



RESEARCH ARTICLE

Phenotypic and anatomical characterisation of rice genotypes for drought tolerance under rainfed conditions

Shambhavi Dubey¹, Vidya Bhushan Kuruwanshi¹, Ujjwal Kumar^{1*}, Pragya Mahobe¹, Annu Verma² & Sashi Prakash Tiwari¹

¹Department of Plant Physiology, Agricultural Biochemistry, Medicinal and Aromatic Plants, Indira Gandhi Krishi Vishwavidyalaya (IGKV), Raipur 492 012, Chhattisgarh, India

²Department of Vegetable Science, Indira Gandhi Krishi Vishwavidyalaya (IGKV), Raipur 492 012, Chhattisgarh, India

*Correspondence email - uk8210@gmail.com

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Abstract

In rainfed agroecosystems, water scarcity reduces the yield of rice by impairing the functionality of roots and reducing water uptake. The study evaluated morphological and anatomical properties of roots of 28 rice varieties that were planted under both irrigated and rainfed conditions in a rainout shelter during the 2020–21 kharif season. Root characteristics 45 days following sowing were measured using mini-rhizotrons and WinRhizo imaging; identified genotypes were subsequently analysed by scanning electron microscopy (SEM) to measure cortical architecture and aerenchyma development. There was a great variation in the genotypes in cumulative root length, surface area, mean diameter and volume. Under rainfed conditions, DT-122 retained longer root length, surface area and volume with preserved cortical cells and aerenchyma structure. Contrary to this, DT-127 was also found to reduce root length and volume, impair cortical cells and generate less aerenchyma. These different reactions suggest two different adaptive patterns: DT-122 use a mixture of anatomical stability and wide soil exploration whereas DT-127 seems to be more adaptable to irrigated areas. Even though aerenchyma promotes aeration and mechanical support of flooded soils, it can impair root functionality during droughts, which is a trade-off in drought tolerance. Combination of morphological and anatomical studies produced a more detailed evaluation of the performance of genotypes in water stress. DT-122 is a potential candidate to upland rice breeding, but multilocation trials to determine the correlation between root characteristics and water extraction depth and grain yield are required to determine its usefulness.

Keywords: aerenchyma; drought tolerance; rice genotypes; root morphology; root anatomy

Introduction

Drought remains one of the biggest factors of variability in yield in rainfed rice systems because the soil moisture can reduce suddenly at critical periods of growth (1). Under this condition, root systems are required to find and transfers water to maintain transpiration and distribute carbon to the growing panicle. As a result, root characteristics outline the main limitations of plant water absorption and temporary resilience to water shortage (2).

The degree of soil that the plant will explore is controlled by root architecture, size and internal movement of water and gases is controlled by the anatomical properties (3). The morphological traits of augmented total root length, increased surface area and augmented root volume increase soil contact and often augment hydraulic conductance; they have been linked to excellent drought performance of various crops, including rice (4). At the same time, change of the stele (e.g., induction of aerenchyma, cortical cell size changes and deposition of lignin or suberin) and the cortex (altering hydraulic resistance, oxygen diffusion and mechanical integrity) are influenced by anatomical changes. The reconciliation of these disparate organisational levels clarifies the possibility of distinct

functional results of analogous architectural parameters in genotypes and environmental settings (5,6).

An example of a common trade-off is seen in the creation of low-resistance airways in the cortex by aerenchyma. These forms enable the internal aeration of flooded soils and reduce the respiratory loss of roots that are exposed to hypoxia (7, 8). However, the augmentation of porosity may lower the mechanical integrity of roots, making them more vulnerable to collapse during desiccation and soil dryness. In turn, the traits that provide a selective benefit in the presence of waterlogging might have the costs of fitness when conditions are not wet (9, 10). Such trade-offs are essential to be appreciated by rainfed agricultural systems and in rainfed agriculture soils often switch between waterlogged and dry states during a single growing season (11). Although this conceptual framework, the phenotype-anatomy association is not well studied at the level of the genotype. Most phenotyping research focuses on architectural features studied using rhizotrons, imaging or excavation or descriptive anatomical studies of a small number of cultivars (12). The number of studies that simultaneously measure morphology and anatomy on a large and varied panel under conditions of contrasting moisture levels is small. Such a methodological segregation makes it

difficult to distinguish genotypes that can be both very exploratory of the soil and very strong of the tissue structure (13). Recent advances in high-throughput root imaging and combined methods of analysis have made paired morphological and anatomical screening an ever more achievable goal. However, there is not much literature regarding applied research using these tools to assess breeding material (14).

