

RESEARCH ARTICLE

ROOT ARCHITECTURAL TRAITS AND THEIR CONTRIBUTION TO YIELD IN F₂ POPULATIONS OF SELECTED RICE CROSSES UNDER CONTRASTING SOIL CATENA CONDITIONS

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ABSTRACT

Rice yields in Sri Lanka's Wet Zone are frequently constrained by soil and drainage limitations, yet root traits remain underutilized in breeding programs. This study evaluated four F₂ populations of rice crosses, their parents, and two check varieties at the Rice Research Station, Labuduwa, under upper and lower catena positions to evaluate genotype × environment effects under contrasting drainage conditions and to (i) compare root and shoot morphological traits and (ii) quantify associations between root traits and yield components. Plot-level means were analyzed using a two-way model with Cross and Catena effects, and significant Cross × Catena interactions were detected for several traits. Across environments, Crosses 2 and 4 exhibited superior root architecture, characterized by greater root zone width, number of roots, root strength, root volume, and root dry weight, along with competitive yield components. Moderate to high phenotypic and genotypic coefficients of variation for key root and yield traits indicated substantial scope for selection. False discovery rate-controlled correlation analysis revealed positive associations of root zone width, number of roots, root strength, and root volume with effective tiller number, shoot biomass, and total panicle weight. These findings demonstrate the value of targeted selection for root traits to enhance yield stability under contrasting drainage conditions in the Wet Zone of Sri Lanka.

Keywords: Genotypic coefficient of variation, Phenotypic coefficient of variation, Rice crosses, Root morphology, Soil

INTRODUCTION

Rice (*Oryza sativa* L.) is a major staple crop providing more than 20% of the global dietary energy requirement and serving as an important source of carbohydrates, minerals, and vitamins (Verma and Shukla, 2011). Globally, rice ranks third among the most widely cultivated cereals, after maize and wheat (FAO, 2021). In Sri Lanka, rice production declined markedly from 3.06 million metric tons in the 2020–2021 *Maha* season to 1.93 million metric tons in 2021–2022 *Maha*, primarily due to climate variability, pest and disease incidence, and labour shortages (Department of Census and Statistics, 2022; Ministry of Agriculture,

2023). These trends underscore the need to develop high-yielding, stress-tolerant rice varieties to ensure food security under changing environmental conditions.

Root systems play a fundamental role in rice growth and productivity by facilitating anchorage, water and nutrient uptake, and physiological regulation (Meng, 2019). In the Low Country Wet Zone (LCWZ) of Sri Lanka, rice cultivation is constrained by fluctuating moisture regimes, frequent flooding, intermittent drought, nutrient leaching, iron (Fe²⁺) toxicity, and poor soil aeration. Under such conditions, increased root volume and stronger root systems are critical for maintaining nutrient uptake and

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mitigating toxicity effects, while deeper and thicker roots enhance tolerance to temporary moisture stress (Yamamoto *et al.*, 2012).

Rice breeding programs have traditionally focused on above-ground traits because of their well-documented association with grain yield (Shyamalee and Ranawake, 2024). However, poor root development caused by anaerobic soil conditions and low nutrient availability remains a major yield-limiting factor in wetland rice ecosystems of Sri Lanka (Perera *et al.*, 2017; Fernando and Wijeratne, 2015). Some rice genotypes in Sri Lanka have exhibited high survival under drought stress, with certain accessions maintaining tolerance across multiple stress conditions (Ranawake and Hewage, 2014). Further, previous studies have demonstrated that a large, deep, and thick root system with high oxidizing capacity is essential for rice adaptation in wet-zone environments (Yamamoto *et al.*, 2012). Despite advances in understanding the role of roots in drought tolerance, lodging resistance, and nutrient-use efficiency (Kashiwagi *et al.*, 2008; Uga *et al.*, 2013; Zhang *et al.*, 2007), root traits remain under-exploited in breeding programs due to phenotyping difficulties and strong environmental influences (Wu and Cheng, 2014).

