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Assessment of Rice Varieties from Ghana under Mild Water Stress at Both Early Seedling and Reproductive Stages

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Abstract

Drought is a major climatic constraint, reducing rice physiological performance and biomass accumulation by over 30% across growth stages. This study examined drought responses of nine rice varieties released in Ghana in August 2022, focusing on seedling and reproductive stages. The set comprised six lowland types (CRI-Korea Mo, CRI-Kang Mo, CRI-Agyapa, CRI-Baakoye, CRI-Tuo Mo, CRI-Onuapa) and three upland types (CRI-Ofosu, CRI-Cho, CRI-KAFACI). A 2 × 9 factorial within a randomized complete block design, with six replications, was conducted in a controlled screen house. Water stress was imposed at 30% of water-holding capacity, while controls were maintained at 100%. Physiological traits assessed included photosystem II quantum yield, leaf greenness, relative leaf water content, and morphological parameters such as leaf area and plant height, measured after 7 and 14 days of stress. ANOVA revealed significant drought effects ($P \leq 0.05$) on most variables, whereas genotype and interaction effects were generally non-significant ($P \geq 0.05$). Notably, all genotypes exhibited ~70% reductions in photosystem II efficiency, leaf area, and grain yield compared to well-watered controls. These findings suggest that lowland and upland rice varieties responded similarly under drought conditions, highlighting the need for breeding programs targeting enhanced drought resilience.

Keywords: *drought, physiological performance, reproductive stage, rice, seedling stage.*

Introduction

Rice (*Oryza sativa* L.) is the second most important cereal crop in Ghana and the chief staple food for most Ghanaians, particularly those living in urban areas (Ankrah et al., 2021; Baffour-Ata et al., 2021; Tasila Konja et al., 2019). Although efforts are underway to increase production of preferred local rice, much of urban demand is met by imported rice (Ayeduvor, 2018; Ragasa et al., 2020). Although rainforest and savanna ecologies are generally more favourable to lowland rice, upland NERICAs are nevertheless widely cultivated in these environments (Abraham et al., 2024; Alagbo et al., 2022). Establishment in rainfed lowlands is typically characterized by standing water of variable depth (Chartzoulakis & Bertaki, 2015). However, drought or flooding at any stage may lead to submergence, particularly in fields located in depressions (Kato et al., 2019; Kumar et al., 2021). The high-water table and waterlogged soils in some areas often render lowland rice production impossible, particularly in the derived savanna and transitional forest-savanna zones (Callo-Concha et al., 2013; Manik et al., 2019; Michael et al., 2023; Panda & Barik, 2021). In the subhumid savannas, lowlands are scarce, but where they exist, they provide the most reliable source of rainfed rice, from which settlers are often able to obtain a crop in the first year (Balasubramanian et al., 2007; Senayah et al., 2009). In the Guinea savanna and the transition to this zone, flat, low-lying areas often become waterlogged and swampy, creating favourable conditions for lowland rice (Akinyemi, 2013; Balasundram et al., 2023; Bationo et al., 2018; Bradford & Hsiao, 1982; Kaur et al., 2020; Opoku & Adu-Asare, 2021). Deep pools or temporary swamps are often encountered throughout the southern zones in the valleys of small rivers. A wide range of lowland environments therefore occurs in Ghana, and given the importance of rice in the Ghanaian diet, the potential to increase local rice production is considerable (Asante et al., 2023; Ragasa et al., 2020; Teeken & Temudo, 2021).

Water stress is a fundamental growth constraint for upland rice in the savannas and some derived savanna transitional forest zones, particularly during the delay to the wet season, known as the "mid-dry season drought", when early-planted crops are at risk (Cm et al., 2023). It also forms the basis of climatic discrimination between upland and lowland rice ecologies in sub-Saharan Africa (Langangmeilu et al., 2023; Luo et al., 2020). Studies on the effects of water stress on upland NERICA's and other upland rice varieties have been carried out under field and screenhouse conditions in West Africa since the late 1990s (Langangmeilu et al., 2023; Purwanta et al., 2017; Saito et al., 2010). The approach has been to impose a fixed period of water deficit on the vegetative stages. In the case of complete water withdrawal, this often results in total crop failure. Documented responses of upland rice to water stress include leaf rolling, reduced stomatal conductance and transpiration, wilting, reduced leaf area, and low tissue water potential. Recovery growth can occur if stress is later relieved, but this is usually insufficient to restore yields to those of unstressed crops (Alou et al., 2018; Lanna et al., 2021; Zu et al., 2017). Substantial progress has been made in our understanding of the physiological and molecular bases of drought resistance in upland rice, and a comprehensive review of this work has been provided (da Mata et al., 2023; HUANG et al., 2019; Oladosu et al., 2019).