The proposed study aims to address the gap by measuring the root morphology and anatomy of 28 genotypes of rice grown in an irrigated and rainfed regime in a rainout shelter. We perform the mini-rhizotron/WinRhizo phenotyping together with the microscopic observation of cortical structure and aerenchyma. The aim is to define genotype-specific combinations of traits that are indicative of resilience to episodic water deficit and to clarify anatomical designs that either promote or defeat drought adaptation in rainfed rice.

Materials and Methods

Experimental site and plant material

The experiment was conducted in a rainout shelter that was managed by the Department of Plant Physiology, Agricultural Biochemistry, Aromatic and Medicinal Plants, Indira Gandhi Krishi Vishwavidyalaya, Raipur (Chhattisgarh) in the kharif season of 2020–21. The experiment was conducted under controlled rainfed conditions in a rainout shelter to impose drought stress by excluding natural rainfall. After crop establishment, irrigation was withheld to simulate rainfed stress conditions. A uniform pre-sowing irrigation was applied to ensure proper germination, followed by one life-saving irrigation at the seedling establishment stage. Thereafter, no supplemental irrigation was provided and soil moisture depletion was allowed to progress naturally, thereby creating water-limited conditions throughout the vegetative and reproductive stages. Soil moisture status was monitored periodically and all genotypes were exposed to identical stress intensity to ensure uniform drought conditions. A total of 28 rice genotypes were included, including 27 testing lines (DT-101 to DT-127), obtained at the Indian Institute of Rice Research, Hyderabad (AICRP on rice) and a local control genotype, Indira Barani, obtained at Indira Gandhi Krishi Vishwavidyalaya (IGKV), Raipur.

Experimental design and treatments

The plants were planted with a completely randomized design (CRD) with 3 replicas and 2 different water regimes, i.e., irrigated (IR) and rainfed (RF). As a growth and observation system, mini-rhizotron units (glass-plate rhizotrons) were used. The rhizotrons were filled with air-dried and sieved soil collected from the experimental farm of IGKV, Raipur. The soil was classified as clay loam in texture, with near-neutral pH (approximately 6.5) and moderate organic carbon content, typical of rice-growing soils in the region. Prior to filling the rhizotrons, the soil was thoroughly homogenised to ensure uniform physical and chemical conditions across all treatments. The seedlings of a single genotype were placed in each rhizotron and spacing and potting were performed under similar treatment protocols. The 45 days after sowing (DAS) were used to grow the plants and levels of root measurements and tissue sampling were done.

Root phenotyping and image analysis

Root samples were carefully excavated, rinsed with tap water to remove any adherent soil and kept briefly in 25 % ethanol in Falcon tubes until further scanning. Three single plants (one per replication)

of each genotype under each water regime were used for root analysis ($n = 3$ per genotype per treatment), resulting in a total of 168 rhizotron units (28 genotypes $\times$ 2 water regimes $\times$ 3 replications). Root assemblies were placed inside acrylic trays and they were filled to about three quarters full of water to reduce overlap before scanning with an Epson Perfection V700/V750 device. WinRHIZO Reg. 2009 software was used to process the digital images at 600 dpi. The automatic thresholding option of the software was initially applied to distinguish roots from the background. Subsequently, manual corrections were performed using the built-in editing tools of the software to remove non-root debris, soil particles and artefacts by adjusting threshold levels and deleting unwanted objects before final analysis. Parameters extracted included total root length (mm), root surface area (cm^2), mean root diameter (mm) and root volume (cm^3). The raw image files and processed output files were stored for further reference.