Rice root systems also exhibit pronounced plasticity along toposequential gradients. In the LCWZ, upper catena soils are relatively well-drained, whereas lower catena soils are frequently waterlogged, resulting in contrasting root growth patterns, nutrient dynamics, and plant stability (Wijesekara *et al.*, 2013). These contrasting environments intensify genotype \times environment interactions, highlighting the importance of evaluating genotypes across both catena positions to identify stable and adaptive breeding materials (Kirk, 2003). Root traits such as depth, thickness, and oxidizing power are therefore key targets for improving yield stability and resilience across heterogeneous rice-growing landscapes (Yang, 2011; Meng *et al.*, 2019).

The present study was conducted at the Rice Research Station, Labuduwa, Sri Lanka, to evaluate root and shoot morphological

variation in an F₂ rice population developed for root improvement under contrasting upper and lower catena soil conditions. The specific objectives were to: (i) characterize variability in root and shoot morphological traits, (ii) determine relationships between key root traits and yield-related components, (iii) assess the effects of soil catena position and genotype \times environment interactions on plant performance, and (iv) identify root traits with potential as selection indices for improving nutrient uptake, stress tolerance, and yield stability in rice breeding programs.

MATERIALS AND METHODS

Four crosses were selected from F₁ evaluations based on the performance advancement to the F₂ generation (Table 1).

Table 1: Four crosses of respective parents for the evaluation

| Cross | F ₂ | Female | Male |
|-------|-------------------------------|-------------|----------------|
| 1 | Ld 20-12-12/ Ld 20-15-14 | Ld 20-12-12 | Ld 20-15-14 |
| 2 | Ld 20-14-12/ Ld 20-15-14 | Ld 20-14-12 | Ld 20-15-14 |
| 3 | Ld 20-11-03/ Ld 21-06-18-2 | Ld 20-11-03 | Ld 21-06-18-02 |
| 4 | Ld 20-15-14/ Ld 20-22-04 | Ld 20-15-14 | Ld 20-22-04 |

Two field trials were conducted in upper- and lower-catena soils at Rice Research Station, Labuduwa, with two replicates per condition during the 2022/23 *Maha* season. Germinated seeds of each cross, relevant parents and standard check varieties were planted with a spacing of 15 cm x 15 cm with a single seed per hill. Three hundred plants were included in each cross in each replicate; gaps were filled with the same-aged plants grown in parachute trays within seven days. All cultural practices were adopted in accordance with the Department of Agriculture's recommendations.

Data collection

Data were recorded using 25 selected plants per F₂ population of four crosses. Morphological characteristics of plants at maturity were recorded using selected plants from each cross and parents, in two replicates per soil condition.

Shoot traits, plant height (cm), number of tillers per plant, number of effective tillers per plant, flag leaf length (cm), flag leaf width (cm), and shoot dry weight (g), yield traits such as panicle length (cm), seed per panicle, single panicle weight (g), total panicle weight per plant (g), filled and unfilled grains, 1000 grain weight (g) and root traits, length of root zone (cm), width of root zone (cm), number of roots, root volume (ml), and root dry weight (g) were collected at the maturity stage of the trial. The length, width, and number of roots were recorded after carefully washing adhering soil; root volume was assessed by immersing the roots in a measuring cylinder and measuring the increase in water volume as root volume. The shoot-to-root ratio was calculated based on the shoot and root dry weights.

Data analysis

Analysis of variance was performed, and the Duncan Multiple Range Test was carried out to perform mean separation. Correlation analysis between root traits and yield-related traits was performed to assess the strength and direction of linear relationships. Pearson's correlation coefficients were calculated in SAS 9.4 (SAS Institute, Cary, NC, USA) to assess linear relationships between traits.

To account for multiple testing and control the expected proportion of false positives, p-values from correlation analyses were adjusted using the False Discovery Rate (FDR) method as proposed by Benjamini and Hochberg (1995). In this study, FDR-adjusted p-values were computed in SAS software (version 9.4; SAS Institute, Cary, NC, USA) using the PROC MULTTEST procedure. The procedure ranks the individual p-values and calculates adjusted p-values that control the expected proportion of Type I errors among significant results. Correlations with FDR-adjusted p-values < 0.05 were considered statistically significant.

Genetic parameters were estimated separately for all crosses. Genotypic variance was estimated by partitioning the total variance using the method formulated by Weber and

Moorthy (1952).

