett's test was used for mean separation (Lee & Lee, 2018). Visual representation of interactive effects of Water-Deficit, P, and genotypes was done in Microsoft Excel 2013.

3. Results

3.1 Plant leaf physiological and morphological responses

3.1.1 Relative water content

At 13 days of Water-Deficit (DWD), RWC remained consistent across water levels, but P levels significantly influenced RWC, showing an increase with higher P levels (Table 1). Genotypic differences were observed, with the low soil P tolerant genotype AFR708 displaying significantly ($P = 0.004$) higher RWC than the check genotype. The three-way interaction of water level, P, and genotypes was not significant at 13 DWD.

Table 1. Influence of water and P levels on relative water content of low soil P tolerant bean, greenhouse-Uganda

Factor	Level	Relative water content (%), n = 36	
		13 DWD	**23 DWD**
Water level	WD	77±2.10a	72±2.13a
	WW	80±2.00a	84±1.62b
Phosphorus	P0	75±2.21a	72±2.80a
	P1	78±2.66ab	78±2.58b
	P2	83±2.23b	85±1.69c
Genotypes	K131	78±1.90a	77±2.58a
	AFR703-1	74±1.92a	75±2.43a
	AFR708	86±2.53b	82±3.23b
Sources of variations			
Water level (W)		NS	<0.001
Phosphorus (P		0.04	<0.001
Genotypes (G)		0.004	0.007
W*P		NS	NS
W*G		NS	NS
P*G		NS	NS
W*P*G		NS	0.037

Note: *WW = Well-Watered; WD = Water-Deficit; DWD = days of Water-Deficit; P0, P1, and P2 represent 0, 6, and 16 mg P kg^{-1} of soil, respectively; K131 = check genotype; Means for a given treatment factor in the same column followed by the identical letters are not statistically different; NS = non-significance.*

Figure 1 (a) at 23 DWD, displayed a significant (*P = 0.037*) three-way interaction influenced leaf RWC, with AFR708 showing a notable reduction under WD without P. However, this difference diminished with increased P levels. While AFR703-1 and the check exhibited no significant RWC variations in WD without P compared to WW condition without P, AFR708 responded to P applied to the soil in WD conditions (Figure 1 a and b).