Root anatomical analysis

Based on the phenotypic tests, genotypes were classified as tolerant, intermediate and susceptible and a subsequent anatomical study was then undertaken accordingly. For anatomical observations, root segments were collected from the maturation zone, approximately 2–4 cm above the root tip, to ensure uniformity and avoid meristematic or senescent tissues. Root segments were fixed in a formaldehyde-acetic acid-ethanol (FAA) solution (70 % ethanol: formaldehyde: glacial acetic acid in the ratio of 90:5:5, v/v), with a few drops of Tween-20 added as a wetting agent. After fixation, the samples were dried with a series of tertbutanol/ethanol dilutions and then infiltrated with a solution of tertbutanol and Para-last (1:1) at 55–60 °C. The tissues that were infiltrated were embedded in Para-last and sectioned at 10–16 μm using rotary microtome, placed in slides and observed under light microscopy to record cortical architecture, cortical thickness (μm) and aerenchyma proportion (percentage of cortical area). Also, chosen root fragments were examined using scanning electron microscopy (SEM) at the collaborating laboratory- the Directorate of Onion and Garlic Research Institute, Pune by following the preparation and imaging procedures set up by that institution to easily view cortical porosity and cellular integrity.

Statistical analysis

The effect of genotype, treatment and the combination of these variables were tested using the analysis of variance (ANOVA) on the WinRhizo output data. Mean comparisons were made, which were critical difference (C.D.) at $p = 0.05$, standard error (SE) and coefficient of variation (CV). To summarise genotype responses, the percentage change between the irrigated and rainfed treatment was calculated.

Results

Root characteristics showed a visible genotypic difference between the IR and RF treatments. Analysis of variance revealed significant effects of genotype, water regime and their interaction on all measured root traits ($p < 0.05$), with corresponding f -values and degrees of freedom provided in Table 1. Root length was similar across the panel (mean IR = 524.04 mm; mean RF = 532.96 mm), but root surface area and root volume were lower in the rainfed case (surface area: mean IR = 62.83 cm^2 ; mean RF = 50.37 cm^2 ; volume: mean IR = 0.514 cm^3 ; mean RF = 0.343 cm^3). The average root diameter was slightly higher when rainfed (mean IR = 0.282 mm; mean RF = 0.311 mm).

Table 1. Mean performance of root traits of different rice genotypes under rainfed (RF) and irrigated (IR) conditions during kharif 2020

Genotypes	Root length (mm)		Root surface area (cm ²)		Average root diameter (mm)		Root volume (cm ³)	
	IR	RF	IR	RF	IR	RF	IR	RF
DT-101	250.3	435.4	41.0	68.9	0.3	0.2	0.3	0.2
DT-102	339.6	343.9	43.7	63.1	0.2	0.2	0.3	0.3
DT-103	149.4	472.0	48.7	41.3	0.3	0.2	0.2	0.2
DT-104	261.0	780.0	118.1	40.2	0.3	0.3	1.2	0.2
DT-105	582.6	956.5	96.9	76.6	0.3	0.4	0.7	0.2
DT-106	1322.5	790.7	94.9	76.8	0.3	0.3	0.9	0.7
DT-107	372.8	266.8	44.6	34.5	0.3	0.3	0.3	0.2
DT-108	1072.8	890.9	75.1	67.2	0.4	0.3	0.7	0.6
DT-109	326.3	376.0	64.4	33.0	0.3	0.2	0.4	0.2
DT-110	151.6	355.8	23.0	33.2	0.4	0.2	0.2	0.2
DT-111	175.5	141.9	17.1	18.0	0.3	0.3	0.1	0.1
DT-112	843.0	1400.9	113.1	73.7	0.2	0.3	0.7	0.6
DT-113	932.0	457.6	42.1	55.1	0.3	0.3	0.3	0.2
DT-114	545.2	277.8	93.8	57.1	0.3	0.5	1.2	0.3
DT-115	434.1	482.3	38.4	74.8	0.3	0.3	0.2	0.3
DT-116	1146.7	395.1	84.8	58.3	0.2	0.3	1.0	0.5
DT-117	121.9	151.0	16.5	12.3	0.3	0.3	0.1	0.6
DT-118	135.3	266.5	62.6	52.1	0.2	0.4	0.3	0.6
DT-119	313.9	178.5	23.0	13.5	0.2	0.4	0.1	0.2
DT-120	170.8	193.1	26.3	13.8	0.3	0.3	0.2	0.3
DT-121	423.7	350.4	63.4	62.0	0.2	0.4	0.7	0.3
DT-122	242.2	1208.1	45.5	83.1	0.2	0.3	0.2	0.5
DT-123	255.6	143.7	43.9	16.0	0.3	0.3	0.3	0.2
DT-124	275.0	777.5	48.8	47.4	0.3	0.4	0.4	0.2
DT-125	360.6	1255.0	73.9	64.9	0.3	0.3	0.2	0.6
DT-126	1107.2	990.7	116.0	83.1	0.3	0.4	0.9	0.7
DT-127	1499.6	321.5	140.9	63.9	0.3	0.3	1.3	0.2
Indira Barani	861.9	263.3	58.6	26.4	0.3	0.3	1.0	0.2
Mean	543.03	532.9	62.86	50.42	0.31	0.35	0.56	0.38
C.D.	111.8	114.4	9.75	5.83	0.04	0.06	0.24	0.21
SE(m)	39.3	40.2	3.43	2.05	0.01	0.02	0.08	0.07
CV	12.99	13.07	9.44	7.04	6.68	10.21	25.96	32.05

