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RESEARCH ARTICLE

Analysis of root system architecture in rice indicates limited varietal adaptations

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Abstract

Plant roots are the primary organs that sense and respond to soil-derived stresses. A healthy root system architecture reflects a plant's adaptive potential. In this study, we analyzed root traits of 286 rice varieties grown in hydroponic and pot culture systems. The results revealed considerable variation and significant correlations for root traits across both systems. Cluster analysis partitioned the genotypes into two clusters, with total root length, surface area and root diameter as major determinants of variation. The results highlight marginal changes in root system traits within the *indica* group, resulting in distinct behaviors under pot culture conditions. However, the *Aus/Boro* subgroup did not exhibit similar patterns. The study underscores the importance of further investigating root system traits to achieve adaptive improvements, aiming to enhance the efficiency and effectiveness of root breeding programs. Understanding these variations can lead to the discovery of desirable traits and the development of superior rice varieties with efficient root systems.

Keywords: Root system architecture, rice, diversity, adaptive grouping

Introduction

Rice (*Oryza sativa* L.) is a key food staple for the world population, significantly contributing to global food security. Approximately 90% of rice cultivation takes place in irrigated and lowland rainfed ecosystems in Asia, where it is vulnerable to several environmental challenges (Bindraban et al. 2015). Among these, soil-based abiotic stresses such as drought, nutrient starvation and soil salinization are most prominent. The impact of climate change can exacerbate soil-related abiotic stresses, making it particularly challenging to sustain field crop productivity, especially for rice (Hu et al. 2014).

Plant roots are the primary organs that sense and suffer from soil-derived stresses. Given their crucial role in the uptake and translocation of water and nutrients, a robust root system is essential for plant health (Uga et al. 2013). Root system architecture (RSA), the spatial configuration of a plant's root system in the soil, is vital for plant adaptation to the soil matrix, defining its ability to access water and nutrients, interact with soil microorganisms, and anchor itself. RSA includes root depth, length, branching, angle, density, and diameter. Similar to aerial parts of plants, RSA shows significant variation among different varieties, allowing them to adapt differently to various environmental conditions and stresses. Therefore, understanding and optimizing RSA is key to enhancing crop resilience and yield. Root developmental plasticity is an inherent adaptation of the plant that reflects its genetic potential and is crucial for modulating root system development (Malamy 2005). Governed by intrinsic constitutive pathways, root system development is both temporal and spatial as the plant grows, and stress factors influence it throughout the plant's

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growth period. A comprehensive understanding of RSA traits among rice varieties in different growing systems is critical for aiding breeding efforts aimed at enhancing climate resilience and sustaining yield under nutrient-limited conditions.

Despite the humongous success of modern plant breeding in securing food security, the genetic variability among cultivars rapidly eroded as new high-yielding cultivars replaced traditional low-yielding ones (Bhandari et al. 2017). A substantial part of the post-green revolution research was focused on above-ground agro-morphological features, particularly grain yield. The RSA has been largely ignored as a target trait in crop improvement programs, resulting in RSA diversity being less documented in rice germplasm. Additionally, the indirect impact of selection made during the green revolution era on the RSA remains poorly understood. Studying root systems is inherently challenging due to the requirement for destructive sampling. Among various methods for observing root systems, hydroponics and pot culture are widely used. Hydroponics offers a rapid, low-cost, and non-destructive means of evaluating root traits (Price et al. 1997), while pot culture provides more realistic soil-based conditions, albeit being more challenging, manual, destructive, and expensive (Vejchasarn et al. 2016). This study, while exploring the root phenotypic variation among a large panel of rice genotypes, also compares the RSA under both the above culture systems to delineate the relationships between root traits and growing environments.

Materials and methods

Plant material

The study utilized 281 rice germplasm of Indian origin included in the 3K rice genome project that had rice accessions from 89 countries (3000 Rice Genome Project, 2014). The Indian subset consisted of 60 *aus*, 13 Basmati, 171 *indica*, 21 tropical *japonica*, three temperate *japonica*, 12 intermediate types, and one unclassified *japonica* genotype. Additionally, five checks—Kalinga III (*indica*), Salumpikit (*indica*), IR64 (*indica*), Nagina 22 (*aus*), and Dagad Deshi (*indica*)—were also used. Among these, Salumpikit (Comas et al. 2013), Nagina 22 (Poli et al. 2013), and Dagad Deshi (Sinha et al. 2015) are drought-tolerant landraces with large and deep root systems, while Kalinga III (Steel et al. 2006) and IR64 (Uga et al. 2015) possess shallow root systems. All plant materials were sourced from the Genetics Division of ICAR-Indian Agricultural Research Institute (IARI), New Delhi. Details of the accessions are provided in Supplementary Table S1.

Growth environments

Two cultivation systems were used in the study: hydroponics and pot culture. Hydroponic cultivation was conducted at the National Phytotron Facility at IARI during the wet seasons of 2020 and 2021. Seeds of 286 lines were surface sterilized with 1% sodium hypochlorite (Sauer and Burroughs 1986) and pre-germinated in petri dishes for 3 days at 37°C. Germinated seedlings were carefully transferred into 100 mm^2 punch wells made in 25 mm thick rectangular expanded polystyrene sheets layered with nylon mesh underneath and floating on modified Yoshida nutrient solution (Supplementary Table S2) in rectangular plastic crates. The nutrient solution was replaced every seven days, maintaining a constant pH of 5.5 for 35 days under natural light. The experiment was designed as a completely randomized trial with two replications.

In the pot culture system, 286 genotypes were initially field-grown in raised bed nurseries as practiced in wetland rice cultivation and maintained for 21 days. Then, 21-day-old seedlings were transplanted into plastic pots filled with puddled sandy loam wetland soil. Each pot received one plant, which was allowed to grow until the flowering stage at the Nanaji Deshmukh Plant Phenomics Centre at IARI. The pots were arranged in a completely randomized design with three replications per genotype. The experiment was repeated twice during the *kharif* seasons of 2020 (June-September) and 2021 (June-September).

Phenotyping

After 35 days of hydroponic culture, individual plants were carefully removed from the wells, ensuring all roots remained intact. These plants were then placed on a plain glass surface, and the maximum root and shoot lengths were measured using a ruler; the sum of these measurements was taken as the plant height (PH). Subsequently, the roots were separated at the collar region and positioned in a transparent acrylic tray placed atop a desktop scanner (EPSON 11000 XL) for image acquisition. Images obtained from the scanner were analyzed using the WinRHIZO® system (Arsenault et al. 1995). RSA traits, such as primary root length (PRL) total root length (TRL), projected area (PA), surface area (SA), average diameter (AD), and root volume (RV) were measured (Bauhus and Messier 1999). The roots and shoots were then separately oven-dried at 55°C for 72 hours. The dry weights of the roots (RDW) and shoots (SDW) were determined. The combined weight of these components represented the total dry biomass (BM) of the seedlings.