In order to improve rice production in the lowlands and uplands. Farmers need to choose the proper varieties with higher water-use efficiency. Although various studies have examined plant responses across different ecosystems, very little work has compared upland and lowland plant varieties within the same agroecosystem. Therefore, this study aims to compare the water stress responses of

lowland and upland rice varieties and to understand their better utilization or tolerance to reduced water availability. Globally, rainfed lowland rice production covers nearly 75 million hectares, and it is grown by resource-poor farmers with low inputs compared to traditional consumers (Akinyemi, 2013; Asante et al., 2023; Manik et al., 2019). Upland rice is typically cultivated using traditional practices. Because of this, upland rice is considered to be a subsistence crop. In Ghana, most rice cultivation occurs in the lowlands, accounting for more than 60%, while the remainder is grown in the uplands (Abdul-Rahaman et al., 2021; Tanko et al., 2019).

Since gaining independence in 1957, Ghana has consistently worked towards achieving food security for its people (Dompreh et al., 2021; Samal et al., 2022). However, rice remains a heavily imported commodity, and its local production needs to be increased to meet national demand (Nyarko & Kassai, 2017; Yeboah et al., 2020). Rice yields in Ghana are generally low, averaging 2 t ha^{-1} compared to the attainable yield of 5 t ha^{-1} (Akolgo, 2021; Buri et al., 2015; Ragasa & Chapoto, 2017). One of the leading causes of this is environmental factors, such as drought. Ghana could benefit from developing rice production techniques for different rice ecologies to increase rice production in its rainfed (upland) areas, especially during the dry season in its lowlands. This study aims to assess the response of Ghanaian lowland and upland rice varieties to water stress. It also compares their morphophysiological characteristics, growth, and yield under water stress. The goal is to identify varieties with superior water-use efficiency and to provide insights to improve local rice production and enhance food security.

Methodology

Study area and Plant materials

The experiments were conducted in a screenhouse at CSIR-Crops Research Institute in Fumesua-Kumasi, Ghana (6˚ 43'05 ``N 1˚ 32` 01`` W) to investigate the drought responses of nine rice varieties at both the seedling and reproductive stages. In August 2022, CSIR-CRI released nine rice varieties in Ghana: six lowland ecology-preferred ones (CRI_Korea Mo, CRI_Kang Mo, CRI_Agyapa, CRI_Baakoye, CRI_Tuo Mo, CRI_Onuapa) and three dry/upland rice varieties (CRI_Ofosu, CRI_Cho, and CRI_KAFACI). These varieties were selected for their adaptability and performance in different rice-growing agroecological conditions in Ghana (CSIR-CRI, 2022) and used in our study.

Experimental design and data collection

The varieties, released in August 2022, included six preferred for lowland ecology and three for dry/upland conditions. To reflect the ecological adaptations of the two rice groups, different water regimes were applied to the control treatments. For the lowland varieties, pots were maintained under shallow waterlogged conditions, with approximately 5 mm of standing water above the soil surface to simulate flooded lowland fields. For the upland varieties, pots were irrigated to field capacity (100% water-holding capacity), representing the well-drained conditions typical of upland rice cultivation. For the drought treatment, however, the same stress regime was applied across both groups: soil moisture was reduced to 30% of water-holding capacity. This uniform stress treatment ensured comparability of drought responses between upland and lowland varieties.

In the seedling-stage experiment, plants were grown in small plastic pots (5 cm deep, 3.5 cm wide) filled with sandy loam topsoil for three weeks. Water stress was induced by irrigating pots to 30% of the water holding capacity (WHC), with a control group maintained at 100% WHC for 7 days in the second week after emergence. After three weeks, plants were harvested

and analyzed for root length, shoot height, estimated leaf area, and chlorophyll content. Root length (cm) or root depth, as may be described, was measured with a ruler after root washing from the base of the plant to the tip of the longest root lying on a flat surface. Plant height (cm) or shoot length was measured with a ruler from the shoot base to the tip of the longest leaf when held together at the top. Leaf area (cm^2) was determined by manually measuring the leaf length and maximum width with a ruler. The estimated leaf area was then calculated using the equation: leaf area = length × width × k, where k is the shape factor (0.70 for rice leaves, Boudiar et al., 2020).