Genotype responses (percent change RF versus IR) were heterogeneous across the traits and dependent on them (Fig. 1–4). The total root length grew significantly in a group of genotypes and decreased in others. The strongest growth in length was observed in DT-122 ($\approx +399\%$ increase relative to irrigated control), but DT-127 had the strongest decrease ($\approx -78.6\%$). In root surface area, DT-115 showed the strongest positive response ($+94.8\%$) and DT-104 showed the strongest negative response (-66.0%). Some genotypes had doubled the average root diameter: DT-118 had the greatest positive significant change of $+100\%$ and DT-110 had the greatest negative significant change of (-50%). Root volume changes were the most changing: DT-117 showing an approximately 500% increase under rainfed conditions relative to a low irrigated baseline, whereas DT-127 exhibited an approximate 84.6% reduction under rainfed conditions. The summary statistics and the entire genotype table have been given above (raw WinRhizo outputs and computed percent-change columns were stored).

The differences in the reactions of the genotypes are in line with the anatomical observation as provided in this paper. Using microscopic analysis of representative genotypes showed that there are different anatomical arrangements, which are associated with the phenotypic patterns as observed previously. Fig. 5 shows representative transverse sections. The most pronounced increase in length observed of genotype DT-122 under conditions of limited flooding (RF) was observed to maintain cortical integrity and functional aerenchyma by microscopy. Conversely, genotype DT-127 that suffered length and volume loss in RF showed cortical cell damage and a parallel loss in aerenchyma (SEM micrographs).

These findings are consistent with existing literature that shows that root anatomical features (e.g., the degree of aerenchyma, the state of cortical cells) are synergistically related to root architecture in determining drought resilience. Aerenchyma is beneficial in hypoxic conditions although it may be detrimental where mechanical strength is needed during drying cycles. The detected surface area decrease in multiple genotypes under RF could also indicate the elevated soil mechanical resistance and cause the compensatory changes in root hydraulic properties, such as changes in aquaporin expression.

Discussion

The anatomical and phenotypic trends observed in this study indicate that DT-122 possesses both architectural advantages and tissue-level resilience that likely contribute to its superior performance under rainfed conditions. DT-122 maintained higher total root length, surface area and volume under rainfed treatment and microscopic observations revealed intact cortical cells with functional aerenchyma. Increased root length and surface area enhance soil exploration and water uptake potential, while conserved cortical structure supports radial water transport and minimises loss of functional tissue during transient drought stress. These relationships between root architecture and drought response are consistent with recent studies emphasising the importance of integrated root phenotyping for identifying drought-adapted rice genotypes (15–18).