Phenotyping from the pot culture system was conducted at the reproductive phase while the root system was fully active. Plants that had reached panicle initiation were carefully removed from the pots to ensure no damage to the roots. Prior to removal, agro-morphological data, including PH and number of tillers (NT), were recorded. The uprooted plants were then soaked overnight in a container filled with water. The following morning, the plant roots were meticulously rinsed under running water to remove any adhering soil. The shoot portion was carefully excised from

the collar region while keeping the root system intact. The lengths of the shoot (SL) and root (RL) were measured from the collar region to their respective ends using a ruler and summed to obtain the PH. The RSA of the mature plants was also determined using digital scans, as previously described. Given the extensive root system of mature plants, the roots were radially dissected into smaller segments for easier handling. Data from these segments were aggregated to deduce the total RSA parameters for individual plants. Following root data acquisition, samples were oven-dried to determine their biomass traits, such as RDW and SDW.

Data analyses

The data were statistically analyzed to assess the phenotype variation and to evaluate the interrelations of various traits. All statistical analyses were performed in the R environment using various packages, as well as standalone software tools like STAR v2.0.1 (IRRI, 2014). Methods employed included mixed model analysis of variance (ANOVA), correlations, principal component analysis (PCA), and clustering. The genotypic best linear unbiased predictors (BLUEs) generated were used for performing PCA.

Results

Phenotypic variation of RSA and shoot traits

ANOVA performed separately on the phenotypic data collected under hydroponics and pot culture revealed significant variation ($\alpha = 0.05$) between the genotypes for root and shoot traits under both growing systems. A descriptive summary of phenotypic variation for root and shoot traits under hydroponics and pot culture is represented in Table 1.

In hydroponics, the PH of the seedlings ranged from 29.3 to 73.5 cm, with an average of 52.6 cm. At panicle initiation, under pot culture conditions, PH ranged from 69.1 to 139.8 cm, with an average of 106.0 cm. NT of the mature plants ranged from 7.0 to 13.8, with an average of 10.2. Seedling SDW averaged 148.0 mg among all the genotypes, varying between 56.8 and 249.4 mg. The average SDW of the pot-cultured plants was 16.2 g, varying between 6.3 and 25.2 g. Among the root characteristics, PRL, with an average of 12.4 cm, ranged from 5.3 to 19.4 cm under hydroponics and from 17.4 to 39.3 cm under pot culture, with an average of 27.7 cm. RDW ranged from 11.0 to 53.1 mg, with an average of 30.9 mg in hydroponics, and from 0.4 to 2.2 g under pot culture, with an average of 1.3 g. TRL under hydroponics averaged 209.1 cm, ranging from 72.5 to 378.9 cm, while under pot culture, the average was 4913.9 cm, ranging from 1674.6 to 8214.6 cm. PA averaged 8.6 cm^2, falling between 3.3 and 15.0 cm^2 under hydroponics, and 223.6 cm^2, ranging from 76.6 to 413.8 cm^2 under pot culture. SA among the tested genotypes ranged from 10.4 to 47.1 cm^2 under hydroponics and from 240.8 to 1300.1 cm^2 under pot culture, with corresponding averages of 27.0 and 701.7 cm^2, respectively. AD ranged from 306.0 to 535.3 µm, with an average of 415.9 µm in hydroponics, and from 300.0 to 595.6 µm under pot culture, with an average of 452.0 µm. RV ranged from 90.6 to 556.4 mm^3, with an average of 283.3 mm^3 in hydroponics, and from 265.0 to 1626.0 mm^3 under pot culture, with an average of 810.0 mm^3. The coefficient of variation (CV) for the traits under hydroponic screening ranged between 2.5% for SDW and 9.9% for RV, while CV under pot culture ranged between 3.1% for PH and 12.08% for NT.

Association among RSA and shoot traits

Pearson's correlation coefficients were found to be significant and positive among most of the traits under both hydroponic and pot culture screenings (Fig. 1). The magnitude of correlation was relatively higher under hydroponics than under pot culture. The shoot traits, PH and SDW, were strongly correlated with each other in both screenings and showed high positive correlations with several root traits, except for AD. The association of PH with AD was negative and significant under hydroponics, while they were uncorrelated under pot culture. Other RSA traits—primary root length (PRL), RDW, TRL, PA, SA and RV—indicated positive relationships among themselves, with very strong associations under hydroponics compared to pot culture. AD, however, showed weak negative to no correlations with RSA traits such as PRL, RDW, and TRL. The relation of AD with PA and SA was positive under pot culture but uncorrelated under hydroponic screening. No significant correlations were, however, found between both systems for any of the traits.

Stratification of total variation for genotype grouping

The PCA identified the first two principal components (PCs) accounting for 96.2% of total variation under the hydroponic and 76.5% of variation under pot culture (Fig. 2). Under the hydroponic system, the first PC accounted for 81.3% and the second PC, 14.9%. Major traits contributing to the PC1 were agronomic and root system traits such as PH, BM, PRL, TRL, PA, SA and RV, while AD alone was found to significantly contribute to the PC2. Under pot culture, the PC1 explained 61.5% of the total phenotypic variation, followed by 15% by PC2. The trait contributions trend was similar to that of the hydropic system but relatively with a lesser degree of influence (Supplementary Table 3). Among the PC1 contributing traits, PRL and PH had relatively less influence under both screening systems. Additionally, NT did not contribute significantly to PC1 under pot culture screening.

K-means clustering of the PC scores of the genotypes revealed two clusters each within the test panel, both the growth systems. In both the screening systems, cluster I comprised 119 genotypes. In comparison, cluster

Table 1. Summary statistics of root and shoot traits under hydroponic (H) and pot culture (P) systems

Traits	Unit	System	Min	Max	Mean	Variance components				SE	CV%
						σ^2_G	σ^2_S	σ^2_{GS}	σ^2_E		
PH	cm	H	29.3	73.5	52.6	202.9**			4.9	0.6	4.2
	cm	P	69.1	139.8	106.0	993.7**	14586.0	199.3	11.0	0.9	3.1
NT	-	P	7.0	13.8	10.2	9.3**	79.7	1.4	1.5	0.1	12.1
SDW	mg	H	56.8	249.4	148.0	4662.6**			13.9	2.9	2.5
	g	P	6.3	25.2	16.2	84.2**	73.7	11.1	1.5	0.3	7.4
RDW	mg	H	11.0	53.1	30.9	232.7**			4.3	0.6	6.7
	g	P	0.4	2.2	1.3	0.7*	4.3	0.1	0.0	0.0	6.4
PRL	cm	H	5.3	19.4	12.4	17.1**			0.4	0.2	5.2
	cm	P	17.4	39.3	27.7	84.8**	26.6	15.8	4.2	0.3	7.4
TRL	cm	H	72.5	378.9	209.1	9966.3**			81.8	4.2	4.3
	cm	P	1674.6	8214.6	4913.9	9403228.8**	15547148.5	665803.0	116891.2	90.8	7.0
PA	cm^2	H	3.3	15.0	8.6	15.9**			0.3	0.2	5.8
	cm^2	P	76.6	413.8	223.6	21547.7**	18723.3	2215.5	289.5	4.4	7.6
SA	cm^2	H	10.4	47.1	27.0	156.6**			2.4	0.5	5.8
	cm^2	P	240.8	1300.1	701.7	212038.5**	166655.1	21060.4	2798.5	13.6	7.5
AD	µm	H	306.0	535.3	415.9	0.0**			0.0	2.7	4.8
	µm	P	300.0	595.6	452.0	0.0**	0.0	0.0	0.0	3.4	3.1
RV	mm^3	H	90.6	556.4	283.3	0.0**			0.0	0.0	9.9
	mm^3	P	265.0	1626.0	810.0	38.1**	20.9	6.3	0.6	0.2	9.3