The phenotypic and genotypic coefficient of variation were computed as per Burton and Devane (1953).

Phenotypic Coefficient of Variation (PCV) = $(\sqrt{\sigma^2_p} / \text{mean}) \times 100$

Genotypic Coefficient of Variation (GCV) = $(\sqrt{\sigma^2_g} / \text{mean}) \times 100$

Where,

σ^2_p : Phenotypic variance, σ^2_g : Genotypic variance, PCV: Phenotypic coefficient of variation, GCV: Genotypic coefficient of variation. PCV and GCV were classified as 0-10% - Low, 10-20% - Moderate, and >20% - High according to Robinson *et al.* (1956).

Broad-sense heritability estimates as percentages were calculated using the formula proposed by Hanson *et al.* (1956).

$h^2 \% = (\sigma^2_g / \sigma^2_p) \times 100$

$h^2 \% =$ Heritability percentage (broad sense)

Where, broad sense heritability is considered as 0-30%: Low, 30-60%: Moderate, >60%: High

Genetic Advance (GA)

$= K \times \sqrt{\sigma^2_p} \times h^2$

(K = 2.06 at 5% selection intensity) Robinson *et al.*, 1956.

RESULTS AND DISCUSSION

Mean performance of F₂ populations of rice crosses under contrasting catena conditions

The present study revealed significant variation among rice crosses in a range of agronomic and root-related traits across contrasting toposequence positions, upper catena (well-drained) and lower catena (poorly drained) soils. This highlights the importance of genotype \times environment interaction in determining performance under varying edaphic conditions (Cooper & Hammer, 1996).

The mean performance of four rice crosses revealed a significant variation among most

morphological and yield-related characters under both upper and lower catena conditions (Table 2). Plant height ranged from 107.9 cm (cross 3) to 118.3 cm (cross 2), indicating genetic diversity among the parental combinations. Crosses 2 and 4 exhibited better performance across most morphological traits. Cross 2 exhibited better performance for several traits, including root

strength, root volume, and shoot dry weight, compared to crosses 1 and 2 in both environments, suggesting its better adaptability, especially in lower catena soils through enhanced anchorage and nutrient uptake. In terms of yield components, the number of filled seeds ranged from 104.5 (cross 3) to 195.6 (cross 1), while total panicle weight was highest in cross 2 (21.6 g).

Table 2: Mean comparison of agronomic and root traits of four F₂ populations of rice crosses evaluated under upper and lower catena conditions

| Character | Cross | | | | Significance | | | |
|-----------|--------------------|--------------------|--------------------|--------------------|--------------|-------|--------------|------|
| | 1 | 2 | 3 | 4 | Soil | Cross | Cross X Soil | CV |
| PH (cm) | 116.1 ^a | 118.3 ^a | 107.9 ^b | 115.9 ^a | ** | * | * | 8.9 |
| RL (cm) | 15.8 ^a | 16.9 ^a | 15.71 ^a | 14.3 ^b | ** | ** | ** | 26.5 |
| RW (cm) | 4.5 ^a | 4.6 ^a | 3.8 ^b | 4.0 ^b | NS | * | NS | 20.8 |
| NR | 154.5 ^b | 177.8 ^a | 117.2 ^c | 158.0 ^b | ** | ** | ** | 44.2 |
| NT | 8.6 ^a | 8.4 ^a | 6.9 ^b | 8.6 ^a | ** | ** | ** | 34.9 |
| NET | 8.0 ^a | 8.1 ^a | 6.7 ^b | 8.4 ^a | ** | ** | ** | 36.7 |
| FLW (cm) | 1.5 ^b | 1.6 ^a | 1.2 ^c | 1.5 ^b | ** | ** | ** | 22.3 |
| RS (N) | 19.7 ^b | 22.8 ^a | 17.4 ^c | 19.9 ^b | ** | ** | ** | 28.2 |
| RV (ml) | 42.4 ^a | 46.3 ^a | 26.8 ^c | 32.9 ^b | ** | ** | NS | 49.0 |
| NSPP | 283.1 ^a | 302.2 ^a | 284.9 ^a | 291.7 ^a | ** | ** | ** | 28.2 |
| FS | 195.6 ^a | 170.6 ^b | 104.5 ^d | 145.4 ^c | ** | ** | ** | 45.5 |
| RDW (g) | 8.6 ^b | 9.7 ^a | 5.9 ^c | 8.1 ^b | ** | ** | NS | 49.4 |
| SDW (g) | 16.7 ^b | 20.4 ^a | 14.4 ^c | 20.2 ^a | ** | ** | NS | 44.4 |
| SPW (g) | 3.3 ^a | 3.3 ^a | 3.3 ^a | 2.5 ^b | ** | ** | ** | 44.6 |
| TPWPP (g) | 19.9 ^{ab} | 21.6 ^a | 16.0 ^c | 18.3 ^{bc} | ** | ** | ** | 48.7 |

