ATATÜRK ÜNİVERSİTESİ YAYINLARI
ATATURK UNIVERSITY PUBLICATIONS

Research Article *Araştırma Makalesi* DOI: 10.17097/agricultureatauni.1431751

Enhancing Growth of Upland Rice in Low-Phosphorus Soil by Leveraging Root Morphological Traits

Düşük Fosforlu Topraklarda Kök Morfolojik Özelliklerinden Yararlanarak Yayla Pirincinin Büyümesinin Artırılması

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ABSTRACT

Low phosphorus (P) in the upland ecosystems negatively influence rice growth and cause significant yield losses. Upland rice to effectively adapt to low P in upland agroecosystems requires a suite of novel root traits. However, studies to identify these traits in upland rice grown in low P agroecosystems have received limited attention in Kenya. In the present study, nine (9) upland rice cultivars were screened to identify root traits that support low-P soil growth in a cement tank. Upland rice cultivars showed significant ($p \leq 0.05$) variation in number of root tips (NRT), number of root branching points (NBP), total root length (TRL), whole root network area (NA), average root diameter, root volume (RV), root surface area (RSA), first-order root length (FORL), and second order root length (SORL). BW01 and ITA01 recorded the highest NRT, NBP, TRL, RV, NA, RSA, FORL, and SORL, while NERICA04 had the lowest, representing 5.8, 8.0, 7.6, 6.8, 9.0, 5.8, and 9.3 differences in these traits under low P soil. NRT was significantly and positively correlated with NBP, TRL, NA, RV, RSA, and FORL, indicating the role of these traits in foraging for soil nutrients. Principal component analysis (PCA) showed that NRT, NBP, TRL, RSA, and SORL are important and effective root traits for selection in rice breeding under low P soil. BW01 and ITA01 recorded well-developed root systems, indicating that they are more P-efficient than the P-inefficient NERICA04 under low P soil conditions. Therefore, BW01 and ITA01 can be targeted for cultivation in P-deficient soils and used as trait donors to improve P-inefficient rice cultivars.

Keywords: Low phosphorus, Phosphorus efficiency, Root trait variation, Rice breeding, Upland rice

ÖZ

Yayla ekosistemlerdeki düşük fosfor (P) seviyeleri, pirincin büyümesini olumsuz etkileyerek önemli verim kayıplarına neden olur. Yayla pirincinin yayla tarımsal ekosistemlerindeki düşük P'ye etkili bir şekilde uyum sağlaması için bir dizi yeni kök özellikleri gerekmektedir. Ancak, Kenya'da düşük P içeren agroekosistemlerde yetiştirilen yayla pirinçlerinde bu özellikleri belirlemeye yönelik çalışmalar sınırlı ilgi görmüştür. Bu çalışmada, bir çimento tankında düşük P'li toprakta büyümeyi destekleyen kök özelliklerini belirlemek amacıyla dokuz (9) yayla pirinç çeşidi taranmıştır. Yayla pirinç çeşitleri, kök uç sayısı (NRT), kök dallanma noktası sayısı (NBP), toplam kök uzunluğu (TRL), tüm kök ağ alanı (NA), ortalama kök çapı, kök hacmi (RV), kök yüzey alanı (RSA), birinci derecede kök uzunluğu (FORL) ve ikinci derecede kök uzunluğu (SORL) açısından anlamlı ($p \leq 0,05$) varyasyon göstermiştir. BW01 ve ITA01, NRT, NBP, TRL, RV, NA, RSA, FORL ve SORL için en yüksek değerleri kaydederken, NERICA04 en düşük değerlere sahip olup, düşük P toprakta bu özelliklerde sırasıyla %5,8, %8,0, %7,6, %6,8, %9,0, %5,8 ve %9,3 oranlarında farklılık göstermiştir. NRT, NBP, TRL, NA, RV, RSA ve FORL ile anlamlı ve pozitif bir şekilde ilişkilidir, bu da bu özelliklerin toprak besin maddeleri için forajlamadaki rolünü göstermektedir. Temel bileşen analizi (PCA), NRT, NBP, TRL, RSA ve SORL'nin düşük P toprakta pirinç ıslahı için önemli ve etkili kök özellikleri olduğunu göstermiştir. BW01 ve ITA01, iyi gelişmiş kök sistemleri kaydederek, düşük P toprak koşullarında P-verimsiz NERICA04'ten daha P-verimli olduklarını göstermiştir. Bu nedenle, BW01 ve ITA01, P bakımından fakir topraklarda yetiştirilmek ve P-verimsiz pirinç çeşitlerini iyileştirmek için özellik donörleri olarak hedeflenebilir.