PH = Plant height in cm; NT = number of tillers; SDW = Shoot dry weight in mg; RDW = Root dry weight in g; PRL = Primary root length in cm; TRL = Total = oot length in cm; PA = Projected root area in cm^2; SA = Surface area in cm^2; AD = Average root diameter in mm; RV = Root volume in mm^3; H = Hydroponic; P = Pot culture; σ^2_G, σ^2_S, σ^2_{SG}, σ^2_E, are variance components respectively for genotypes (G), seasons (S), genotype:season (GS) and residual (E); SE = Standard error of mean and CV% = coefficient of variation in %.

Fig. 1. Correlation matrices among root and shoot traits in hydroponics and in pot culture and between both systems

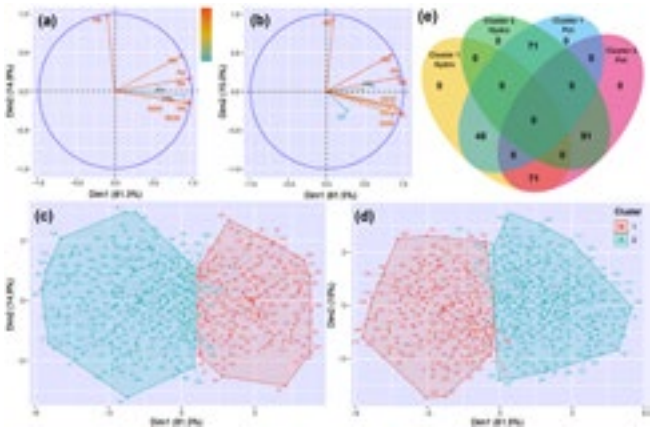

Fig. 2. Multivariate clustering followed by principal component analysis revealed significant contribution of traits towards major principal components in (a) hydroponics and (b) pot culture. Two clusters were identified in both the evaluation systems, (c) hydroponics and (d) pot culture, with common genotypes shared across the methods shown in a Venn diagram (e)

II contained 162 genotypes (Fig. 2). Cluster centroids indicated that, under hydroponics, cluster II genotypes had significantly higher mean values for all the traits except AD (Table 3). In the pot culture system, the cluster mean of the first cluster was found to be significantly higher than that of cluster II for all the traits. There was a marked departure of genotypes between clusters across the culture systems.

Visually illustrating the relationships and overlaps between the different clusters, the Venn diagram (Fig. 2e) under both growing systems indicated that cluster I

Table 3. Cluster centroids for root and shoot traits (a) in hydroponics and (b) in pot culture

Trait	Cluster I	Cluster II	p-value	Cluster I	Cluster II	p-value
PH	44.06	58.92	7.5E-49	118.7	96.5	1.6E-42
NT	-	-	-	10.7	9.8	2.6E-06
SDW	103.61	180.57	5.4E-62	20.1	13.4	9.6E-46
RDW	20.61	38.41	8.1E-70	1.6	1.0	6.1E-45
TRL	143.07	257.49	1.5E-65	6351.9	3861.0	1.7E-65
PRL	9.88	14.32	7.2E-53	29.5	26.3	2.8E-09
PA	5.99	10.52	6.0E-64	295.7	171.0	2.1E-77
SA	18.83	33.07	6.0E-64	927.9	536.7	2.0E-77
AD	421.86	411.73	6.3E-02	462.6	444.8	9.9E-03
RV	201.28	343.64	2.9E-44	10.9E03	6.1E03	2.3E-55

PH = Plant height in cm; NT = Number of tillers; SDW = Shoot dry weight in mg; RDW = Root dry weight in g; PRL = Primary root length in cm; TRL = Total root length in cm; PA = Projected root area in cm^2; SA = Surface area in cm^2; AD = Average root diameter in mm and RV = Rroot volume in mm^3

of hydroponics shared 48 genotypes with cluster I of pot culture. Similarly, cluster II of both the culture systems had 91 genotypes in common. The overlapping region between cluster I in hydroponics and cluster II in pot culture and vice-versa contained 71 genotypes, making a total of 142 genotypes (50.5%) getting cross-classified among the clusters between both the screening systems.

Varietal and spatial patterns among the root system clusters

Based on root system traits, the two genotype clusters each contained six varietal patterns, equally distributed except for the *indica* group in pot culture. The chi-square probability indicated no significant difference in class frequency (Table 4). Both clusters comprised 21% *Aus*/*Boro* types, 5% Basmati/Sadri types, 61% *indica*, 4% intermediates, 1% temperate *japonica*, and 8% tropical *japonica* types.

A similar pattern emerged when genotypes were grouped by their place of origin (Fig. 3). The current assembly's genotypes originated from 32 locations, including four outside India. Each foreign location had one genotype. Of the remaining 28 Indian locations, one group was labeled 'Location uncertain,' and another broadly as 'Northeast India' without assigning to a specific state. The remaining 86% of genotypes came from 26 Indian states. Under both screening systems, the distribution of cluster I and cluster II genotypes across the states was non-significant, except for a few states such as Assam, Manipur, and Meghalaya under hydroponic culture, and the genotype groups from location uncertain, Chhattisgarh, and Kerala under pot culture (Supplementary Table S4).

Discussion

Root system architecture is a crucial heritable trait that must be emphasized in breeding programs. Unlike shoot phenotyping, root phenotyping presents significant challenges (Uga 2021). As the root system is the primary sensor of water and nutrient imbalances in the soil, as well as other edaphic factors such as salinity, acidity, metal toxicity, oxygen status, and soil temperature, understanding root system variability, is essential for determining genotypes' plasticity in confronting challenging soil conditions. By evaluating the diversity of root system architectural traits in various rice accessions, breeders can identify and select the most promising genotypes for future breeding and improvement (Guimarães et al. 2020). Although identified as a priority area, research on root adaptive mechanisms (Panda et al. 2021) has a relatively short history in crop improvement.

Table 4. The varietal pattern among the root system clusters in hydroponic and pot culture

Varietal group	Hydroponic culture		χ^2*p*-value	Pot culture		χ^2*p*-value
	Cluster I	Cluster II		Cluster I	Cluster II	
Aus/boro	23	37	0.07	26	34	0.30
Basmati/sadri	5	8	0.41	7	6	0.78
indica	75	97	0.09	67	105	0.00*
Intermediate type	5	7	0.56	6	6	1.00
Temperate *japonica*	2	1	0.56	0	3	0.08
Tropical *japonica*	9	12	0.51	13	8	0.28

*Significant at 5% level

Fig. 3. Distribution of cluster I and cluster II genotypes at their geographical origins in India. Red pies indicate the proportion of cluster I genotypes under hydroponic culture, and green pies indicate the same under pot culture. The white sector indicates cluster II proportions

This is particularly significant in semi-aquatic crops like rice, where the root system adapts to a broad range of growth conditions, from upland to lowland, aerobic to submerged, and various cropping systems, such as direct seeding to transplanting.