PH: Plant height, RL: Root length, RW: Root width, NR: Number of roots, NT: Number of tiller, NET: Number of effective tiller, FLW: Flag leaf width, RS: Root strength, RV: Root volume, NSPP: Number of seeds per panicle, FS: Filled seeds, RDW: Root dry weight, SDW: Shoot dry weight, SPW: Single panicle weight, TPWPP: Total panicle weight per plant, Means followed by the same letter within a row are not significantly different at $p \leq 0.05$

** highly significant, *significant, NS: not significant

In contrast, cross 3 expressed lower root volume and root dry weight, implying weaker root development. Notably, cross 3 showed significantly lower performance in terms of total panicle weight and number of filled seeds, especially in lower catena soil, indicating poor sink development, possibly due to reduced assimilate partitioning. The performance of cross 2 for most yield and root traits suggests that this cross possesses favourable allelic combinations for yield potential and stress adaptation.

These findings agree with the previous study by Kumar *et al.* (2020) who reported that crosses with balanced root vigour and shoot growth exhibit higher grain yield under variable water regimes. The increased root strength and volume can enhance nutrient and water uptake, especially under less favourable

conditions (Henry *et al.*, 2011; Uga *et al.*, 2013). The high variability among crosses in root length, root width, and dry weight indicates the presence of diverse root architectural types that could be useful for selection under moisture-deficit conditions.

The significant interaction effects (cross \times soil position) observed for traits such as root length, root width, shoot dry weight, and root dry weight underscore the need to evaluate genotypes across topographic gradients (Wickramasinghe & Mallawatantri, 2003). Cross 4, although not consistently superior, showed potential under upper catena conditions for traits such as flag leaf length and total seeds, indicating it may possess desirable traits for aerobic soil adaptation (Pandey *et al.* 2002).

Overall, the findings emphasize the importance of multi-environment testing and selection for specific adaptation in rice breeding programs, especially in landscapes with variable soil conditions (Khush, 1995; Linquist *et al.* 2006). Root architectural traits should be given priority during selection to ensure resilience under both drought-prone

upland and waterlogged lowland conditions.

Effect of soil catena position on morphological traits

The comparison between lower- and upper-catena conditions revealed distinct environmental effects on most traits (Table 3).

Table 3: Comparison of performance between upper and lower catena conditions

| Characters | Lower catena | Upper catena | CV % |
|---------------------------|--------------------|--------------------|------|
| PH (cm) | 116.6 ^a | 112.6 ^b | 8.9 |
| Culm height (cm) | 87.6 ^a | 83.0 ^b | 8.7 |
| Root length (cm) | 20.2 ^a | 11.2 ^b | 26.6 |
| Root width (cm) | 4.2 ^a | 4.3 ^a | 20.8 |
| No of roots | 182.0 ^a | 121.8 ^b | 44.3 |
| No of tillers | 7.6 ^b | 8.7 ^a | 34.9 |
| No of effective tillers | 7.3 ^b | 8.3 ^a | 36.7 |
| Flag leaf width (cm) | 1.5 ^a | 1.4 ^b | 22.3 |
| Root strength (N) | 18.7 ^b | 21.3 ^a | 28.3 |
| Root volume (ml) | 46.4 ^a | 27.9 ^b | 49.0 |
| Panicle length (cm) | 21.9 ^a | 22.3 ^a | 15.2 |
| No of seeds | 308.9 ^a | 272.1 ^b | 28.2 |
| Filled seeds | 127.1 ^b | 181.0 ^a | 45.6 |
| Unfilled seeds | 181.8 ^a | 94.0 ^b | 42.6 |
| Root dry weight (g) | 7.3 ^b | 8.8 ^a | 49.4 |
| Shoot dry weight (g) | 19.0 ^a | 16.9 ^b | 44.1 |
| Total panicle weight (g) | 15.3 ^b | 22.6 ^a | 48.8 |
| Single panicle weight (g) | 2.2 ^b | 4.0 ^a | 44.7 |
| 1000 grain weight (g) | 15.8 ^b | 17.0 ^a | 32.7 |