Anahtar Kelimeler: Düşük fosfor, Fosfor verimliliği, Kök özellik varyasyonu, Pirinç ıslahı, Yayla pirinci

Received / Geliş Tarihi 05.02.2024
Accepted / Kabul Tarihi 03.09.2024
Publication Date / Yayın Tarihi 29.09.2024

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Cite this article: Mutembei, J. & Nyongesa, B.O. (2024). Enhancing Growth of Upland Rice in Low-Phosphorus Soil by Leveraging Root Morphological Traits. *Research in Agricultural Sciences, 52*, 175-182.

Introduction

Rice is a principal cereal crop that provides the global population with calories. Increased preference of rice in sub-Saharan Africa (SSA) due to a shift in consumer preference away from traditional crops toward rice consumption has triggered rice production to lag behind local demand for rice in Kenya. Therefore, there is a need to maximize production in traditional irrigated ecosystems and expand cultivation into upland ecosystems to meet Kenya's demand for rice. In upland acidic soils, free iron and aluminum oxides bind to native and applied phosphorus (P), whereas in calcareous soils, abundant calcium and magnesium compounds bind tightly to inorganic phosphates, making P inaccessible to plant roots (Alewell et al., 2020). This has contributed to over 80% of the soils in western Kenya becoming P deficient (Jama & Straatan, 2006). Therefore, P deficiency is one of the factors that limit rice production in upland rice ecosystems. The drought occasioned by climate change is likely to contribute to enhanced P deficiency because P mobility decreases with the decline in soil moisture in upland ecology (Marin et al., 2021). Low P levels in the soil are likely to affect rice seedling establishment and development because soil foraging by roots is insufficient to acquire immobile P. One strategy that can reduce P limitations is to search for varieties or cultivars with novel root traits that yield well under low P soil conditions (Rakotoson et al., 2020; Anandan et al., 2022).

Plants can withstand low P in soil by developing root morphological changes that enhance P uptake and increase internal P use efficiency (Kale et al., 2021a; Dinh et al., 2023). Previous studies have shown that rice root morphological and biomasses vary under P-deficient conditions (Wissuwa et al., 2020; Kale et al., 2021b; Anandan et al., 2022; Ranaivo et al., 2022). The genotypic differences in P uptake observed in rice are attributed to variations in the root growth and, to a lesser extent, differences in the quantity of P acquired per root size or root efficiency (Mori et al., 2016; Wissuwa et al., 2020). Rapid seedling root development drives differences in P acquisition ability during early rice seedling stages (Pariasca-Tanaka et al., 2015). The variation observed in these studies indicates that there is an opportunity to exploit root traits to improve the performance of rice cultivars under low P conditions. Although significant root morphological traits that enhance rice growth have been identified in low P soil, the characteristics of many rice varieties and cultivars grown by farmers in upland ecology in Kenya is unknown. Therefore, the yield of upland rice in P-deficient upland ecology is extremely low. Consequently, there is a need to search for root functional phenotypes that confer better establishment of upland rice in low P soil. This is likely to support better crop establishment, sustain rice production, and reduce the economic burden of the farmers that rely on fertilizer imports. The present study aimed to screen nine (9) upland rice varieties/cultivars in a cement tank to identify novel root traits that support growth under low P conditions.

Materials and Methods

Plant materials

Nine rice cultivars sourced from the Kenya Agricultural Research Organization were used in this study. These cultivars were named as BW01, IR01, IR02, IR64, ITA01, Komboka, Mnuri, NERICA01, and NERICA04, respectively.