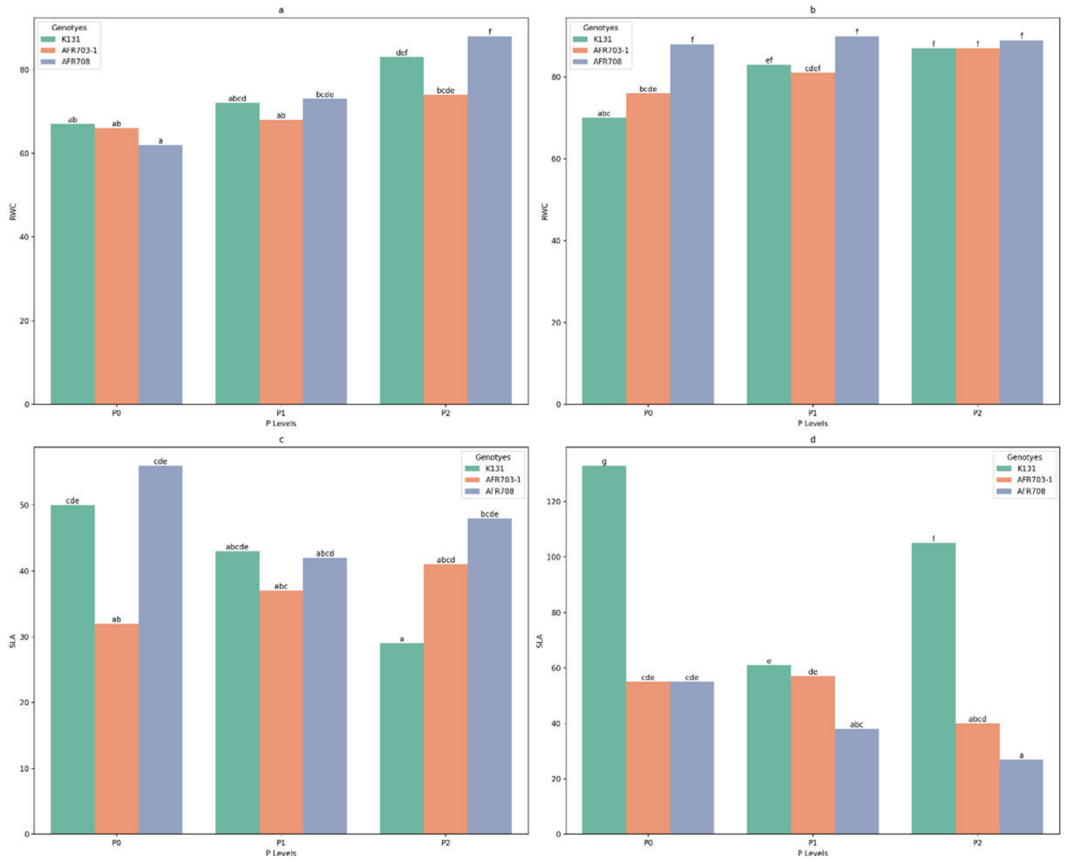

Figure 1. Interactive effect of water treatment, P, and genotypes on plant leaf relative water content (%) and specific leaf area ($cm^2\ g^{-1}$) assessed at 23 days of Water-Deficit, greenhouse-Uganda. *The plots on the left (a and c) illustrate Water-Deficit treatments, while those on the right (b and d) show Well-Watered treatments. RWC = relative water content; SLA = Specific Leaf Area. P_0, P_1, and P_2 denote phosphorus levels at 0, 6, and 16 mg P kg^{-1} of soil, respectively; K131 serves as the check genotype; Letters above each bar indicate statistical differences, with bars sharing the same letter not being significantly different from one another.*

3.1.2 Net assimilation rate

The three-way interaction of water treatment, P, and genotypes was not significant on the Net Assimilation Rate (NAR) at 23 DWD, but the interaction of water levels and genotypes was significant ($P < 0.01$). Genotype AFR703-1 and the check exhibited higher NAR values in WD compared to WW conditions, while AFR708 showed the opposite trend at 23 DWD (Table 2).

Table 2. Influence of water and P levels on net assimilation rate of low soil P tolerant beans, greenhouse-Uganda

Factor	Level	Net assimilation rate (g m^{-2} day $^{-1}$), n = 36	
		13 DWD	**23 DWD**
Water levels	WD	2.37±0.20a	3.25±0.41b
	WW	2.70±0.28a	2.33±0.22a
Phosphorus	P0	2.76±0.21a	2.23±0.38a
	P1	2.76±0.31a	3.18±0.47b
	P2	2.09±0.36a	2.92±0.37b
Genotypes	K131	2.45±0.24a	3.29±0.55b
	AFR703-1	2.81±.0.28a	3.00±0.31b
	AFR708	2.35±0.36a	2.07±0.27a
Sources of variations			
Water level (W)		NS	<0.001
Phosphorus (P)		NS	0.005
Genotypes (G)		NS	<0.001
W*P		NS	NS
W*G		NS	<0.001
P*G		0.019	<0.001
W*P*G		NS	NS

Note: *WW= Well-Watered; WD= Water-Deficit; DWD= days of Water-Deficit; P0, P1 and P2 represent 0, 6 and 16 mg P kg^{-1} of soil, respectively; K131= check genotype; NS= non-significance. Means for a given treatment factor in the same column followed by the identical letters are not statistically different.*

3.1.3 Specific leaf area

Table 3 summarizes Specific Leaf Area (SLA) results for low soil P-tolerant bean plants. At 13 DWD, neither main treatments nor genotypes significantly affected SLA ($P > 0.05$). By 23 DWD, SLA significantly differed with water treatment ($P < 0.001$), being higher in WW than in WD conditions.

Table 3. Influence of water and P levels on specific leaf area of low soil P tolerant bean, greenhouse-Uganda

Factor	Level	Specific leaf area (cm^2 g^{-1}), n = 36	
		13 DWD	23 DWD
Water level	WD	70±4.0a	42±2.2a
	WW	68±4.4a	64±7.9b
P	P0	70±3.1a	63±9.8b
	P1	71±6.1a	46±3.1a
	P2	66±5.7a	48±8.1a
Genotypes	K131[a]	77±5.3a	70±11.2b
	AFR703-1	64±4.7a	44±3.2a
	AFR708	65±4.6a	44±3.3a
Sources of variations			
Water-Deficit (W)		NS	<0.001
P		NS	<0.001
Genotypes (G))		NS	<0.001
W*P		NS	<0.001
W*G		NS	<0.001
P*G		NS	<0.001
W*P*G		NS	<0.001

Note: *WW= Well-Watered; WD = Water-Deficit; DWD = days of Water-Deficit; P0, P1, and P2 represent 0, 6, and 16 mg P kg^{-1}of soil, respectively; K131 = check genotype; Means for a given treatment factor in the same column followed by the identical letters are not statistically different; NS = non-significance.*

The interactive effect of water treatments, P, and genotypes was significant ($P < 0.001$) on SLA. In WD conditions, only check genotype K131 showed reduced SLA with increasing P levels (Figure 1 b), while in WW conditions SLA in AFR708 and the check decreased significantly with higher soil P levels (Figure 1 c). Across water treatments, genotypes AFR703-1 consistently exhibited significantly lower SLA in WD conditions without P compared to WW conditions without P.