The current investigation, therefore, scrutinizes the phenotypic diversity among the genotype panel and examines the pattern of diversity among different varietal groups and locations of origin. The panel itself was random but were members of an already existing 3K rice genome assembly. Only Indian origin genotypes were selected and were spread across all the regions of India. It was hypothesized that if adaptive patterns exist within the varietal groups or spatial regions, root system diversity would show deviations aligning with such patterns. Such alignment would be phenotypic rather than genotypic. If no alignment pattern emerges, it suggests that no adaptive root system changes have been introduced through breeding, at least within the varietal or spatial origin of the genotypes.

Two culture systems were used in the study: hydroponics and pot culture. Hydroponics, a soil-free growth management system, allows plants to grow and be managed easily under controlled environments (Gericke 1940). It is widely used for experimental and commercial cultivation of both dicots and monocots (Jones 1982). The hydroponic system offers unrestricted opportunities for plant roots to grow and access nutrients from the surrounding growth media. However, it provides minimal root anchorage since plants float over the nutrient mixture (Butler and Oebker 1962). In rice, hydroponics provides root submergence as in the semi-aquatic environment, making it ideal for root system studies, particularly at the seedling stage (Sharma et al. 2018). However, hydroponics does not replicate the actual rice-growing environment where plants are anchored to a soil matrix that remains submerged throughout the crop duration.

Pot culture is, therefore, the next best alternative to simulate field conditions while maintaining close management under a controlled environment. This system ensures maximum similarity to field conditions, including soil puddling and transplanting 35-day-old seedlings. The nutrient profile of the main field is maintained in individual pots, and standing water is retained as in open fields. The advantage of the pot culture system is the ability to harvest the total root system without any loss, which is difficult to achieve under field conditions. However, root extraction is cumbersome and requires careful washing to remove the soil adhering to the roots. By providing two different growth environments in the current study, root system responses under both conditions and at different crop growth phases could be observed. The hydroponic system provided early root responses, while pot culture facilitated responses up to the reproductive stage.

As anticipated, significant variability in the root system was observed among genotypes under both screening systems. The most substantial deviations were noted in total root length, root surface area, and root diameter across all genotypes and culture systems. This indicates that these traits exhibited the most stable expression and accounted for the greatest variation in root system architecture, regardless of the cultural environment. Notably, root diameter demonstrated a poor correlation with other root traits, signifying its independence from common root system characteristics such as root length and biomass. This phenomenon is attributed to the varying root diameters along different root lengths at various root levels, as documented in several cereals, including maize (Wu et al. 2016).

The correlation between the two screening methods was found to be weak, primarily due to significant differences in the growing environments, growth mediums, and developmental stages used during the screening procedure. These distinct characteristics were critical in minimizing potential correlations between the traits studied. Similar findings were reported by Saengwilai et al. (2018) in their study comparing the phenotypic variation of root traits in Thai rice.

The root system traits exhibited maximum variation across both culture systems, with no correlation between them, providing an ideal scenario for analyzing root system

variation among genotypes. Two distinct clusters were identified under each system, with overlapping genotypes showing less consistent patterns between them. When considering the common genotypes shared between clusters in both culture systems, Cluster I of the hydroponic system had 17% of its genotypes in common with Cluster I of the pot culture and 25% with Cluster II. Similarly, Cluster II of the hydroponic system shared 33% of its genotypes with Cluster II of the pot culture and 25% with Cluster I. This highlights significant deviations between the pot culture and hydroponic systems, likely influenced by the crop growth stage and growth conditions. The root system pattern in hydroponics primarily reflected the seedling stage, whereas in pot culture, it reflected the reproductive stage, characterized by a more robust root system compared to the former. Root system plasticity is a characteristic feature of the adaptive response in rice, where root patterns adjust to phenological stages, cultivation environments, and stress factors (Sandhu et al. 2016). Thus, in this study, we integrated responses from two growth stages and two different cultivation systems to maximize the variability among genotypes for root system traits. Previous studies have shown that increasing total root length, root dry weight, and root volume can enhance plant growth under reduced nitrogen conditions (Guan et al. 2022) and improve the ability of plants to extract water and nutrients from complex soils (Kawai et al. 2022). In our study, genotypes Bokdel, Ratnagiri 45-2, Kanpuri, ARC 12067, Dodgui, Dhaniya Phool, Banikat, and Lal Taura exhibited high total root length and root dry weight in both systems while also expressing finer roots indicated by low root diameter. Genotypes Chundi, ARC 10799, Perunel, ARC 10028, W 398, ARC 18112, and ARC 10100 were found to have thicker and longer roots. Genotypes with robust root systems are known for their tolerance to various abiotic stresses (Khan et al. 2016). It would be valuable to evaluate the potential tolerance of these genotypes to different stress factors. Understanding these genotype patterns is essential for advancing plant breeding applications. Liao et al. (2022) reported that fine root diameters with long specific root lengths can penetrate dry, compacted soils, allowing root systems to grow deeper and maintain plant productivity under drought stress (Comas et al. 2013).

Having maximized the root diversity expression, we examined whether any adaptation pattern exists within the panel when classified into varietal groups or based on locations of origin. If adaptation is present, a skewed distribution of clusters within these classes would be observed; otherwise, an equal distribution is expected. Chi-square analyses on the frequency distribution of clusters within each class revealed predominantly insignificant variation, indicating no specific adaptation associated with either varietal classes or locations of origin. However, there were exceptions, such as the *indica* group in pot culture, which showed a skewness towards cluster II, and certain classes based on original locations, such as Kerala, Chhattisgarh, and locations marked as uncertain. The root system among cluster I and cluster II genotypes, comprising 61% and 39% of the *indica* group, respectively, indicated selective adaptation to pot culture, which was absent under hydroponics. Surprisingly, cluster I exhibited better average root system performance than cluster II. This implies that there have been marginal changes in root system traits within the *indica* group, resulting in a slight but distinct behavior under pot culture conditions. Although this was the largest subgroup in the panel, the next largest subgroup, *Aus/Boro*, did not exhibit similar behavior. The variations found among the location classes appeared random or could be attributed to factors such as low genotype representation for these classes.

Understanding root system architecture diversity can uncover desirable traits and lead to the development of novel rice varieties with efficient root systems through plant breeding. These enhanced root systems improve resource utilization, plant growth, drought tolerance, and adaptability. Our study suggested that germplasm exhibited considerable variation in root traits under both hydroponics and pot culture but with limited improvements over time. This highlights significant opportunities for the enhancement of these traits. The findings from this study call for further investigation into root system traits to achieve adaptive improvements in response to temporal enhancements in above-ground plant biomass. This requires examining a larger panel and associating molecular patterns with these variations to improve the efficiency and effectiveness of root breeding programs.