Phenotyping for phosphorus stress in a cement tank

Low-P soil was collected from the top 15 cm of an unfertilized farm, native grassland vegetation at the University of Eldoret (0.584° N 35.309° E. 2100 masl). The soil was air-dried, sieved through a 2 mm mesh to remove coarse fragments, and thoroughly mixed. Soil pH was measured in a 1:2 (w/v) soil to distilled water suspensions, following the method described by Anderson and Ingram (1993). Total organic carbon was determined using the Walkley-Black method (Nelson and Sommers 1982), whereas Kjeldahl nitrogen was measured according to Jackson (1962). Total P was quantified using the ammonium bicarbonate-diethylenetriaminepentaacetic acid (AB-DTPA) extraction method as per Soltanpour and Workman (1979). Approximately 10 g of soil was placed in a beaker, mixed with 20 ml of extraction solution containing 1 M AB and 5 mM DTPA, shaken for 15 min, and then filtered. The filtrate was analyzed for P content using a colourimeter. For calcium measurement, about 0.5 g of sieved soil was placed in a beaker with 40 ml of 0.5 N HCl, left at room temperature for 5 min, and the filtrate was analyzed (Sahrawat 1987). The physical characteristics of the sieved soil were determined using the hydrometer method as described by Bouyoucos (1962). The soil exhibited the following properties: pH-H_2O 5.73, organic carbon (%) 1.89, total nitrogen (%) 0.15, available P (mg/kg) 5.38, Na (m/kg) 427, Ca (mg/kg) 1770, sand (%) 61, clay (%) 25, and silt (%) 14.

The phenotyping of root morphological traits of nine rice cultivars was carried out in a cement tank following the procedure described by Anandan et al. (2022). The cement tank was filled with air-dried, and sieved soil. Fifteen rice seeds per cultivar were sterilized by adding 10 ml of 10% sodium hypochlorite to a beaker for 10 min. Seeds were rinsed five times with distilled water to remove any sodium hypochlorite. The seeds were imbibed in water for 24 h to accelerate germination. Soaked rice seeds for each cultivar were directly seeded in a cement tank on 1st February 2023 following a completely randomized design with three replicates. Seeds were sown in a single-row plot measuring 80 cm long and spaced 20 cm between plants within a row and 20 cm between the rows. NERICA04 was used as a P-sensitive control to identify P-efficient cultivar in this study. Weeds were manually uprooted during the experiment. No fertilizers or chemicals were applied to the experimental setup.

The soil was irrigated daily, and 15 days after sowing, the seedlings were thinned, leaving only two seedlings per hill. On the 45th day, five plants per cultivar were uprooted and placed in individual plastic bags. The roots were washed with distilled water and stored at 4°C for further analysis. Five intact root samples, including first- and second-order roots, were randomly selected for morphological measurements. Root classification followed the standard method, where first-order roots are the most distal and unbranched, and second-order roots originate at the junction of two first-order roots (Pregitzer, 2002; Freschet & Roumet, 2017). The samples were arranged in water on a transparent tray measuring 30 × 20 × 3 cm, and scanned at 300 dpi using an HP scanner (hp300 version). The following root traits were recorded: number of root tips (NRT), number of root branching points (NBP), total root length (TRL, mm), whole root network area (NA, cm²), average root diameter (ARD, mm), root volume (RV, cm³), root surface area (RSA, cm²), first-order root length (FORL, mm), and second-order root length (SORL, mm). These traits were recorded for each replication and analyzed using RhizoVision version 2 (Seethepalli et al., 2021).

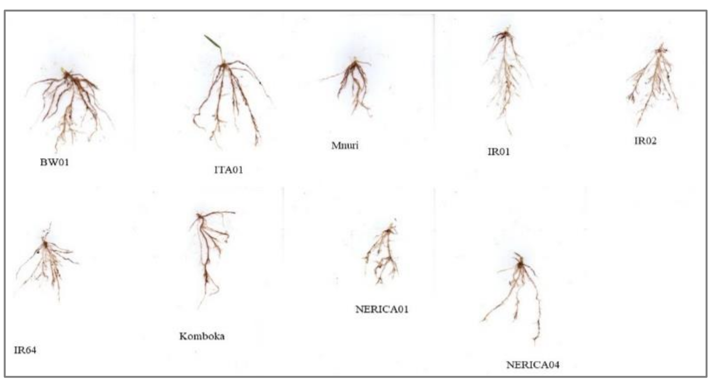

Figure 1.
Root morphological traits of nine rice cultivars grown under low phosphorus soil conditions.