Chlorophyll content, photosystem II efficiency, and leaf fluorescence measurements were performed using a handheld device, the Flour Pen 100. The FluorPen FP 100 is from Photon System Instruments: https://handheld.psi.cz/. The second fully expanded leaf from the top was used.

The reproductive-stage experiment was conducted in pots (20 cm deep, 12 cm wide) to evaluate the performance of rice varieties under water stress during the flowering and grain-filling stages (Figure 1). Stress was induced by suspending irrigation until soil moisture declined to 30% of field capacity. Harvested panicles were analyzed for grain number, weight, and filling rate. Data on wilting and senescence were collected to measure water stress tolerance.

Both experiments used a randomised complete block design with six replications per treatment. For the reproductive-stage experiment, the stress treatment was applied at the booting stage (BBCH 45) for 14 days (Figure 1). Afterwards, the plants were rewatered and harvested at maturity.

Statistics

The data collected from these measurements were analyzed to identify significant differences between the two rice varieties and their responses to water stress. Statistical analysis included a two-way analysis of variance (ANOVA) with Type III error terms in JASP 0.18, and Tukey's HSD post hoc tests after confirming the homoscedasticity and homogeneity assumptions (JASP Team, 2024). The two-way ANOVA (Type III) was used to identify significant differences in the morphophysiological responses of lowland and upland rice varieties to water stress at the early seedling and reproductive stages. Tukey's HSD test was used to compare mean differences in the effects of water stress levels and rice varieties on morphophysiological parameters. Results were considered statistically significant at $P < 0.05$, and findings were presented in graphs to illustrate the differences. Trait-relatedness was analyzed using the Pearson correlation coefficient at the 95% confidence interval.