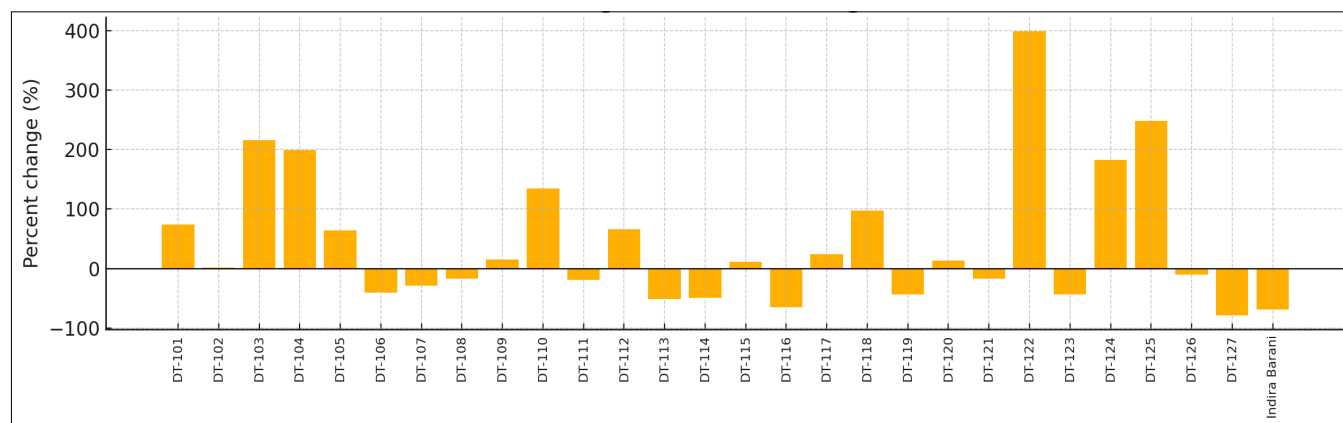


Fig. 1. Percent change in total root length (RF vs IR) across 28 rice genotypes. Genotype DT-122 showed the highest increase in root length under rainfed treatment, whereas DT-127 exhibited the most significant decline.

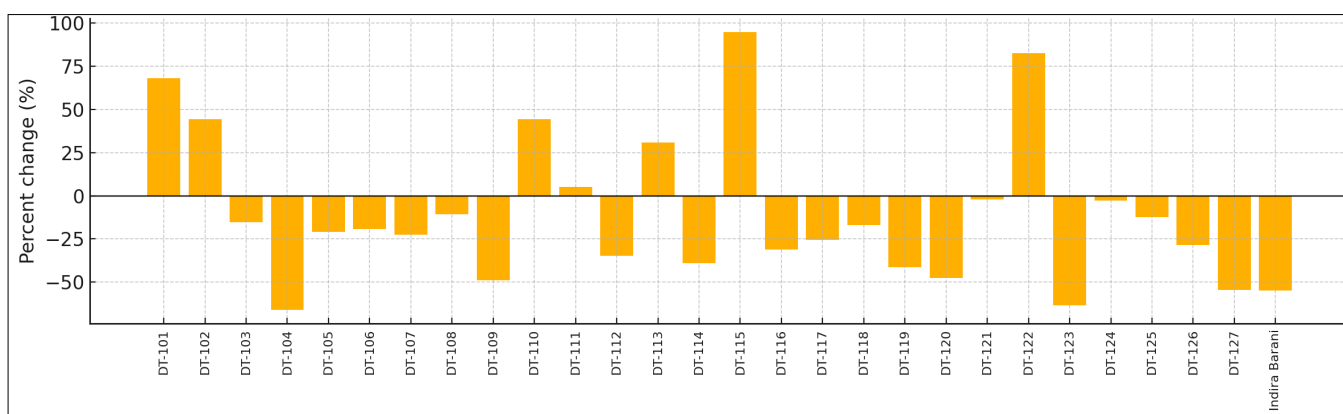


Fig. 2. Percent change in root surface area (RF vs IR) across 28 rice genotypes. Genotype DT-115 showed the most significant increase under rainfed conditions, whereas DT-104 and DT-127 exhibited substantial declines.