Statistical Analysis

Phenotypic data: NRT, NBP, TRL, NA, ARD, RV, RSA, FORL, and SORL were subjected to one-way analysis of variance (ANOVA) to determine the response of genotype variation in low-P soil. ANOVA was performed using IBM SPSS Statistics for Windows, version 23.0 (Armonk, NY: IBM Corp), based on a general linear model at $p \le .05$. Cultivar means in low-P soil were compared using Tukey's significance difference test. Pearson's correlation coefficient was used to determine the relationship among the root traits using IBM SPSS version 23. Principal component analysis (PCA) was performed on root morphological traits to identify novel root traits that can be used to select genotypes for cultivation and breeding to improve P use efficiency under low-P conditions. PCA analysis was executed using the GenStat (GenStat, 2003)

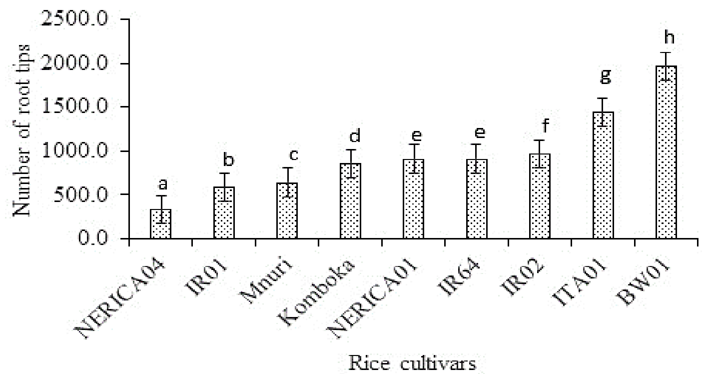

Figure 2.
Number of root tips of rice cultivars grown under low soil phosphorus soil conditions. Bar graph columns with different letter(s) sindicate that the means differ significantly at p ≤ .05.

Results

Root morphological trait variation among rice cultivars

One-way ANOVA revealed highly significant ($p \le .05$) variation in NRT, NBP, TRL, NA, ARD, RV, RSA, FORL, and SORL among the upland rice cultivars, as presented in Table 1 and Figure 1. There was a 5.8-fold difference in NRT, ranging from 336 for NERICA04 to 1865 for BW01 (Figure 2). In low-P soil, NBP varied significantly, with an 8-fold difference varying from 216.7 in NERICA04 to 1775.3 in BW01 (Figure 3). BW01 recorded the highest TRL at 505.4 mm, whereas NERICA04 had the lowest at 66.6 mm, showing a 7.6-fold difference among cultivars under low-P soil (Table 2). The rice cultivars showed a 6.8-fold variation in NA, with BW01 having the highest of 63.0 cm², while NERICA04 had the lowest of 9.3 cm² (Table 2). The rice cultivars exhibited a 1.9-fold in average root diameter, with Mnuri recording the highest value of 2.76 mm, while IR02 had the lowest value of 1.46 mm (Table 2). The root volume (RV) varied significantly, with BW01 recording the highest value of 65.48 cm³, whereas IR01 had the lowest value of 4.54 cm³, indicating a 14.4-fold difference among rice cultivars (Table 2). IR02, NERICA04, IR64, and NERICA01 recorded RV values less than 10.0 cm³, with no significant differences among them. The rice cultivars exhibited a 9-fold difference in RSA, with BW01 recording the highest value of 449.4 cm², while IR01 and NERICA04 had the lowest values of 47.97 cm² and 54.12 cm², respectively, in low-P soil (Figure 4). BW01 recorded the highest FORL at 120.81 mm, whereas NERICA04 and IR01 had the lowest value at 20.78

mm and 22.30 mm, respectively, showing a 5.8-fold difference among rice cultivars (Table 2). The SORL of the rice cultivars showed a 9.3-fold difference in response to low-P soil, with BW01 recording the highest value of 304.86 mm, while NERICA04 and IR01 had the lowest values of 32.72 mm, and 33.70 cm, respectively (Table 2).

Table 1.