Supplementary material

Supplementary Tables S1 to S4 are provided, which can be accessed at www.isgpb.org

Authors' contribution

Conceptualization of research (KKV, AKS); Designing of the experiments (KKV, KNG, VC); Contribution of experimental materials (RKE, AK); Execution of field/lab experiments and data collection (KNG, PKB, RP, SK); Analysis of data and interpretation (KNG, KKV, GKS, RKE, HP); Preparation of the manuscript (KNG, KKV).

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Supplementary Table S1. Particulars of genotypes used in the study

S.No.	IRGC No	IRIS ID	Variety name	Varietal group	Native
1	5999	313-9083	Pankhari 203	Basmati/sadri	Gujarat
2	117327	313-10349	CSR-90 IR-2	Indica	Haryana
3	76296	313-9610	Dangar	Aus/boro	Gujarat
4	117346	313-10404	K 479-2-3	Indica	Uncertain
5	35154	313-8771	Simul Khuri	Aus/boro	West Bengal
6	20709	313-9137	ARC 10100	Aus/boro	Meghalaya
7	21780	313-8554	ARC 11959	Aus/boro	Arunachal Pradesh
8	22710	313-7736	Nona Bokra	Indica	West Bengal
9	26971	313-7780	Sona(IET 1991)	Indica	Andhra Pradesh
10	122259	313-8147	T 757	Indica	Uncertain
11	27594	313-9108	Rayada	Aus/boro	Bangladesh
12	67707	313-8796	Dudh Kadar	Indica	Madhya Pradesh
13	52523	313-8631	Dudre	Indica	Karnataka
14	49790	313-8559	Keeripala Chill Paddy	Indica	Kerala
15	63113	313-8647	Perunel	Indica	Tamil Nadu
16	61667	313-8435	UPRH233	Indica	Uttar Pradesh
17	12524	313-9609	ARC 10594	Indica	Meghalaya
18	12603	313-8986	ARC 10754	Indica	Meghalaya
19	12631	313-9313	ARC 10799	Indica	Meghalaya
20	21348	313-9176	ARC 11359	Tropical japonica	Meghalaya
21	14567	313-8999	ARC 11430 B	Intermediate type	Arunachal Pradesh
22	42672	313-8946	ARC 11524	Indica	Arunachal Pradesh
23	21528	313-9392	ARC 11626	Intermediate type	Arunachal Pradesh
24	40972	313-9560	ARC 11857	Indica	Arunachal Pradesh
25	41068	313-9053	ARC 12536	Intermediate type	Nagaland
26	22163	313-8967	ARC 12576	Indica	Nagaland
27	41216	313-9347	ARC 13778	Indica	Assam
28	42256	313-9427	ARC 18092	Indica	Assam
29	42274	313-8982	ARC 18112	Indica	Assam
30	12144	313-9424	ARC 5840	Indica	Assam
31	53715	313-9403	Baduie	Indica	Uttar Pradesh
32	6179	313-8957	BAM 9	Indica	Odisha
33	67720	313-8988	Banikat	Indica	Madhya Pradesh
34	52807	313-9384	Barik Kudi	Indica	Goa
35	45197	313-9348	BK26	Indica	Uncertain
36	45255	313-10148	Cauvery	Indica	Tamil Nadu
37	67485	313-9484	Chnnor	Indica	Madhya Pradesh
38	15777	313-9023	CR60-10	Indica	Odisha
39	52184	313-8924	Kutta	Indica	West Bengal
40	74757	313-9547	Labra	Indica	Madhya Pradesh
41	77529	313-9557	Mullikuruva	Indica	Kerala
42	51932	313-9605	NCS194	Indica	Uttar Pradesh
43	62202	313-9492	NCS237	Indica	Uncertain

S.No.	IRGC No	IRIS ID	Variety name	Varietal group	Native
44	62604	313-9400	NCS964 c	Indica	Uncertain
45	50009	313-9351	Para nellu	Aus/boro	Tamil Nadu
46	61133	313-8920	Patalasafed Sunghawado	Indica	Madhya Pradesh
47	46695	313-9120	Sonapatnai	Tropical japonica	Uncertain
48	52261	313-9611	Wanga Barugulu	Indica	West Bengal
49	117326	313-10348	CSR-89 IR-15	Indica	Haryana
50	61127	313-8757	Nirguni	Indica	Madhya Pradesh
51	8948	313-8244	Pokkali	Indica	Kerala
52	39735	313-9566	RP9-4	Indica	Andhra Pradesh
53	74779	313-8303	Surmatiya	Indica	Madhya Pradesh
54	74782	313-8754	Type 50	Indica	Uttar Pradesh
55	117357	313-10417	UPR 1201-1-20-1	Indica	Uttar Pradesh
56	5891	313-8450	498-2ABR 8	Indica	West Bengal
57	22417	313-8603	ARC 12884	Indica	Nagaland
58	43299	313-8453	ARC 18597	Indica	NE India
59	50690	313-9522	RPW9-4(SS1)	Indica	Telangana
60	67742	313-8731	Nibari	Indica	Madhya Pradesh
61	12190	313-9201	ARC 6044	Indica	Assam
62	46907	313-9190	Unnamed	Tropical japonica	Uncertain
63	45733	313-9259	G 25	Indica	Uncertain
64	45701	313-9433	Gokulganja	Indica	West Bengal
65	74763	313-9258	Makro	Indica	Madhya Pradesh
66	46693	313-9287	Sonamukhi	Indica	West Bengal
67	21074	313-8386	ARC 10812	Indica	Meghalaya
68	42328	313-8414	ARC 18202	Indica	NE India
69	20491	313-8498	ARC 7091	Aus/boro	Meghalaya
70	12331	313-9172	ARC 7229	Indica	Meghalaya
71	10105	313-8530	Dhane Burwa	Indica	West Bengal
72	46459	313-10150	N 22	Indica	Uttar Pradesh
73	62530	313-9516	NCS840	Aus/boro	West Bengal
74	53630	313-8614	Rajhusai(ACR12)	Indica	Uncertain
75	54792	313-8727	T 315	Indica	Andhra Pradesh
76	52785	313-8305	Uraibool	Indica	Uncertain
77	6671	313-8622	Xitto	Indica	Goa
78	21727	313-8585	ARC 11901	Indica	Arunachal Pradesh
79	33967	313-11152	AC74	Indica	Uncertain
80	6254	313-10527	ADT12	Indica	Tamil Nadu
81	81783	313-12052	Adukkan	Indica	Tamil Nadu
82	53942	313-11493	AR 133	Tropical japonica	Tripura
83	12514	313-10671	ARC 10581	Indica	Meghalaya
84	21082	313-10857	ARC 10825	Indica	Meghalaya
85	12653	313-10673	ARC 10843	Aus/boro	Meghalaya
86	21122	313-10858	ARC 10894	Indica	Meghalaya
87	12673	313-10676	ARC 10916	Indica	Meghalaya
88	21278	313-10861	ARC 11276	Aus/boro	Meghalaya