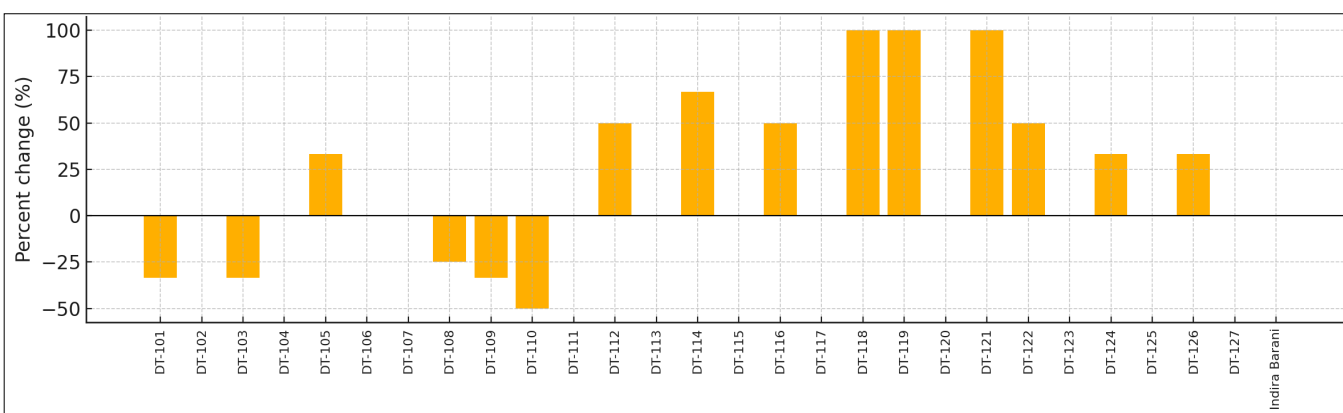


Fig. 3. Percent change in average root diameter (RF vs IR) across 28 rice genotypes. The most significant increase was observed in genotypes DT-118, DT-119 and DT-120, whereas DT-110 exhibited the most significant decline under rainfed treatment.

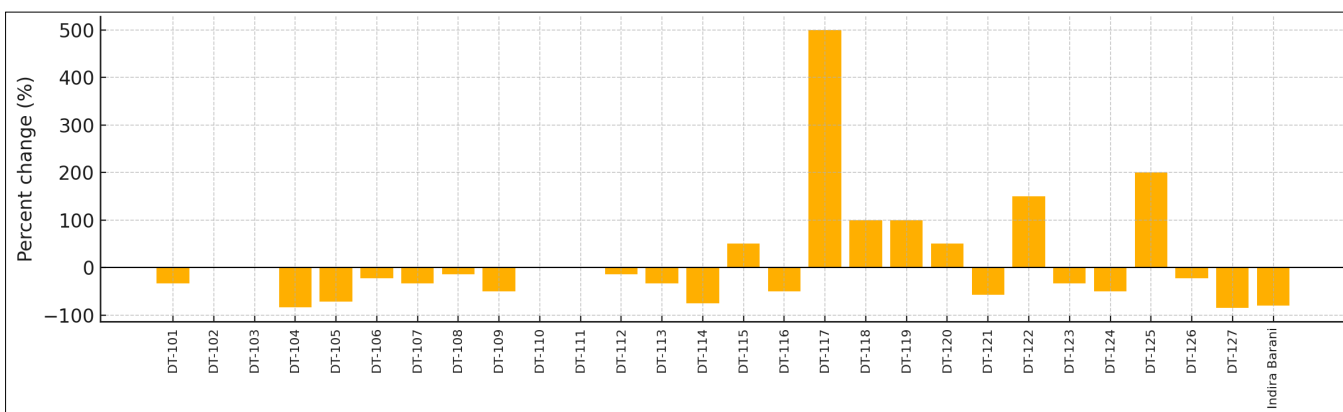


Fig. 4. Percent change in root volume (RF vs IR) across 28 rice genotypes. Genotype DT-117 showed the highest increase ($\approx +500\%$), while DT-127 exhibited the steepest decline in root volume under rainfed conditions.