3.1.4 Leaf mass ratio

Table 4 presents Leaf Mass Ratio (LMR) results for low soil P-tolerant common beans. At 13 DWD, a significant ($P < 0.001$) interactive effect of water, P, and genotypes on LMR was observed. AFR703-1 exhibited the lowest LMR in Water-Deficit (WD) conditions at 16 mg P kg^{-1} soil, while in WW condition, LMR in AFR703-1 significant ($P < 0.001$) reduced with increasing P. At 23 DWD, the interaction of water treatment, P, and genotypes was significant on LMR, revealing a significant ($P < 0.001$) decline in LMR in AFR genotypes as P increased in WD conditions, while an inconsistent trend was observed among genotypes in WW conditions (Table 4).

Table 4. Influence of water and P treatments on leaf mass ratio of low soil P tolerant bean, greenhouse- Uganda

Water level	P level	LMR AT 13 DWD			LMR AT 23 DWD		
		Genotypes					
		K131	AFR703-1	AFR708	K131	AFR703-1	AFR708
WD	P0	0.54cd	0.56cde	0.57cde	0.57f	0.56f	0.59g
	P1	0.54cde	0.46ab	0.57cde	0.44b	0.5d	0.56f
	P2	0.57cde	0.57cde	0.58de	0.64h	0.49c	0.54e
WW	P0	0.55cde	0.6de	0.56cde	0.55ef	0.47c	0.55ef
	P1	0.51ab	0.58cde	0.57cde	0.51d	0.59g	0.56f
	P2	0.61e	0.4a	0.58de	0.35a	0.45b	0.66i
Source of variation							
Water-Deficit (W)		NS			<0.001		
P		NS			<0.001		
Genotypes (G)		0.007			<0.001		
W*P		0.017			<0.001		
W*G		NS			<0.001		
P*G		0.001			<0.001		
W*P*G		<0.001			<0.001		

Note: *WW = Well-Watered; WD= Water-Deficit; DWD = days of Water-Deficit; P0, P1, and P2 represent 0, 6, and 16 mg P kg^{-1} of soil, respectively; K131 = check genotype; Means for a given treatment factor in the same column followed by the identical letters are not statistically different; NS = non-significance.*

2.1.5 Relative growth rate

In Table 5, significant two-way interactions between water levels and genotypes were observed for the Relative Growth Rate (RGR) at both 13 ($P < 0.05$) and 23 DWD ($P < 0.001$). At 13 DWD, the AFR genotype showed a significantly lower RGR than the check-in Water-Deficit treatment, while AFR708 had a smaller RGR than the check, and AFR703-1 did not differ significantly under WW conditions.

Table 5. Influence of water and P levels on relative growth rate of low soil P tolerant bean, greenhouse-Uganda

Water treatment	Relative Growth Rate at 13 DWD			Relative Growth Rate at 23 DWD		
	Genotype					
	KI31	AFR703-1	AFR708	KI31	AFR703-1	AFR708
WD	0.10c	0.06a	0.07ab	0.136d	0.092c	0.044a
WW	0.097bc	0.096bc	0.078a	0.080bc	0.063ab	0.077bc
Sources of variation						
Water-Deficit (W)	NS			0.017		
P	<0.001			0.030		
Genotypes (G)	0.007			<0.001		
W*P	NS			NS		
W*G	0.021			<0.001		
P*G	0.09			<0.001		
W*P*G	NS			NS		

Note: *WW= Well-Watered; WD = Water-Deficit; DWD = days of Water-Deficit; P0, P1, and P2 represent 0, 6, and 16 mg P kg^{-1} of soil, respectively; K131= check genotype; Means for a given treatment factor in the same column followed by the identical letters are not statistically different; NS = non-significance.*

At 23 DWD, a significant (P < 0.001) interactive effect of water level and genotypes on RGR was observed. The check (K131) had the highest RGR (0.136), followed by AFR703-1 (0.092), and the lowest value was recorded in AFR708 (0.044) under the Water-Deficit treatment (P < 0.05). However, under WW treatment, all test genotypes exhibited similar RGR values to the check at the same sampling stage (23 DWD; results omitted).