Analysis of variance for root morphological traits among nine rice cultivars in low phosphorus soil

Parameters	Genotype			
	Df	Mean square	F value	P value
NRT	8	709134.0	4310.4	< .001
NBP	8	725571.8	1697.6	< .001
TRL	8	57052.7	1587.2	< .001
NA	8	948.7	272.9	< .001
ARD	8	0.5	8.7	< .001
RV	8	1287.8	853.6	< .001
RSA	8	48826.4	859.8	< .001
FORL	8	3932.9	250.4	< .001
SORL	8	23884.6	870.7	< .001

NRT = number of root tips, NBP = number of root branching points, TRL = total root length, NA = whole root network area, ARD = average root diameter, RV = root volume, RSA = root surface area, FORL = First order root length, SORL = second order root length. $p \leq .05$

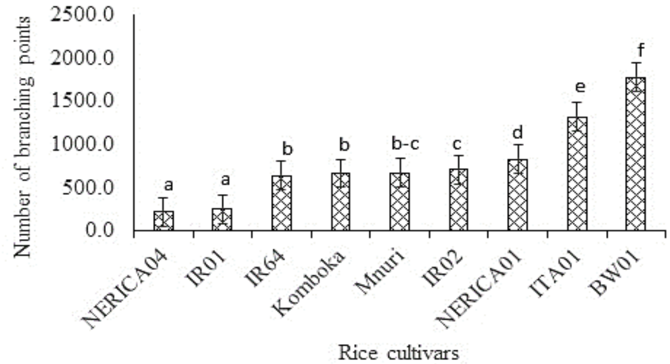

Figure 3.

Number of root branching points of rice cultivars grown under low phosphorus conditions. Bar graph columns with different letter(s) sindicate that the means differ significantly at $p \leq .05$.

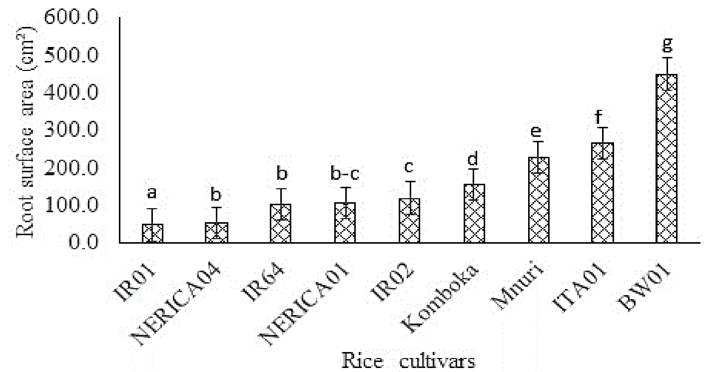

Figure 4.

Root surface area of rice cultivarss grown low soil phosphorus soil conditions. Bar graph columns with different letter(s) sindicate that the means differ significantly at $p \leq .05$.

Table 2

Mean values of root morphological traits of nine rice cultivars s grown in low-phosphorus soil

Genotype	Mean					
	TRL (mm)	NA (cm²)	ARD (mm)	RV (cm³)	FORL (mm)	SORL (mm)
BW01	$505.5^{g}\pm1.0$	$63.0^{f}\pm1.0$	$2.4^{de}\pm0.3$	$65.5^{f}\pm0.8$	$120.8^{f}\pm0.9$	$304.9^{g}\pm0.4$
IR01	$82.0^{b}\pm0.5$	$11.1^{a}\pm3.6$	$1.7^{ab}\pm0.1$	$4.5^{a}\pm0.1$	$22.3^{a}\pm1.6$	$33.7^{a}\pm0.4$
IR02	$272.4^{e}\pm10.3$	$22.7^{c}\pm1.3$	$1.5^{a}\pm0.2$	$7.1^{b}\pm1.4$	$105.7^{e}\pm2.4$	$107.2^{c}\pm8.9$
IR64	$201.8^{c}\pm14.3$	$17.6^{b}\pm2.5$	$1.6^{ab}\pm0.1$	$8.8^{b}\pm0.1$	$61.0^{cd}\pm10.5$	$79.8^{b}\pm10.6$
ITA01	$387.2^{f}\pm1.9$	$48.0^{e}\pm1.0$	$1.8^{ac}\pm0.4$	$24.3^{d}\pm0.3$	$103.0^{e}\pm0.6$	$226.5^{f}\pm1.1$
Komboka	$207.8^{c}\pm1.2$	$25.5^{c}\pm2.1$	$2.1^{bd}\pm0.3$	$14.9^{c}\pm0.7$	$45.5^{b}\pm3.5$	$126.2^{d}\pm1.2$
Mnuri	$218.9^{d}\pm1.0$	$32.1^{d}\pm0.7$	$2.8^{e}\pm0.3$	$43.2^{e}\pm3.2$	$54.5^{c}\pm0.3$	$135.4^{e}\pm2.2$
NERICA01	$208.2^{c}\pm1.8$	$17.2^{b}\pm1.4$	$1.7^{ab}\pm0.1$	$9.3^{b}\pm0.7$	$63.6^{d}\pm3.0$	$83.5^{b}\pm6.9$
NERICA04	$66.6^{a}\pm1.2$	$9.3^{a}\pm1.3$	$2.2^{cd}\pm0.2$	$8.3^{b}\pm0.3$	$20.8^{a}\pm0.4$	$32.7^{a}\pm0.7$