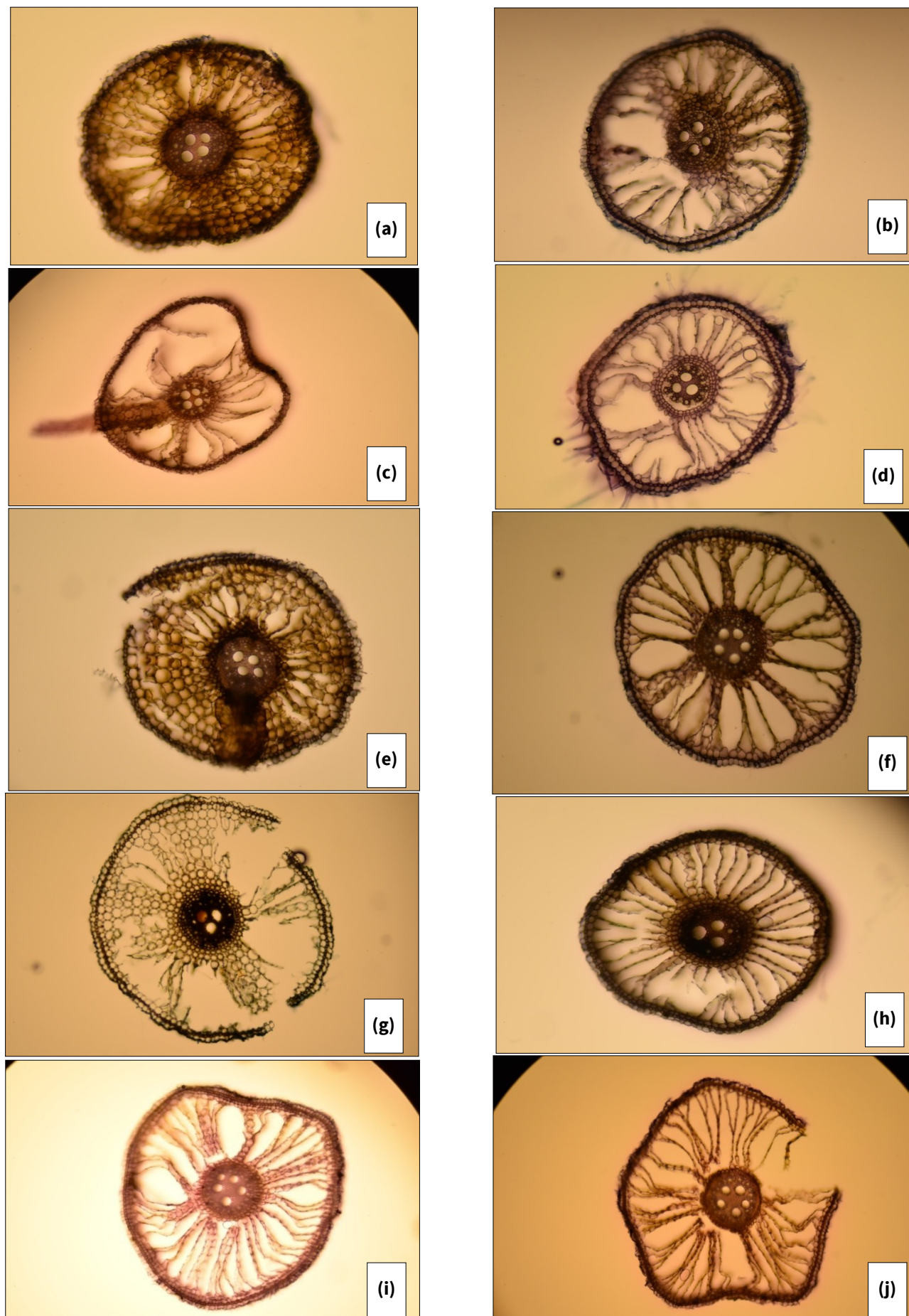


Fig. 5. Transverse sections of rice roots showing anatomical differences between irrigated (IR) and rainfed (RF) treatments in selected genotypes. (a-b) DT-112 under IR and RF conditions, respectively; (c-d) DT-122 under IR and RF conditions; (e-f) DT-127 under IR and RF conditions. Higher-magnification micrographs showing cortical and aerenchyma features are presented for (g-h) DT-112, (i-j) DT-122 and DT-127 under corresponding treatments. DT-122 maintained an intact cortex and well-developed aerenchyma under rainfed conditions, whereas DT-127 exhibited cortical cell collapse and reduced aerenchyma under rainfed stress. Scale bars = 100 μ m (a-f) and 50 μ m (g-j).

The exceptionally high increase in root length observed in DT-122 under rainfed conditions likely reflects strong adaptive plasticity rather than absolute growth alone. This large relative increase was amplified by comparatively lower root length under irrigated conditions. Pronounced root elongation under water limitation has been widely reported in drought-adapted rice genotypes and is commonly interpreted as a strategy to enhance soil exploration and access deeper or residual soil moisture. The maintenance of cortical integrity and functional aerenchyma in DT-122 further suggests that this response represents a coordinated architectural and anatomical adaptation rather than stress-induced damage.

Greater root thickness and tissue robustness may represent additional mechanistic contributors to the phenotypic performance of DT-122. Previous studies have shown that transcription factors such as OsNAC10 and OsNAC5 enhance root diameter and overall root development in rice, traits that are associated with improved drought tolerance under field conditions. Although the involvement of these genes was not examined in the present study, the observed phenotypic similarities suggest that increased root thickness and preserved cortical structure may enhance functional stability during intermittent moisture deficit (2, 19).

The root architectural and anatomical patterns documented here are broadly consistent with earlier studies employing controlled root phenotyping systems such as rhizotrons and imaging platforms. Drought-tolerant rice genotypes identified using these approaches typically exhibit increased root length, maintenance of surface area and preserved cortical integrity under water-limited conditions. Although the present study was conducted under rainout shelter conditions, these traits have frequently been associated with improved drought performance under field conditions, particularly through enhanced water acquisition and avoidance mechanisms.