S.No.	IRGC No	IRIS ID	Variety name	Varietal group	Native
89	21283	313-10862	ARC 11281	Tropical japonica	Meghalaya
90	21329	313-10864	ARC 11338	Basmati/sadri	Meghalaya
91	42664	313-11295	ARC 11397	Intermediate type	Arunachal Pradesh
92	21614	313-10869	ARC 11751	Aus/boro	Arunachal Pradesh
93	21639	313-10871	ARC 11777	Aus/boro	Arunachal Pradesh
94	21677	313-10873	ARC 11822	Aus/boro	Arunachal Pradesh
95	21837	313-10875	ARC 12021	Aus/boro	Arunachal Pradesh
96	21881	313-10876	ARC 12067	Aus/boro	Arunachal Pradesh
97	21888	313-10877	ARC 12079	Aus/boro	Arunachal Pradesh
98	21907	313-10878	ARC 12101	Aus/boro	Arunachal Pradesh
99	21929	313-10879	ARC 12124	Aus/boro	Arunachal Pradesh
100	22558	313-10894	ARC 13204	Aus/boro	Nagaland
101	22608	313-10895	ARC 13257	Tropical japonica	Nagaland
102	42743	313-11298	ARC 13544	Aus/boro	Arunachal Pradesh
103	43016	313-11302	ARC 14899	Indica	Tripura
104	41811	313-11274	ARC 14901	Aus/boro	Tripura
105	41848	313-11275	ARC 14975	Indica	Tripura
106	41938	313-11277	ARC 15129	Aus/boro	Manipur
107	43106	313-11304	ARC 15163	Indica	Manipur
108	43174	313-11306	ARC 15385	Indica	Manipur
109	53799	313-11490	ARC 15480	Indica	Manipur
110	51756	313-11443	ARC 18533	Indica	Uncertain
111	12196	313-10664	ARC 6052	Indica	Assam
112	42510	313-11290	ARC 6579	Intermediate type	Assam
113	20436	313-10849	ARC 7001	Aus/boro	Meghalaya
114	40914	313-11255	ARC 7056	Indica	Meghalaya
115	20606	313-10852	ARC 7336	Aus/boro	Meghalaya
116	42538	313-11291	ARC 7425	Aus/boro	Meghalaya
117	44978	313-11348	Aus paddy(red)	Aus/boro	NE India
118	34831	313-11164	Bak Tulsi	Aus/boro	West Bengal
119	52067	313-11448	Baramanj	Indica	West Bengal
120	52410	313-11454	Bari Sutar	Aus/boro	Rajasthan
121	60893	313-11596	Bhainsa Mundariya	Indica	Chhattisgarh
122	60895	313-11597	Bhata Pyagi	Aus/boro	Chhattisgarh
123	34861	313-11166	Bhut Muri	Aus/boro	West Bengal
124	53889	313-11491	Bir Bahadur	Aus/boro	Bihar
125	61085	313-11606	Bokdel	Basmati/sadri	Madhya Pradesh
126	74734	313-11917	Butnapar	Aus/boro	Madhya Pradesh
127	67486	313-11737	Chundi	Indica	Madhya Pradesh
128	45368	313-11355	CN44-40-7	Indica	West Bengal
129	49573	313-11409	Cuttack 29	Indica	Odisha
130	6445	313-10534	D 204-1	Aus/boro	Uncertain
131	17038	313-10756	Damodar	Indica	Haryana
132	70811	313-11824	Dhaniya Phool	Basmati/sadri	Madhya Pradesh
133	6688	313-10544	Dongrem	Indica	Goa

S.No.	IRGC No	IRIS ID	Variety name	Varietal group	Native
134	19560	313-10833	Edakkadan 0-69-27	Indica	Uncertain
135	60944	313-11598	Godadani	Indica	Chhattisgarh
136	66269	313-11712	Gora Dhan 2	Indica	Jharkhand
137	61105	313-11607	Holdiganthi	Indica	Madhya Pradesh
138	50674	313-11432	Iswar Kora	Tropical japonica	Maharashtra
139	60960	313-11599	Jugray	Indica	Chhattisgarh
140	55017	313-11505	K 1074	Indica	Uncertain
141	55043	313-11506	K 15591-4	Indica	Uncertain
142	36778	313-11197	K 17-9-1-1	Indica	Uncertain
143	34954	313-11168	Kada Chopa	Aus/boro	West Bengal
144	67718	313-11742	Kalibajari	Basmati/sadri	Uncertain
145	53670	313-11489	Kalu T 139	Indica	Punjab
146	53278	313-11477	Kanpuri	Indica	Gujarat
147	77128	313-11963	Karangi	Aus/boro	Uttar Pradesh
148	49774	313-11414	Karunjeeraga Samba	Indica	Karnataka
149	34154	313-11156	Khudwani ACC 202	Tropical japonica	Jammu & Kashmir
150	52168	313-11449	Kodia Phul	Aus/boro	Odisha
151	52456	313-11456	Kolamba	Aus/boro	Rajasthan
152	75448	313-11937	Kunjukunju	Indica	Kerala
153	74760	313-11919	Lakha Kuar	Indica	Madhya Pradesh
154	70854	313-11828	Lali Gurmatia	Temperate japonica	Chhattisgarh
155	35017	313-11170	Lal Taura	Aus/boro	West Bengal
156	52343	313-11452	Local Bhat	Indica	Maharashtra
157	35054	313-11171	M 142	Aus/boro	West Bengal
158	61004	313-11602	Malchi	Aus/boro	Madhya Pradesh
159	50707	313-11433	MR136-1	Tropical japonica	Karnataka
160	52009	313-11446	Napdai	Indica	Manipur
161	51854	313-11445	NCS102	Indica	Bihar
162	62216	313-11636	NCS271 A	Indica	Uncertain
163	62247	313-11638	NCS331	Indica	Uncertain
164	62290	313-11640	NCS458	Indica	Uncertain
165	62373	313-11642	NCS599	Indica	Uncertain
166	62377	313-11643	NCS603 B	Indica	Uncertain
167	62478	313-11645	NCS766	Indica	Uncertain
168	62483	313-11646	NCS771 A	Indica	Uncertain
169	62502	313-11647	NCS809 A	Indica	Uncertain
170	62568	313-11650	NCS901 A	Temperate japonica	Uncertain
171	19581	313-10835	Perunel 0-69-18	Indica	Tamil Nadu
172	28611	313-11041	Poongar	Indica	Tamil Nadu
173	53418	313-11480	PR106	Aus/boro	Punjab
174	35109	313-11172	Rani Bhog	Aus/boro	West Bengal
175	39709	313-11243	Ratnagiri 45-2	Aus/boro	Maharashtra
176	35117	313-11173	Sada Aus	Aus/boro	West Bengal
177	52833	313-11462	Salsi	Indica	Goa
178	46659	313-11371	Sathi	Aus/boro	Uttarakhand