3.1.6 Association between Relative Growth Rate (RGR) and observed plant response traits

Table 6 displays two multivariate regression models; model 1, which considers only the components of RGR, and model 2 in which relative water content was introduced. Considering Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) values, model 2 provides the most suitable explanation for the relationship between RGR and the measured traits. According to model 2: MVREG RGR = LMR, SLA, NAR, RWC; the RGR significantly increased with increasing SLA (P < 0.01) and NAR (P < 0.001) when assessed under WW condition. Similarly, when assessed under the Water-Deficit condition; RGR noticeably increased with increasing LMR (P < 0.05), SLA (P = 0.05), and NAR (P < 0.001).

Table 6. Relationship between the measured response traits and relative growth rate based on multivariate regression analysis

Variables	Model 1		Model 2	
	WW	WD	WW	WD
	Coefficient	Coefficient	Coefficient	Coefficient
LMR	0.018	0.133*	0.022	0.131*
SLA	0.001**	0.001	0.001**	0.001*
NAR	0.041***	0.027***	0.040***	0.028***
RWC			0.000	0.001
Constants	- 0.07	- 0.110*	- 0.11	- 0.155**
R^2	0.80	0.93	0.81	0.95
P-valve	0.000	0.000	0.00	0.00
AIC	-104		-107	
BIC	-101		-102	

Note: *Model 1: MVREG RGR = LMR, SLA, NAR; Model 2: MVREG RGR = LMR, SLA, NAR, RWC; MVREG = Multivariate Regression, WW = Well-Watered; WD = Water-Deficit; RGR = Relative Growth Rate, LMR = Leaf Mass Ratio, SLA = Specific Leaf Area, NAR: Net Assimilation Rate, RWC = Relative Water Content, AIC = Akaike's Information Criterion; BIC = Bayesian Akaike's Information Criterion.*

3.2 Root development as an adaptive mechanism

3.2.1 Basal roots

In the Water-Deficit Nakasongola site, a significant interaction between P and genotypes impacted basal root numbers. AFR708 displayed significantly more basal roots than the local check at 12 kg P ha^{-1}, while AFR707-1 showed no differences at the same P level (Figure 2 a).

In the Well-Watered Environment (WWE), a significant P and genotype interaction influenced basal roots, with AFR703 and AFR708 showing higher basal roots than K131 when P was not applied (Figure 2 b). Evaluation of roots across study sites indicated no significant impact caused by variations in rainfall between sites on the number of basal roots per plant (Table 7).