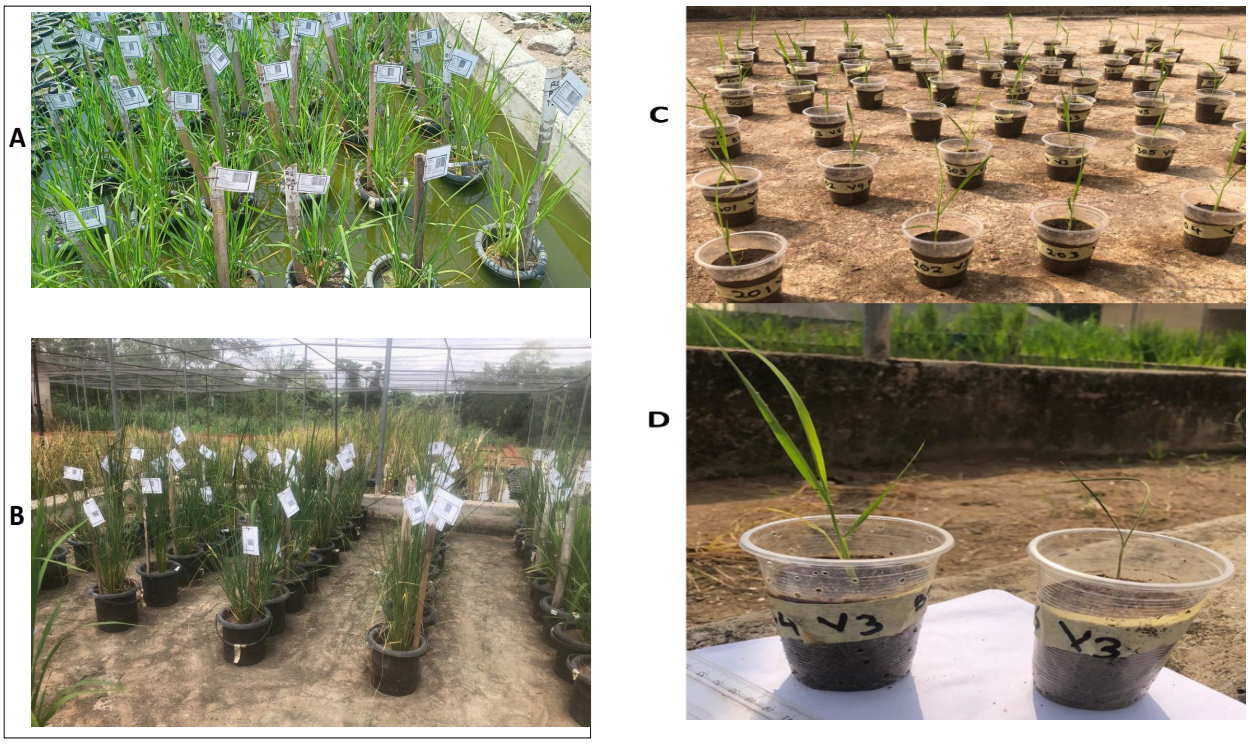

Figure 1: Pictures illustrating the experimental setup. (A) Control plants during the reproductive-stage stress treatment. (B) Water-stressed plants during the reproductive-stage stress treatment. (C) Control plants for seedlings during the stress treatment stage. (D) Comparing control and stress plants side by side during the seedling stage of stress treatment.

Results

Variation among genotypes across treatments at both seedling and reproductive stages

Analysis of variance revealed significant variation among the estimated traits across the well-watered control and drought stress treatments at the seedling stage (Table 3.1). At this stage, genotypic effects for all studied traits were not significant ($P > 0.05$). However, treatment effects were significant for all traits. Specifically, treatment effects were significant at $P < 0.01$ for leaf area (LA), dry root weight (DRW), root-shoot ratio (RSR), and fresh root weight (FRW), while they were highly significant at $P < 0.001$ for plant height (PH), dry biomass (DBM), chlorophyll content (FT), and quantum yield of photosystem II (QTY II). Among the estimated traits, only plant height exhibited a significant genotype × treatment interaction ($P < 0.05$).

At the reproductive stage, analysis of variance revealed significant variation among genotypes in genotypic, treatment, replication, and genotype × treatment interactions for some of the estimated traits (Table 3.2). At this stage, genotypic effects were highly significant ($P < 0.001$) for plant height (PH), fresh root weight (FRW), dry root weight (DRW), and tiller number (TN), while the remaining traits were not significant ($P > 0.05$). Treatment effects were also highly significant ($P < 0.001$) for PH, FRW, DRW, dry biomass (DBM), chlorophyll content (FT), quantum yield of photosystem II (QTY II), TN, and dry grain weight (DGW), whereas leaf area (LA) was significant at $P < 0.01$. The genotype × treatment interaction was highly significant ($P < 0.001$) for PH, FRW, DRW, and TN, significant at $P < 0.01$ for DBM, and significant at $P < 0.05$ for the root-shoot ratio (RSR). Replication effects were significant at $P < 0.01$ for DRW, DBM, and

QTY II, and highly significant ($P < 0.001$) for RSR.

Table 3.1. Mean sum of squares from ANOVA for traits across treatments at the seedling stage

TRAITS	Df	pH	LA	FRW	DRW
GENO	8	9.65170	1.1698ns	0.0473ns	0.0008ns
TRT	1	274.5633***	15.1781**	0.2509**	0.0055**
REP	5	3.32640	1.9879ns	0.0344ns	0.0006ns
GENO X TRT	8	29.0954*	2.458ns	0.0036ns	0.0002
RESIDUALS	85	11.13020	1.548	0.0239	0.0006

Table 3.1 continued

TRAITS	Df	RSR	DBM	FT	QTYII
GENO	8	2.7461ns	0.0011ns	690926ns	0.0286ns
TRT	1	27.1337**	0.027***	202423078***	2.6164***
REP	5	5.408ns	0.0011ns	1062639ns	0.0257ns
GENO X TRT	8	1.1946ns	0.0002ns	1770042ns	0.038ns
RESIDUALS	85	3.0809	0.0008	1256128.164	0.0299

GENO: Genotype; TRT: treatment; REP: replication; GENO X TRT: genotype interaction treatment; Df: degree of freedom; PH: plant height; LA: leaf area; DRW: dry root weight; RSR: root-shoot ratio; DBM: dry biomass; FT: chlorophyll content; QTYII: quantum yield of photosystem II.

Table 3.2. Mean sum of squares from ANOVA for traits across treatments at reproductive stage

TRAITS	Df	PH	LA	FRW	DRW	RSR
GENO	8	903.58***	1196323.2ns	21804.48***	3921.94***	0.16ns
TRT	1	15056.81***	8230317.57**	337010.08***	52096.15***	0.01ns
REP	5	117.94ns	678106.82ns	2631.28ns	625.38**	0.52***
GENO X TRT	8	830.01***	628245.45ns	24493.17***	3909.34***	0.24*
RESIDUALS	85	116.7	1009582.92	2456.49	178.16	0.09

Table 3.2 continued.