S.No.	IRGC No	IRIS ID	Variety name	Varietal group	Native
179	53930	313-11492	Sirhanti	Indica	Bihar
180	35157	313-11174	SLO 19	Aus/boro	Andhra Pradesh
181	35160	313-11175	Sona Aus	Aus/boro	Odisha
182	61059	313-11604	Sugarkand	Indica	Madhya Pradesh
183	35175	313-11176	SxC216	Indica	Uncertain
184	8892	313-10608	T 21	Aus/boro	Uttar Pradesh
185	61615	313-11619	UPRH166	Aus/boro	Uttar Pradesh
186	61641	313-11620	UPRH197	Indica	Uttar Pradesh
187	61689	313-11621	UPRH265	Indica	Uttar Pradesh
188	61503	313-11616	UPRH31	Aus/boro	Uttar Pradesh
189	61525	313-11618	UPRH58	Aus/boro	Uttar Pradesh
190	52805	313-11461	Vaikatharyan	Aus/boro	Kerala
191	53339	313-11479	Vankali	Indica	Gujarat
192	19588	313-10836	Vella Peruvazha 0-68-12	Indica	Kerala
193	46787	313-11374	W 398	Aus/boro	Uncertain
194	42557	313-11292	ARC 10120	Indica	Meghalaya
195	12656	313-10674	ARC 10846	Indica	Meghalaya
196	21150	313-10859	ARC 10939	Indica	Meghalaya
197	42651	313-11294	ARC 11245	Indica	Assam
198	21315	313-10863	ARC 11322	Indica	Assam
199	21380	313-10865	ARC 11424	Tropical japonica	Arunachal Pradesh
200	21487	313-10868	ARC 11571	Basmati/sadri	Arunachal Pradesh
201	21965	313-10880	ARC 12180	Indica	Arunachal Pradesh
202	41047	313-11256	ARC 12411	Indica	Nagaland
203	22148	313-10885	ARC 12559	Indica	Nagaland
204	22288	313-10888	ARC 12726	Tropical japonica	Arunachal Pradesh
205	41095	313-11257	ARC 12757	Intermediate type	Nagaland
206	42720	313-11296	ARC 12800	Indica	Nagaland
207	22622	313-10896	ARC 13276	Aus/boro	Nagaland
208	41126	313-11258	ARC 13502	Basmati/sadri	Arunachal Pradesh
209	41134	313-11259	ARC 13515	Basmati/sadri	Arunachal Pradesh
210	41177	313-11260	ARC 13591	Indica	Arunachal Pradesh
211	41288	313-11262	ARC 13888	Indica	Assam
212	41313	313-11263	ARC 13919	Indica	Assam
213	42889	313-11299	ARC 14299	Indica	Nagaland
214	41517	313-11266	ARC 14347	Indica	Assam
215	41523	313-11267	ARC 14358(gold hull)	Indica	Assam
216	41650	313-11269	ARC 14632	Intermediate type	Assam
217	41671	313-11270	ARC 14663	Intermediate type	Assam
218	42976	313-11300	ARC 14709	Indica	Assam
219	41793	313-11273	ARC 14860	Indica	Tripura
220	43009	313-11301	ARC 14868	Indica	Tripura
221	43166	313-11305	ARC 15373	Indica	Manipur
222	43175	313-11307	ARC 15387	Indica	Manipur
223	43183	313-11308	ARC 15403	Indica	Manipur

S.No.	IRGC No	IRIS ID	Variety name	Varietal group	Native
224	42040	313-11279	ARC 15455	Indica	Manipur
225	43269	313-11310	ARC 15929	Indica	Nagaland
226	42423	313-11287	ARC 18371	Indica	Odisha
227	42429	313-11288	ARC 18434	Indica	Odisha
228	12343	313-10668	ARC 7255	Indica	Meghalaya
229	45003	313-11349	Bachhaikalma	Indica	Odisha
230	45024	313-11350	Bajal	Basmati/sadri	Odisha
231	49440	313-11407	Batcha Bhog(scented)	Indica	Andhra Pradesh
232	36849	313-11200	BR52-87-1	Indica	Odisha
233	45237	313-11352	Buchi	Basmati/sadri	Odisha
234	45352	313-11354	CAC75	Indica	Odisha
235	45297	313-11353	Chile Boro	Aus/boro	Odisha
236	49524	313-11408	Chitrakali	Indica	Tamil Nadu
237	46865	313-11375	Code No 31225	Intermediate type	Odisha
238	39247	313-11240	CR157-392-4	Indica	Odisha
239	26850	313-10989	Gutti-Akkullu	Indica	Odisha
240	45996	313-11361	Kalikalma	Indica	Odisha
241	46117	313-11362	Keya Nunia	Basmati/sadri	Odisha
242	16948	313-10754	KH998	Indica	Odisha
243	24135	313-10929	Kolongi Bao	Indica	Odisha
244	46236	313-11365	Lanjali	Indica	Odisha
245	46289	313-11367	Makarandasail	Indica	Odisha
246	49891	313-11418	Matali	Indica	Punjab
247	46500	313-11368	Panikelash	Indica	Odisha
248	46567	313-11369	Ranachandrabhog	Indica	Odisha
249	10803	313-10640	SR26 B	Indica	Odisha
250	46698	313-11372	Sufaldhula	Indica	Odisha
251	36842	313-11199	Synthetic Sativa	Indica	Uncertain
252	46760	313-11373	T 3	Basmati/sadri	Uttarakhand
253	50192	313-11421	Tulasibas	Indica	Odisha
254	60878	313-11595	Amakoyali	Indica	Chhattisgarh
255	20981	313-10856	ARC 10537	Indica	Meghalaya
256	21418	313-10866	ARC 11478	Tropical japonica	Arunachal Pradesh
257	21463	313-10867	ARC 11538	Tropical japonica	Arunachal Pradesh
258	22514	313-10893	ARC 13156	Tropical japonica	Nagaland
259	22691	313-10897	ARC 13373	Indica	Nagaland
260	74738	313-11918	Dilbaksh	Indica	Madhya Pradesh
261	6666	313-10543	Dodgui	Aus/boro	Goa
262	70840	313-11826	Hira Nakhi	Indica	Chhattisgarh
263	6394	313-10531	HR22	Intermediate type	Telangana
264	19573	313-10834	IARI 11387	Tropical japonica	New Delhi
265	53973	313-11494	IC25690	Tropical japonica	Arunachal Pradesh
266	52324	313-11451	Kalisal	Aus/boro	Maharashtra
267	52664	313-11458	Karahani	Temperate japonica	Chhattisgarh
268	60982	313-11600	Kotodeshi	Aus/boro	Madhya Pradesh