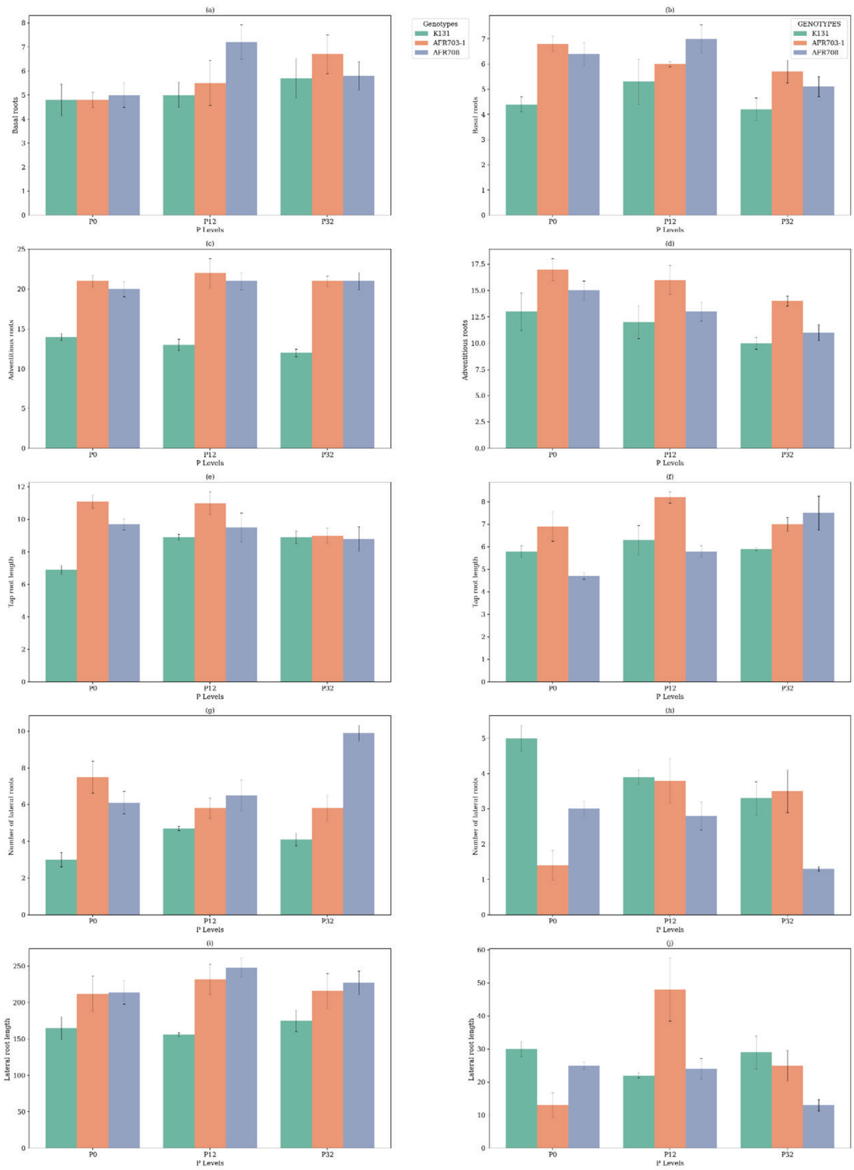

Figure 2. Influence of P on basal roots (#), adventitious roots (#), tap roots (cm), number of lateral roots, and lateral root length (cm) in low soil P tolerant bean assessed in Nakasongola and Mukono Districts, Uganda. *The plots on the left (a, c, e, and g) illustrate Water-Deficit Environment (Nakasongola site), while those on the right (b, d, f, and h) represent Well-Watered Environment (Mukono site). # = number; P0, P12, and P32 represent phosphorus at 0, 12, and 32 kg P ha^{-1}, respectively; K131 serves as the check genotype. Standard errors are represented by bars over the mean.*

3.2.2 Adventitious roots

In the Water-Deficit (WD) site, a notable interaction between P and genotypes affected adventitious roots. AFR703-1 and AFR708 exhibited 1.5 times more adventitious roots than the local check without P, with AFR708 surpassing the check at 12 kg P ha^{-1} under WD in Nakasongola (Figure 2 c). Similar trends were observed under WWE in Mukono, where AFR703-1 significantly produced more adventitious roots than the check at 12 kg P ha^{-1} (Figure 2 d).

There was a significant variation in the adventitious roots of AFR708 across different P levels, with a reduction in roots at 32 kg P ha^{-1} compared to the control (P0), while other genotypes showed no such variation. Comparing adventitious roots across environmental conditions, WDE significantly promoted more growth than in WWE (Table 7).

Table 7. Comparisons of root variables in the bean plant behavior in WDE and WWE conditions, Uganda

Root variables	WWE	WDE	Difference
Adventitious roots $plant^{-1}$ (numbers)	13	16	*
Basal roots $plant^{-1}$ (numbers)	5.3	5.5	NS
Taproot length $plant^{-1}$ (cm)	6.3	8.5	***
Lateral roots on tap root $plant^{-1}$ (numbers)	2.7	5.3	***
Length of Lateral roots on tap root $plant^{-1}$ (cm)	22	47	***
Total root length $plant^{-1}$ (cm)	176	186	NS
Specific root length (cm g^{-1})	271	315	*
Root biomass (kg ha^{-1})	117	109	*
Root-to-shoot	0.12	0.15	*

Note: *, **, ***, *designate that treatment variations within the same row are significant at* P = 0.05*, 0.01, and 0.001, respectively; NS = non-significant; WDE = Water-Deficit Environment (Nakasongola District); WWE = Well-Watered Environment (Mukono District).*

3.2.3 Tap roots

Significant tap root elongation variability among genotypes was observed under WDE, with AFR703-1 and AFR708 displaying significantly longer tap roots than the check. Similarly, the interaction between genotypes and P significantly influenced tap root length in WDE, with AFR genotypes exhibiting longer tap roots than the check without P application (Figure 2 e).

In Mukono, AFR703-1 exhibited significantly longer tap roots in WWE compared to the check, and the two-way interaction between P and genotype was also significant ($P < 0.05$). AFR703-1 was non-responsive to P, while tap root length in AFR708 increased with P application (Figure 2 f). Comparing environmental conditions, WDE significantly promoted longer tap roots in test genotypes and the check compared to WWE (Table 7).