TRAITS	Df	DBM	FT	QTYII	TN	DGW
GENO	8	7216.6ns	940307.7ns	0.01ns	243.65***	34.99ns
TRT	1	486018.75***	25017781.48***	0.11***	2380.08***	7416.9***
REP	5	19844.19**	1008033.21ns	0.02**	45.14ns	77.52ns
GENO X TRT	8	13886.4**	788671.77ns	0.01ns	257.92***	18.12
RESIDUALS	85	4037.89	1210727.29	0.01	53.88	33.09

GENO: Genotype; TRT: treatment; REP: replication; GENO X TRT: genotype interaction treatment; Df: degrees of freedom; PH: plant height; LA: leaf area; DRW: dry root weight; RSR: root-shoot ratio; DBM: dry biomass; FT: chlorophyll content; QTYII: quantum yield of photosystem II.

Morphological changes of rice to water stress

Significant alterations in the morphological parameters of the genotypes between well-watered (100% WHC) and water-deficient (30% WHC) conditions were observed at the seedling and reproductive stages. The mean plant height of the genotypes at the seedling stage under well-watered conditions was approximately 19 cm, ranging from 8 cm to 24 cm (Figure 2A). Under water stress at the seedling stage, the mean height was approximately 19 cm, with values ranging from approximately 7 cm to 30 cm (Figure 2A). At the reproductive stage, plants under well-watered conditions had an average height of about 83 cm, with a minimum of approximately 35 cm and a maximum of 108 cm (Figure 2A). However, when subjected to water stress during the reproductive stage, the mean height was approximately 58 cm, with heights ranging from approximately 14 cm to 99 cm (Figure 2A).

The average number of tillers for the various genotypes under optimal irrigation conditions during the reproductive phase was 34.76, ranging from 23 to 59 tillers (Figure 2B). Conversely, under water-stress conditions at the reproductive stage, the mean tiller number was 18.35, ranging from 7 to 34 for the same genotypes (Figure 2B).

The mean estimated leaf area for the seedlings' water stress treatment was 4.70 cm, with minimum and maximum values of 2.07 cm and 7.69 cm, respectively (Figure 2C). However, the mean estimated leaf area for the seedlings control was 4.61 cm^2 and spanned between 1.24 cm^2 and 7.92 cm^2 (Figure 2C). During the reproductive stage, under well-watered conditions, an average estimated leaf area of 2061.87 cm^2 was obtained, showing a minimum value of 13.3 cm^2 and a maximum value of 4648.63 cm^2, as illustrated in Figure 2C. Conversely, the average leaf area of the genotypes under water-stress conditions was 1956.47 cm2, ranging from 292.32 cm2 to 4953.38 cm2 (Figure 2C).

The mean seedling fresh root weight obtained from the seedling stage drought stress experiment was 0.255 g, which fell within the range of 0.011 g to 0.872 g (Figure 3A). In contrast, the average fresh root weight for seedlings under well-watered conditions was 0.299 g, ranging from 0.093 g to 0.789 g (Figure 3A).

At the reproductive stage, the average fresh root weight for the genotypes under well-watered conditions was 379.000 g, ranging from 96.000 g to 627.000 g (Figure 3B). Under water stress conditions, the minimum and maximum values for fresh root weight, with a mean of 155.889 g, were 369.000 g and 369.000 g, respectively (Figure 3B).

The mean seedlings' dry root weight of the genotypes in the water stress conditions was 0.06 g, its minimum weight was 0.01 g, and its maximum weight was 0.14 g (Figure 3B). Contrary to that, the mean dry root weight for the control seedlings was 0.05 g, between a minimum weight of 0.01 g and a maximum weight of 0.13 g (Figure 3B). At the reproductive stage, the mean dry root weight for the genotypes under water stress was 82.07 g, between a minimum dry root weight of 9 g and a maximum dry root weight of 234 g (Figure 3B). The mean dry root weight for the genotypes under a controlled water regime was 172.32 g, ranging from 64 g to 420 g (Figure 3B). The mean seedling shoot dry weight under water-stress conditions was approximately 0.04 g, ranging from 0.01 g to 0.09 g (Figure 3B). In contrast, under well-watered conditions, the mean shoot dry weight was also around 0.04 g, with minimum and maximum values of approximately 0.01 g and 0.09 g, respectively (Figure 3B). At the reproductive stage of drought stress, the mean shoot dry weight across genotypes was 24.09 g, ranging from 6 g to 68 g (Figure 3B). On the contrary, the mean

shoot dry weight for the control was 67.02 g, ranging from 14 g to 160 g (Figure 3B).