NRT = number of root tips, NBP = number of root branching points, TRL = total root length, NA = whole root network area, ARD = average root diameter, RV = root volume, RSA = root surface area, FORL = First order root length, SORL = second order root length. Means in the same column followed by a different letter(s) differ significantly at $p \leq .05$.

Table 3

Person's correlation coefficients for pairwise root morphological traits for nine rice cultivars in response to low soil phosphorus

	NRT	NBP	TRL	NA	ARD	RV	RSA	FORL	SORL
NRT	1								
NBP	0.974**	1							
TRL	0.967**	0.982**	1						
NA	0.908**	0.948**	0.953**	1					
ARD	0.045	0.195	0.161	0.398	1				
RV	0.684*	0.767*	0.753*	0.872**	0.737*	1			
RSA	0.876**	0.927**	0.922**	0.983**	0.511	0.940**	1		
FORL	0.880**	0.874**	0.931**	0.799**	-0.091	0.544	0.745*	1	
SORL	0.929**	0.965**	0.968**	0.996**	0.353	0.847**	0.976**	0.822**	1

NRT = number of root tips, NBP = number of root branching points, TRL = total root length, NA = whole root network area, ARD = average root diameter, RV = root volume, RSA = root surface area, FORL = First order root length, SORL = second order root length. ** significant at $p \leq .01$, * significant at $p \leq .05$.

Table 4

Principal component analysis showing eigenvectors, percent and cumulative variation of root morphological traits of nine rice cultivars at low phosphorus soil.

	Components	
Root traits	PC 1	PC2
ARD	0.00008	0.00394
FORL	0.04466	-0.02850
NA	0.02337	0.04746
NBP	0.68318	0.50959
NRT	0.67340	-0.6916
RSA	0.16311	0.44071
RV	0.02148	0.11457
SORL	0.11954	0.20349
TRL	0.18950	0.1007
Eigen values	7.311	1.468
% of Variance	81.238	16.307
Cumulative %	81.238	97.545

NRT = number of root tips, NBP = number of root branching points, TRL = total root length, NA = whole root network area, ARD = average root diameter, RV = root volume, RSA = root surface area, FORL = First order root length, SORL = second order root length.

Correlation coefficients of root morphological traits

Table 3 shows the Pearson's correlation coefficients of the root morphological traits for rice cultivars in low P soil conditions. In the low P soil, NRT significantly and positively correlated with NBP (r = 0.95, $p < .0001$), TRL (r = 0.94; $p < .0001$), NA (r = 0.84; $p = .001$), RV (r = 0.47; $p = .042$), RSA (r =0.77; $p = .002$), FORL (r = 0.77; $p = .002$), and SORL (r = 0.86; $p < .0001$), except for the average root diameter. NBP significantly and positively correlated with all root morphological traits under low P soil conditions, except for ARD. ARD showed a positive significant correlation only with RV (r = 0.54; $p = .024$). RV showed a positive significant correlation with RSA (r = 0.88; $p < .0001$) and SORL (r = 0.72; $p = .004$), while FORL positively and significantly correlated with SORL (r = 0.68, $p = .007$). The two principal component analyses (PCA) revealed a total variability of 97.55%, as shown in Table 4. PC1 and PC2 accounted for 81.24% and 16.31% of variability at low-P soil conditions, respectively. NBP, NRT, and TRL contributed to variation in PC1, whereas RSA and SORL were associated with PC2 (Table 3; Figure 5).