3.2.4 Lateral roots

As displayed in Figure 6, the two-way analysis revealed significant ($P < 0.05$) genotypic differences in the number of lateral root development influenced by the interactive effects of P and environmental conditions. In WDE, the studied genotypes exhibited more lateral roots at P0, and only AFR708 showed an increase at 32 kg P ha^{-1} (Figure g).

Lateral root lengths exhibited a similar trend, with AFR genotypes in WDE developing roots 2 to 2.5 times longer than the check, and in WWE, notable genotypic differences were observed (Figure 2 i). The WDE in Nakasongola significantly ($P < 0.001$) promoted longer lateral roots in low soil P-tolerant bean plants compared to WWE in Mukono (Figure 2 j)

3.2.5 Total roots

Figure 3 (a and e) illustrates significant ($P < 0.05$) variations in total root length influenced by the interactive effects of genotypes and P in the Water-Deficit (WD) Nakasongola site and WW Mukono site. In WD, the studied genotypes exhibited over 30% longer total roots at 12 kg P ha^{-1} compared to the check, while at P0 and 32 kg P ha^{-1}, no significant differences were observed (Figure 3 a). In WW conditions, AFR genotypes, particularly AFR703-1, demonstrated significantly ($P < 0.05$) longer roots than the check at 12 kg P ha^{-1} and 32 kg P ha^{-1} (Figure 3 e).