Under water-stress conditions, the mean root-to-shoot ratio for the seedlings was 1.79 g, ranging from 0.73 g to 5.6 g (Figure 4A). However, the mean root-to-shoot ratio of seedlings under control conditions was 1.4 g, ranging from 0.3 to 2.6 g (Figure 4A). At the reproductive stage, the mean root-to-shoot weight ratio for the water stress at maturity was 20.40 g, with grain weight varying from 6 g to 36 g (Figure 4B). However, water stress imposed during the reproductive stage resulted in an average treatment was 4.4 g, ranging from 0.6 g to 20 g (Figure 4A). Meanwhile, the root-to-shoot ratio for the control under the reproductive stage was 4.07 g, with a minimum-maximum value of 0.75 g – 17.71 g (Figure 4A).

The mean weight of grains obtained from the different genotypes under control conditions

grain weight of 3.96 g, within the range of 0.3 g to 14 g for the identical genotypes (Figure 4B).

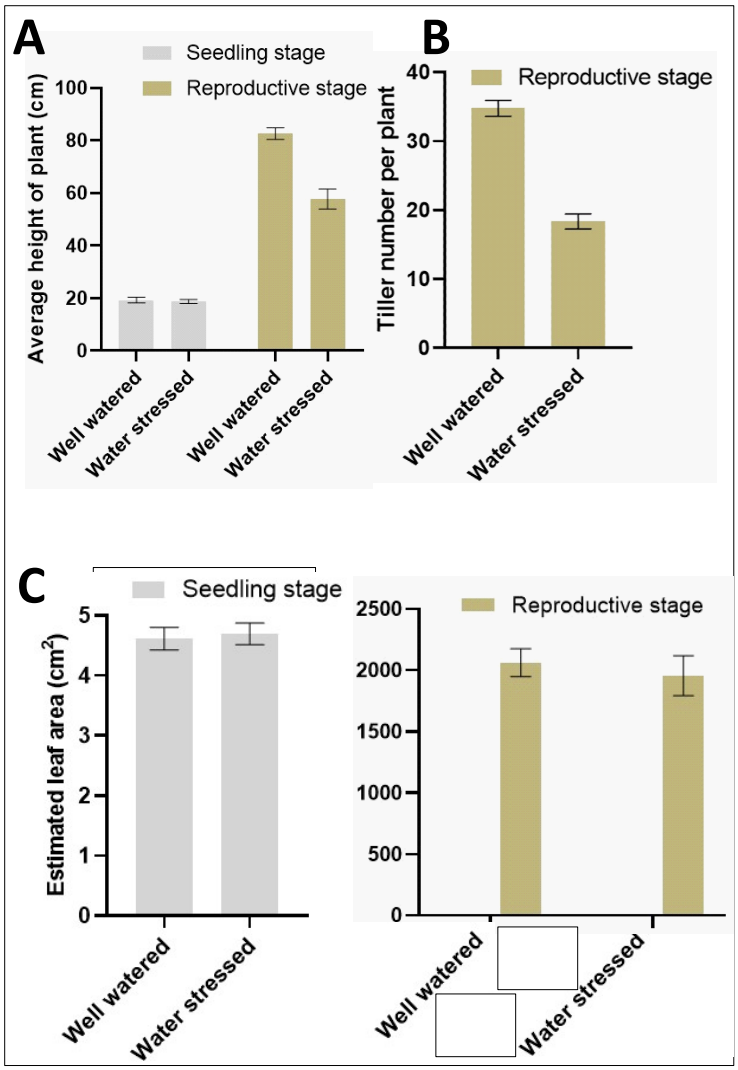

Figure 2: Panel figure of rice morphological traits. Plot showing the response of plants' height (cm) to water stress and well-watered conditions (control) at the seedling stage and reproductive stage, (A). Plot (B) shows the tiller number of plants under water-stress and well-watered (control) conditions at the reproductive stage only. Plot (C) shows the response of estimated leaf area (cm^2) per plant to water stress and well-watered conditions (control) at the seedling stage and reproductive stage. The error bars indicate the absolute variation in the data around the mean.