S.No.	IRGC No	IRIS ID	Variety name	Varietal group	Native
269	74318	313-11913	Buagkog	Tropical japonica	Philippines
270	42316	313-8458	ARC 18175	Indica	Assam
271	21630	313-10870	ARC 11768	Tropical japonica	Arunachal Pradesh
272	42066	313-11281	ARC 15505	Indica	Manipur
273	20370	313-10848	ARC 6188	Tropical japonica	Meghalaya
274	34967	313-11169	Kanai Bashi	Aus/boro	NE India
275	20656	313-10853	ARC 10028	Tropical japonica	Meghalaya
276	41435	313-11265	ARC 14150	Aus/boro	Assam
277	42096	313-11282	ARC 15589	Indica	Manipur
278	20570	313-10850	ARC 7263	Intermediate type	Meghalaya
279	24252	313-10933	ARC 7281	Basmati/sadri	Meghalaya
280	49850	313-11417	Lawangai	Intermediate type	Punjab
281	34514	313-11161	Sadu	Tropical japonica	Liberia

Supplementary Table S2. Composition of Modified Yoshida (stock and culture) nutrient solution

Element	*Reagent*	*Formula*	*Quantity for stock*		*Nutrients*		*Culture solution*	
			g/10L	*g/L*	*%*	*g/L*	*ppm*	*Stock(ml)/4 L*
Stock A								
K+N	Potassium nitrate	KNO_3	567.3	56.73	38.67 K 13.85 N	21.94 K 7.86 N	40	5.0
N	Ammonium sulphate	$(NH_4)_2SO_4$	1138.0	113.80	21.20 N	24.13 N	40	5.0
K+P	Potassium dihydrogen phosphate	KH_2PO_4	351.5	35.15	22.76 P 28.73 K	8.00 P 10.10 K	10	5.0
Stock B								
Ca	Calcium chloride	$CaCl_2$	886.0	88.60	36.11	32.00	40	5.0
Mg	Magnesium sulphate	$MgSO_4.7H_2O$	3240.0	324.00	9.86	31.95	40	5.0
Stock C								
Mn	Manganese chloride	$MnCl_2.2H_2O$	15.0	1.50	33.94	0.51	0.5	5.0
Mo	Ammonium molybdate	$(NH_4)_6Mo_7O_{24}.4H_2O$	0.74	0.074	54.34	0.04	0.05	
B	Boric Acid	H_3BO_3	9.34	0.934	17.48	0.16	0.2	
Zn	Zinc sulphate	$ZnSO_4.7H_2O$	0.35	0.035	22.74	0.008	0.01	
Cu	Copper sulphate	$CuSO_4.5H_2O$	0.31	0.031	25.45	0.008	0.01	
Fe	Ferrous sulphate	$FeSO_4.7H_2O$	79.20	7.92	20.09	1.60	2	
	Citric acid (monohydrate)		119.0	11.9				

Supplementary Table S3. Contribution of traits towards the major principal components derived from the root and morphological data from principal component analysis

Traits	Hydroponic screen		Pot culture screen	
	PC1	PC2	PC1	PC2
PH	11.47	0.26	11.59	3.06
NT	-	-	1.33	4.44
PRL	12.24	1.62	4.02	0.02
RDW	13.07	1.69	13.01	2.02
SDW	13.12	1.67	12.90	5.72
TRL	13.12	1.84	14.46	3.18
PA	13.16	2.12	15.24	2.39
SA	13.16	2.11	15.25	2.35
AD	0.13	72.77	0.15	61.52
RV	10.53	15.93	12.05	15.29

PH = Plant height in cm; NT = Number of tillers; SDW = Shoot dry weight in mg; RDW = Root dry weight in g; PRL = Primary root length in cm; TRL = Total root length in cm; PA = Projected root area in cm^2; SA = Surface area in cm^2; AD = Average root diameter in mm and RV = Rroot volume in mm^3

Supplementary Table S4. Pattern of cluster distribution among the locations of origin based on two screening systems.

No	Origin	Hydroponics						Pot culture					
		Cluster 1	Cluster 2	χ^2	p	Prop	Pie	Cluster 1	Cluster 2	χ^2	p	Prop	Pie
1	Uncertain	13	17	0.53	0.47	43%	j	7	23	8.53	0.00	23%	e
2	Andhra Pradesh	3	2	0.20	0.65	60%	m	1	4	1.80	0.18	20%	e
3	Arunachal Pradesh	10	17	1.81	0.18	37%	h	15	12	0.33	0.56	56%	l
4	Assam	14	4	5.56	0.02	78%	q	10	8	0.22	0.64	56%	l
5	Bangladesh	0	1	1.00	0.32	0%	a	1	0	1.00	0.32	100%	v
6	Bihar	1	2	0.33	0.56	33%	h	1	2	0.33	0.56	33%	h
7	Chattisgarh	5	3	0.50	0.48	63%	n	0	8	8.00	0.00	0%	a
8	Goa	4	1	1.80	0.18	80%	q	3	2	0.20	0.65	60%	m
9	Gujarat	1	3	1.00	0.32	25%	f	3	1	1.00	0.32	75%	p
10	Haryana	0	3	3.00	0.08	0%	a	0	3	3.00	0.08	0%	a
11	Jammu & Kashmir	0	1	1.00	0.32	0%	a	1	0	1.00	0.32	100%	v
12	Jharkhand	0	1	1.00	0.32	0%	a	0	1	1.00	0.32	0%	a
13	Karnataka	0	3	3.00	0.08	0%	a	1	2	0.33	0.56	33%	h
14	Kerala	1	5	2.67	0.10	17%	d	0	6	6.00	0.01	0%	a
15	Liberia	1	0	1.00	0.32	100%	v	1	0	1.00	0.32	100%	v
16	Madhya Pradesh	7	12	1.32	0.25	37%	h	10	9	0.05	0.82	53%	l
17	Maharashtra	1	3	1.00	0.32	25%	f	2	2	0.00	1.00	50%	k
18	Manipur	2	9	4.45	0.03	18%	d	4	7	0.82	0.37	36%	h
19	Meghalaya	9	20	4.17	0.04	31%	g	13	16	0.31	0.58	45%	j
20	Nagaland	6	8	0.29	0.59	43%	j	4	10	2.57	0.11	29%	g
21	NE India	1	3	1.00	0.32	25%	f	2	2	0.00	1.00	50%	k
22	USA	0	1	1.00	0.32	0%	a	1	0	1.00	0.32	100%	v
23	Odisha	18	9	3.00	0.08	67%	o	14	13	0.04	0.85	52%	k

24	Philippines	0	1	1.00	0.32	0%	a	1	0	1.00	0.32	100%	v
25	Punjab	3	1	1.00	0.32	75%	p	1	3	1.00	0.32	25%	f
26	Rajasthan	1	1	0.00	1.00	50%	k	1	1	0.00	1.00	50%	k
27	Tamil Nadu	3	5	0.50	0.48	38%	h	3	5	0.50	0.48	38%	h
28	Telangana	1	1	0.00	1.00	50%	k	0	2	2.00	0.16	0%	a
29	Tripura	3	3	0.00	1.00	50%	k	2	4	0.67	0.41	33%	h
30	Uttar Pradesh	6	7	0.08	0.78	46%	j	6	7	0.08	0.78	46%	j
31	Uttarakhand	0	2	2.00	0.16	0%	a	1	1	0.00	1.00	50%	k
32	West Bengal	5	13	3.56	0.06	28%	f	10	8	0.22	0.64	56%	l

Prop, proportion of Cluster 1 to the total