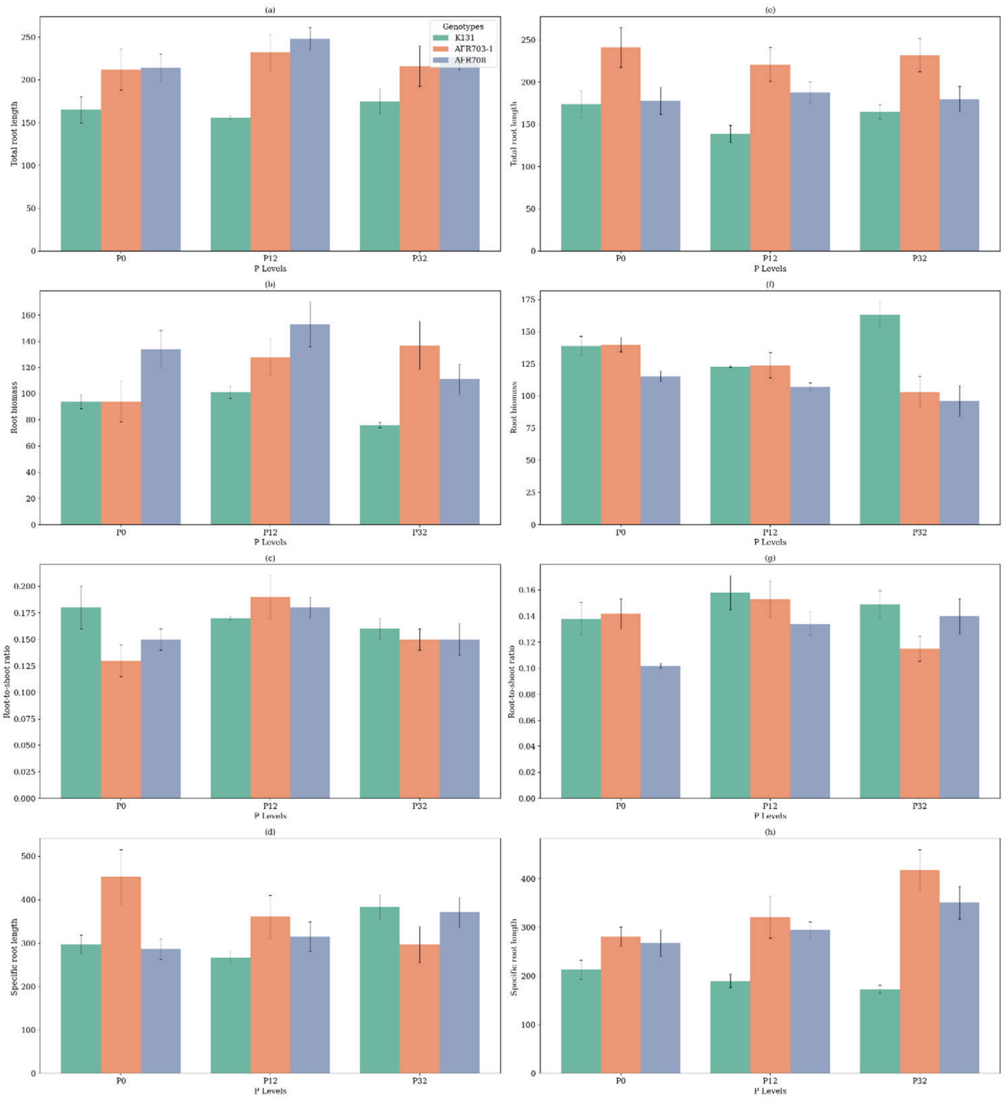

Figure 3. Influence of P on total root length (cm), root biomass (kg ha^{-1}), root-to-shoot ratio an specific root length (cm g^{-1}) in low soil P tolerant bean assessed in Nakasongola and Mukono Districts, Uganda. *The plots on the left (a, b, c, and d) illustrate Water-Deficit Environment (Nakasongola site, while those on the right (e, f, g, and h) represent Well-Watered Environment (Mukono site); P0, P12, and P32 represent phosphorus at 0, 12, and 32 kg P ha^{-1}, respectively; K131 serves as the check genotype; Standard errors are represented by bars over the mean.*

3.2.6 Root biomass

Root biomass per plant exhibited significant genotype-dependent variations under different P levels in WDE. Without P application, root biomass did not significantly differ between test genotypes and the check; however, at 12 kg P ha^{-1} and 32 kg P ha^{-1}, AFR708 and AFR703-1 displayed a significantly ($P < 0.05$) greater root biomass than the check (Figure 3 b). In WWE, the AFR genotypes produced comparable root biomass to the check without P (Figure 3 f). The studied genotypes, significantly ($P < 0.05$) produced less biomass in the roots compared to the check (Table 7).

The three-way interaction resulted in a significant variation in the root-to-shoot ratio ($P < 0.05$). In the Water-Deficit Environment (WDE), the AFR genotypes demonstrated a significantly higher root-to-shoot ratio at P12 kg P ha^{-1}; however, in the same environment, these genotypes exhibited a lower root-to-shoot ratio in the absence of P (Figure 3 c). Assessment of the root-to-shoot ratio between the environmental conditions indicated that the low soil P-tolerant common bean plants grown in the WD-Nakasongola study site significantly ($P < 0.05$) recorded a higher root-to-shoot ratio than their counterparts grown in WW Mukono study site (Table 7).

3.2.7 Specific root length

In WDE, AFR703-1 and AFR708 exhibited significantly higher specific root length (SRL) than the check across various P levels (Figure 3 d). Statistical analysis across P levels showed AFR and check genotypes were nonresponsive to P. Low soil P tolerant common bean plants in WDE (Nakasongola) significantly developed finer SRL than those in WWE (Mukono) (Table 7).

3.2.8 Contribution of root parameters to grain yield in measured field

In the Water-Deficit site in Nakasongola District, grain yield decreased with increasing specific root length (SRL) ($P < 0.05$) and root-to-shoot ratio ($P < 0.05$). Conversely, other measured root parameters did not significantly influence grain yield. In the Well-Watered site in Mukono District, grain yield reduced with increasing root-to-shoot ratio ($P < 0.001$).

4. Discussions and conclusion

4.1 Discussions

4.1.1 Plant leaf physiological and morphological responses

Water-Deficit significantly reduced leaf Relative Water Content (RWC) across all genotypes, regardless of applied P levels (Figure 1 a and b). These findings were consistent with those in beans reported by Rosales et al. (2012). Genotype AFR703-1 maintained stable RWC under Water-Deficit and low soil P conditions, similar to its performance in Well-Watered conditions without P. This resilience mirrors the findings in field pea (Jin et al., 2014).

Despite RWC being a key indicator of coping with Water-Deficit (Rosales et al., 2012), it did not improve the survival of AFR708 under Water-Deficit and low soil P, as the genotype failed to retain water, unlike in Well-Watered conditions with low soil P. However, supplying AFR708 with P alleviated adverse effects on RWC during Water-Deficit, consistent with findings in field peas (Jin et al., 2014).

Application of P improves tolerance in AFR708 to Water-Deficit, likely through enhanced root water absorption, partial stomatal closure, or water conservation. This promotes its survival under water stress, highlighting the significance of genotypic variations in RWC responses (Rosales et al., 2012). The findings underscore the complex interplay of Water-Deficit, P levels, and genotypic responses in common bean physiology, thus emphasizing the crucial role of P in managing water stress and enhancing plant tolerance.