PH: Plant height, CH: Culm height, RL: Root length, RW: Root width, NR: Number of roots, NT: Number of tiller, NET: Number of effective tiller, FLW: Flag leaf width, RS: Root strength, RV: Root volume, NSPP: Number of seeds per panicle, FS: Filled seeds, RDW: Root dry weight, SDW: Shoot dry weight, SPW: Single panicle weight, TPWPP: Total panicle weight per plant. Means followed by the same letter within a row are not significantly different at $p \leq 0.05$

Plants grown in the lower catena showed significantly higher plant height, culm length, and root length. In contrast, plants grown in the upper catena exhibited greater numbers of tillers, effective tillers, and panicle weight. Root traits were highly responsive to differences in moisture regime. Root volume (46.4 ml) and number of roots (182 roots plant⁻¹) were markedly higher in lowland conditions, while root dry weight was greater under upland (8.83 g), possibly due to the formation of thicker, denser roots in aerated soils. These patterns agree with the findings of Sandhu *et al.* (2016), who reported higher root biomass allocation under upland conditions as an adaptive mechanism to drought.

Shoot traits followed a similar pattern, with shoot dry weight and plant height being higher under lowland conditions, reflecting

favourable water and nutrient availability. In contrast, upland-grown plants produced heavier panicles and higher 1000-grain weight, indicating effective partitioning of assimilates under moderate stress. These results collectively demonstrate significant genotype \times environment interactions, suggesting that selection strategies for yield improvement in rice should consider the target production environment.

Genetic variability, heritability, and genetic advance

The estimates of genotypic and phenotypic coefficients of variation (GCV and PCV), broad-sense heritability, and genetic advance are presented in Table 4. A considerable variation was observed among traits, reflecting the genetic segregation expected in F₂ populations.

Table 4: Estimates of genetic parameters for morphological and yield-related traits in rice

| Character | GCV (%) | PCV (%) | Heritability | Genetic Advance (%) |
|-----------------------------|---------|---------|--------------|---------------------|
| Plant height | 19.30 | 21.24 | 82.56 | 41.39 |
| Culm height | 22.30 | 23.93 | 86.87 | 36.53 |
| Root length | 17.10 | 61.37 | 7.76 | 1.54 |
| Root width | 46.87 | 51.28 | 83.52 | 3.73 |
| Number of tillers | 44.30 | 56.43 | 61.65 | 5.83 |
| Number of effective tillers | 43.78 | 57.15 | 58.69 | 5.39 |
| Leaf width | 49.69 | 54.48 | 83.19 | 1.35 |
| Root dry weight | 97.18 | 109.04 | 79.43 | 14.38 |
| Shoot dry weight | 77.88 | 89.69 | 75.40 | 25.01 |
| Total panicle weight | 58.37 | 76.07 | 58.88 | 17.49 |
| Panicle weight | 60.80 | 75.45 | 64.95 | 3.16 |

PCV: Phenotypic coefficient of variation, GCV: Genotypic coefficient of variation

The highest heritability (86.9%) was recorded for culm height, followed by root width (83.5%) and leaf width (83.2%), indicating strong genetic control and low environmental influence, consistent with the observations of Karthikeyan *et al.* (2017). Observed high GCV and heritability values for culm height, root width, leaf width, and root dry weight, suggesting these traits are largely governed by additive gene action and can be effectively improved through simple selection. Similarly, shoot dry weight, total panicle weight, and panicle weight showed moderate to high heritability with substantial genetic advance, indicating good prospects for yield improvement through selection in subsequent generations (F₃ and F₄).