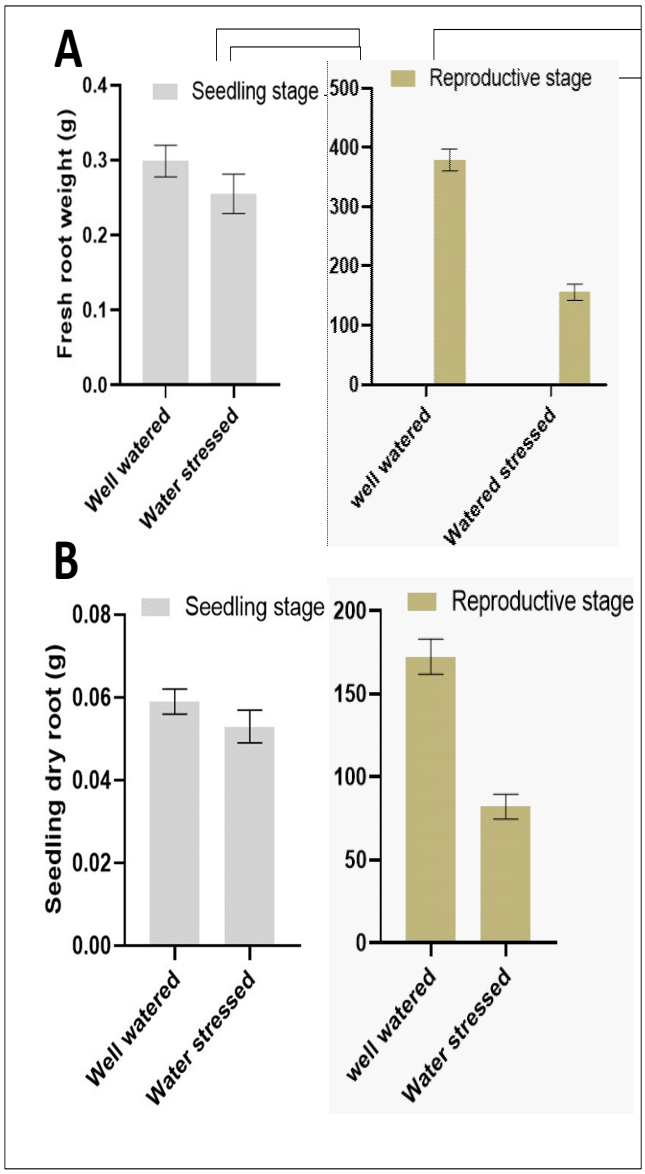

Figure 3: Panel figure of rice root traits. Plot showing the response of plants' fresh root weight (g) to water stress and well-water conditions(control) at the seedlings stage and reproductive stage (A). Plot (B) shows the response of plants' dry root weight (g) to water stress and well-watered conditions (control) at the seedlings stage and reproductive stage. The error bars indicate the absolute variation in the data around the mean.