In addition to the contrasting responses of DT-122 and DT-127, several genotypes exhibited intermediate phenotypic and anatomical responses under rainfed conditions. These genotypes showed partial maintenance of root length or diameter without severe anatomical damage, indicating moderate adaptive capacity. Such intermediate responses likely reflect genotype-specific trade-offs between root expansion, tissue maintenance and metabolic cost and may contribute to stable performance under moderate or intermittent drought stress, where extreme trait expression may not always be advantageous.

In contrast, DT-127 displayed a susceptible response characterised by marked reductions in root length and volume, accompanied by cortical cell damage. Cortical collapse and reduced root volume decrease the effective surface area available for water uptake and increase hydraulic resistance, thereby limiting the plant's ability to sustain transpiration during drought. Structural damage to cortical tissues can disrupt apoplastic pathways and alter the balance between transcellular and apoplastic water transport, ultimately constraining whole-plant hydraulic conductivity. These observations are consistent with earlier reports linking cortical damage to reduced functional performance under drought stress.

A further trade-off highlighted by this study relates to aerenchyma formation. While aerenchyma reduces metabolic costs and improves internal aeration under hypoxic or flooded conditions, increased porosity can reduce mechanical strength and the

proportion of living tissue involved in water uptake. In rainfed systems characterised by alternating wetting and drying cycles, excessive aerenchyma formation may therefore be disadvantageous when soils dry and shrink. The SEM observations showing partial loss of aerenchyma or cortical collapse in some genotypes under rainfed stress support this interpretation (20, 23).

Finally, hydraulic regulation provides an additional framework for understanding genotype-specific responses. Plants may partially compensate for reduced root surface area by adjusting aquaporin-mediated root hydraulic conductance and shoot-root signalling. However, such physiological compensation is limited when anatomical damage occurs or when root system size is substantially reduced. The diverse responses observed among genotypes in this study suggest that drought resilience is governed by interactive effects of root architecture, anatomical integrity and dynamic hydraulic regulation (24, 25).

Implications for breeding and phenotyping

The findings emphasise that selection is based on balanced trait characteristics and not individual traits in the rainfed rice enhancement. The genotypes that combine extended soil exploration ability with maintained cortical integrity, e.g., DT-122, are especially promising since they avoid the strength trade-off that affects other lines. In practice, high throughput architectural evaluations (e.g., rhizotron or imaging methods) should be used in conjunction with specific anatomical analysis of cortical condition and porosity. The two-level system can reduce false positives in case of a genotype that has desirable architectural features but has weak tissue organisation.

Limitations and future work

Plants grown by rhizotron were used in the current study and only a few individuals of each genotype were scanned and hence the extrapolation of the results to the yield of full-size field should be done with caution. It is justified to validate it in different sites, measure the depth of water extraction and draw direct correlations between the water extraction and the grain yield. Also, molecular or physiological measurements, including measures of aquaporin expression and cell wall composition, may clarify the processes underlying the described anatomical resilience.

Our integrated morphological and anatomical assessment identified contrasting strategies in the panel. It supported DT-122 as a candidate for upland breeding because it combined extensive soil exploration with resilient cortical structure. Selecting for such trait combinations and validating them under heterogeneous field conditions should increase the likelihood of breeding rice that performs reliably in rainfed, seasonally variable environments.

Conclusion

DT-122 put together deep root probing with keeping the cortical setup and was marked as the most hopeful type for rain-fed areas. The pair use of rhizotron-based shape checking and inside look proved good at picking out working root plans that setup-only tests would overlook. These results back the adding of aimed inside checks in dryness-resistance lines to cut down on mistakes. DT-122 needs multilocation field proof and use as a giver in growing plans aimed at highland and rain-fed rice.

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Authors' contributions

SD conducted the phenotypic and anatomical evaluations and drafted the manuscript. VBK and SPT supervised the study design and reviewed the manuscript. UK assisted in data analysis, manuscript editing and correspondence. AV and PM contributed to experimental setup, field observations and data recording. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Grammarly to improve language clarity, structuring and editing. After using this tool, the authors carefully reviewed and edited the content and take full responsibility for the final version.

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