Root length exhibited low heritability (7.76%) and low genetic advance, implying a stronger environmental influence and the need for replicated testing or further generation advancement before effective selection.

The overall trend of PCV exceeding GCV across all traits indicates that environmental factors exerted a noticeable influence on phenotypic expression, as expected in segregating F₂ populations. However, the high heritability, coupled with moderate to high genetic advance in root and yield traits, suggests that these crosses possess favourable genetic variability that can be exploited to develop high-yielding, stress-tolerant lines. Although root width exhibited high heritability, its relatively low genetic advance suggests limited expected response to selection in early generations.

Correlation of root traits with yield components

Across both upper and lower catena soils, root traits exhibited strong and FDR-significant associations with key yield components (Table 5).

Table 5. Significance of correlations of root characters and yield components in upper and lower catena soils

| Soil Catena | Cross | Trait | Trait | r | Raw p | FDR-p | Significance |
|-------------|-------|----------|-------|-------|-------|--------|--------------|
| Upper | 1 | RDW | SDW | 0.772 | 0.01 | 0.0267 | ** |
| Upper | 2 | Strength | TGW | 0.508 | 0.01 | 0.0267 | ** |
| Upper | 3 | Volume | SDW | 0.71 | 0.01 | 0.0267 | ** |
| Upper | 4 | Volume | SDW | 0.785 | 0.01 | 0.0267 | ** |
| Lower | 1 | Volume | TPWPP | 0.796 | 0.01 | 0.0267 | ** |
| Lower | 2 | Volume | TPWPP | 0.744 | 0.01 | 0.0267 | ** |
| Lower | 2 | RDW | TPWPP | 0.739 | 0.01 | 0.0267 | ** |
| Lower | 1 | Strength | TPWPP | 0.712 | 0.01 | 0.0267 | ** |
| Lower | 2 | RZW | TPWPP | 0.666 | 0.01 | 0.0267 | ** |

RDW: Root dry weight, RZW: Root zone width, SDW: Shoot dry weight, TGW: 1000-grain weight, TPWPP: Total panicle weight per plant, ** Highly significant

In upper catena soil, root dry weight showed a strong positive correlation with shoot dry weight ($r = 0.77$, $p < 0.05$), suggesting coordinated biomass allocation between above- and below-ground components, while root strength contributed significantly to 1000-grain weight, emphasizing the role of robust root systems in supporting plant biomass and grain development (Kato *et al.*, 2006; Gowda *et al.*, 2011). In lower catena soil, root volume consistently showed the highest correlations with total panicle weight, and root dry weight, root strength, and root zone width also contributed significantly, highlighting the importance of both root biomass and structural traits for reproductive success through improved assimilate translocation or water-use efficiency (Lafitte *et al.*, 2006; Henry *et al.*, 2011).

CONCLUSIONS

The study clearly demonstrates that F_2 populations of rice crosses exhibit differential adaptation to contrasting catena positions, with root traits playing a pivotal role in determining yield performance under variable soil moisture conditions. Traits such as root volume, root dry weight, and root strength were strongly associated with biomass production and grain yield, highlighting the importance of root system architecture in conferring stress tolerance and yield stability. The contrasting trait–yield relationships observed between upper- and lower-catena soils indicate that environment-specific root ideotypes are required, underscoring the need for targeted breeding strategies rather than uniform selection across environments. The superior and relatively stable performance of certain crosses, particularly cross 2, suggests the presence of favourable allelic combinations for both productivity and adaptability. These findings extend previous research by explicitly demonstrating how root–yield relationships vary along a topographic moisture gradient, an aspect rarely addressed in conventional rice breeding studies. By integrating catena-based evaluation with root trait analysis, this study provides a more nuanced understanding of genotype \times environment interactions relevant to heterogeneous rice-growing systems.

Future work should focus on validating these associations across generations and seasons, while integrating root phenotyping with molecular approaches to accelerate selection. Such strategies will support the development of rice varieties with improved resilience and yield stability under diverse and changing production environments.

AUTHOR CONTRIBUTION

MCM designed the study. EKCD and MGNR conducted experiments. MCM and EKCD prepared the manuscript.

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