Discussion

Plants alter root morphological features as an adaptation to improve P acquisition under low P soil conditions (Gutierrez-Alanis et al., 2018). In this study, there were significant differences in root morphological traits: NRT, NBP, TRL, NA, ARD, RV, RSA, FORL, and SORL among the upland rice germplasm grown under low P soil. These variations may have arisen from evolutionary adaptations of upland rice to diverse habitats or indirect selection by farmers over the years. Previous findings indicate that rice landraces collected from different agroecological zones exhibit variations in root morphology, and are well adapted to survive low levels of P in the soil (Panda et al., 2021; Anandan et al., 2022). The observed variation indicates the presence of novel traits that can be harnessed for improved growth of P-sensitive rice cultivars such as NERICA04 under low P soil. These findings are in agreement with previous studies, which reported high variation in root number, total root length, total root surface area, root average diameter, root volume and root tips, and root and shoot biomasses in diverse rice lines under low P soil conditions (Anis et al., 2018; Solangi et al., 2020; Kale et al., 2021; Anandan et al., 2022; Ranaivo et al., 2022).

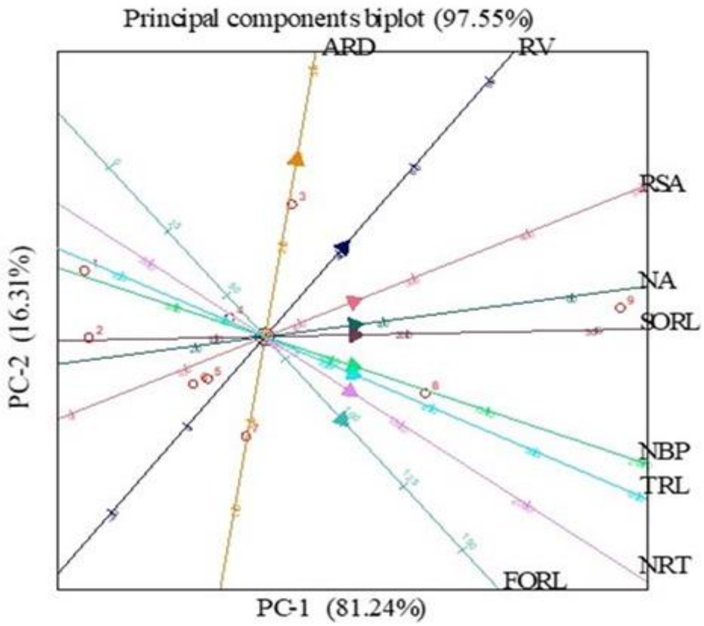

Figure 5.

Principal component analysis of nine root morphological traits of in nine rice cultivars grown at low phosphorus conditions. ARD = average root diameter, RV = root volume, RSA = root surface area, NA = whole root network area, SORL = second order root length, NBP = Number of root branching points, TRL = Total root length, NRT = Number of root tips, FORL = First order root length. Numbers in figure represent genotypes as follows: 1 = NERICA04, 2 = IR01, 3 = Mnuri, 4 = Komboka, 5 = NERICA01, 6 = IR64, 7 = IR02, 8 = ITA01, 9 = BW01.

BW01 and ITA01 recorded higher NRT, NBP, TRL, RV, RSA, FORL, and SORL than NERICA04 and IR01, indicating that they are well adapted to low P soil conditions. Therefore, BW01 and ITA01 are P-efficient rice cultivars, whereas NERICA04 and IR01 are P-inefficient. NERICA04 exhibits slow seedling growth and root development under P-limiting conditions, as reported by Wissuwa et al. (2020) and Ranaivo et al. (2022), which aligns with the findings of this study. Previous findings in Arabidopsis, rice, and cotton have revealed that increasing the root tip density, lateral root density and length, total root length, and number of root tips under low P stress increases the capacity of P to be absorbed (Fitter et al., 2002; Gutierrez-Alanis et al., 2018; Kayoumu et al., 2022; Dinh et al., 2023). De Bauw et al. (2020) similarly reported that root tips and lateral root types are key drivers of P uptake in upland rice. Rice cultivars with high root phenes, such as NRT, NBP, TRL, RV, RSA, FORL, and SORL are suitable for low P conditions.