Genotype AFR703-1 exhibited high water use efficiency by utilizing limited water effectively for photosynthesis and achieving greater biomass production per unit leaf area, in contrast to AFR708. This is consistent with the work of Mahmud et al. (2016). Liang et al. (2013) attributed low NAR to reduced biomass accumulation per unit leaf area and high transpiration rates, thus explaining lower leaf RWC registered by AFR708 under WD without P application compared to WW conditions.

The low SLA values in AFR703-1 under Water-Deficit at P0, compared with Well-Watered conditions, suggest that SLA serves as a morphological adaptation, possibly through thicker, smaller leaves to reduce transpiration (Karimi et al., 2015). This indicates that AFR703-1 can withstand Water-Deficit and maintain high biomass production without P. Low SLA is associated with stomatal closure, reduced transpiration, high water retention, and increased soluble compounds (Rosales et al., 2012; Yan et al., 2019). The application of P decreased SLA in AFR708 under WW conditions, enhanced water use efficiency, and potentially boosted CO_2 fixation per unit of water lost through leaves (Karimi et al., 2015).

The study of genotypes exhibited significantly higher LMR under WD at low soil P levels than in WW conditions without P (Table 4), suggesting increased biomass allocation to leaves under stress. The LMR, a marker for Water-Deficit tolerance, is linked to higher biomass allocation to leaves, enhancing photosynthesis and dry matter accumulation. Application of P decreased LMR in AFR703-1 and AFR708 under WD, indicating a shift in biomass allocation from leaves to roots for better water acquisition (Poorter et al., 2012). The lack of correlation between LMR and SLA indicates independent morphological responses to Water-Deficit. K131 showed inconsistent LMR patterns under WD compared to WW conditions.

Although Water-Deficit reduced RGR in AFR708, it increased in AFR703-1 compared to WW conditions, aligning with the NAR-RGR relationship (Table 6). Both SLA and LMR contributed to RGR in WD; while NAR significantly influenced RGR in both conditions. This indicates that leaf morphological and physiological traits play crucial roles in RGR variations under both conditions, consistent with Liu et al. (2015)

4.1.2 Root development as an adaptive mechanism

The study demonstrated that low soil P tolerant bean genotypes, exhibited superior root development compared to the check genotype under WDE in Nakasongola District, especially without P application (Table 7). These genotypes displayed enhanced basal roots, adventitious roots, tap root, total root length, and specific root length (SRL) in Water-Deficit Environments.

The development of these root traits under WDE conformed to previous findings in common beans (Suriyagoda et al., 2010; Beebe et al., 2013). The application of P, especially at moderate rates (12 kg P ha^{-1}), further improved root development in AFR708 under Water-Deficit, contributing to enhanced water absorption and improved RWC in AFR708.

Multiple root characteristics in AFR genotypes, including tap roots, lateral roots, and specific root length (SRL), enable efficient exploitation of P and water resources, adapting to combined soil P deficiency and Water-Deficit. Basal and adventitious roots efficiently utilize P and water from upper soil layers (Khan et al., 2010). Lateral roots enhance water access by expanding root surface area, crucial during uneven seasonal droughts. The taproot's positive gravitropism allows deep soil penetration for moisture access during Water-Deficits, optimizing water use efficiency (Beebe et al., 2013).

The study found that while low soil P tolerant AFR genotypes exhibited superior root development and beneficial traits under WDE compared to WWE (Table 7), there was no significant relationship between most root traits and grain yield at the Water-Deficit site in Nakasongola District. Increased root biomass, root-to-shoot ratio, total root length, and specific root length (SRL) support nutrient uptake and resilience in drought-prone areas. However, SRL and root-to-shoot ratio were negatively related to grain yield, indicating that these genotypes prioritize water exploitation over grain production.

This aligns with the findings of Porch et al. (2009), which suggest that root adaptations to water deficit and low soil P do not necessarily enhance yield. The results highlight the complex interactions between root traits, P application, and water deficit in the adaptation and productivity of common bean genotypes in challenging environments.

4.2 Conclusion

Genotype AFR703-1 exhibits water deficit tolerance, maintaining leaf relative water content (RWC) under challenging conditions, while AFR708's resilience improves with added soil P. AFR703-1 adapts morphologically with SLA and physiologically with NAR in limited water and P in the soil. Leaf mass ratio aids AFR703-1 under P application. Also, these genotypes show enhanced basal, adventitious, and tap roots, as well as greater total root length and specific root length (SRL), efficient for water and P resource exploitation. This study highlights valuable traits for common bean breeding, emphasizing yield improvement under limited soil P and optimized moisture utilization. However, the improvements in low P tolerance and water deficit observed in the test genotypes do not result in corresponding increases in grain yield.

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