In this study, NRT showed a significant positive correlation with NBP, TRL, NA, RV, and RSA, demonstrating that root morphological traits work synergistically to enhance P foraging in low P soil. Previous studies identified multiple traits, including root volume, total surface area, number of root tips, and total root length, that contribute to phosphorus deficiency tolerance in rice (Panda et al., 2021; Anandan et al., 2022). Kaysar et al. (2022) reported a close relationship among root length, root number, root volume and root porosity when sourcing water and nutrients from the soil in different rice cultivars under subtropical conditions. These findings align well with those of Anis et al. (2018), Kale et al. (2021b), and Anandan et al. (2022), who reported significant positive correlations among root traits in rice under low P. The strong positive correlation among the root traits demonstrates the potential to improve P-inefficient cultivars. PCA identified NBP, NRT, TRL, RSA, and SORL as important root traits that enhance P stress tolerance in upland rice. These results are consistent with previous studies by Fitter et al. (2002) and Kayoumu et al. (2022), which identified the number of root tips and total root length as key traits for improving phosphorus uptake in Arabidopsis and cotton genotypes. Therefore, NRT, NBP, RSA, and SORL are valuable root traits that can be leveraged in breeding programs to improve the growth of P-sensitive upland rice germplasm in low-P soils.

In conclusion, nine rice cultivars revealed wide variation in root morphological traits, with most traits showing significant positive correlations, indicating that they are synergistically linked in enhancing growth under low P soil. PCA showed that NRT, NBP, TRL, and RSA are key traits to target for selection in rice breeding under low soil P supply. BW01 and ITA01 recorded higher NRT, NBP, TRL, and RSA than NERICA01, NERICA04, IR01 and IRO2, among others, under low soil P conditions. Therefore, BW01 and ITA01 are suitable candidates for cultivation in P-limited upland ecosystems, and as potential donors of novel root traits to improve P-inefficient upland rice cultivars.

Peer-review: Externally peer-reviewed.

Acknowledgements: The authors thank Mr. Richard Nyagwachi from the Department of Biological Sciences, University of Eldoret, for assisting with setting up the greenhouse experiment; Mr. Wilson Kwoba Odunga for helping with the root analysis; Dr John Kimani from the Kenya Agricultural Livestock Research for providing rice germplasm.

Author Contributions: Benson O. Nyongesa conceptualized the study, Justus Mutembei and Benson O. Nyongesa designed the study, Benson O. Nyongesa supervised the first author to implement the project, Justus Mutembei conducted greenhouse experiments and performed detailed root analysis, and Justus Mutembei and Benson O. Nyongesa did the data analysis and wrote the manuscript.

Conflict of Interest: The authors have no conflicts of interest to declare.

Financial Disclosure: This research project was supported by the International Foundation for Science grant number 1-3-C-6639-1.

Hakem Değerlendirmesi: Dış bağımsız.
Teşekkür: Teşekkürler: Yazarlar, sera deneyinin kurulumunda yardımları için Eldoret Üniversitesi Biyolojik Bilimler Bölümü'nden Bay Richard Nyagwachi'ye; kök analizi konusunda yardımları için Bay Wilson Kwoba Odunga'ya; pirinç germ plazmasını sağladığı için Kenya Tarım Hayvancılık Araştırmalarından Dr. John Kimani'ye teşekkürlerini sunarlar.
Yazar Katkıları: Çalışmanın kavramsallaştırılmasını Benson O. Nyongesa üstlendi, Justus Mutembei ve Benson O. Nyongesa çalışmayı tasarladı, Benson O. Nyongesa projenin uygulanmasında birinci yazara danışmanlık yaptı, Justus Mutembei sera deneyleri yürüttü ve detaylı kök analizi yaptı ve Justus Mutembei ve Benson O. Nyongesa veri analizini yaptı ve makaleyi yazdı.
Çıkar Çatışması: Yazarlar, çıkar çatışması olmadığını beyan etmiştir.
Finansal Destek: Bu araştırma projesi Uluslararası Bilim Vakfı tarafından 1-3-C-6639-1 numaralı hibe ile desteklenmiştir.

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