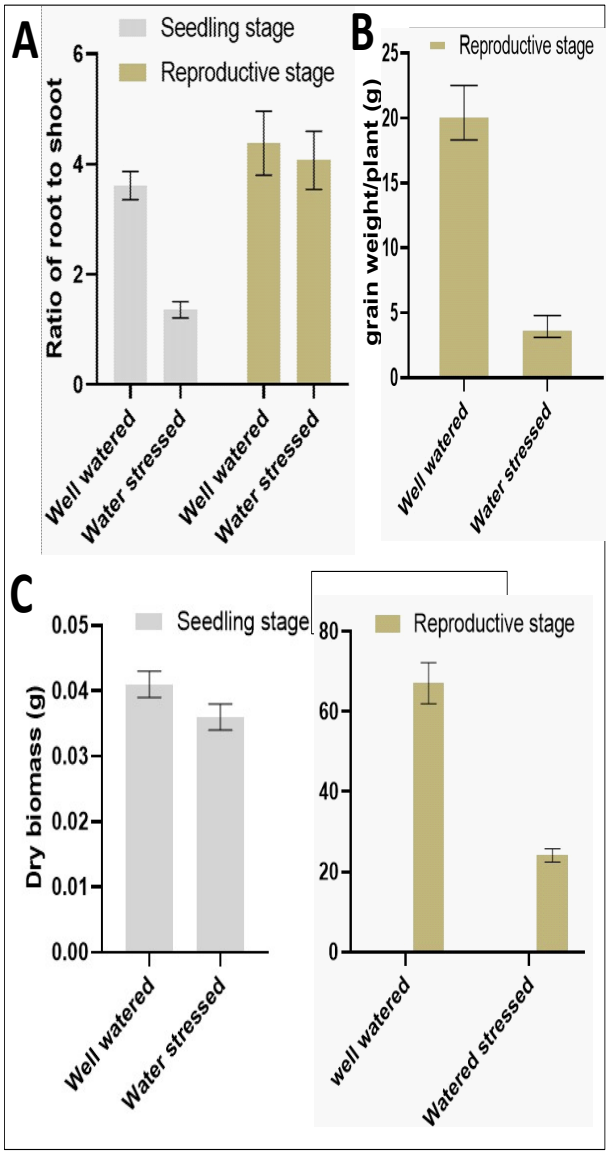

Figure 4: Panel figure of rice plant traits. Panel figure of rice plant traits. Root-shoot ratio under water stress and well-watered (control) conditions at the seedling and reproductive stages (A). Plot (B) shows the response of grain weight per plant under drought stress and well-watered conditions at maturity of the reproductive stage experiment. Plot (C) shows the response of plants' dry biomass or shoot dry weight (g) to water stress and well-watered conditions (control) at the seedling stage and reproductive stage. The error bars indicate the absolute variation in the data around the mean.

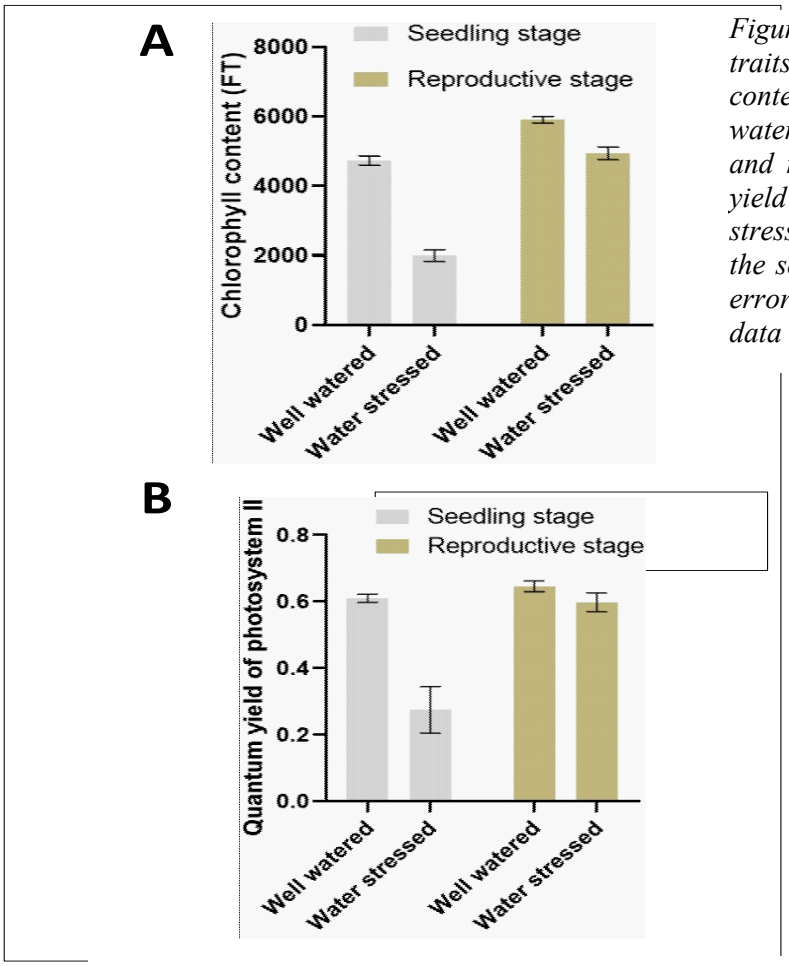

Figure 5: Panel figure of rice physiological traits. Bar plot showing the leaf chlorophyll contents of plants under water stress and well-watered conditions (control) at the seedlings and reproductive stages (A). Plot of quantum yield of photosystem II of plants under water stress and well-watered conditions (control) at the seedlings and reproductive stages (B). The error bars indicate the absolute variation in the data around the mean.

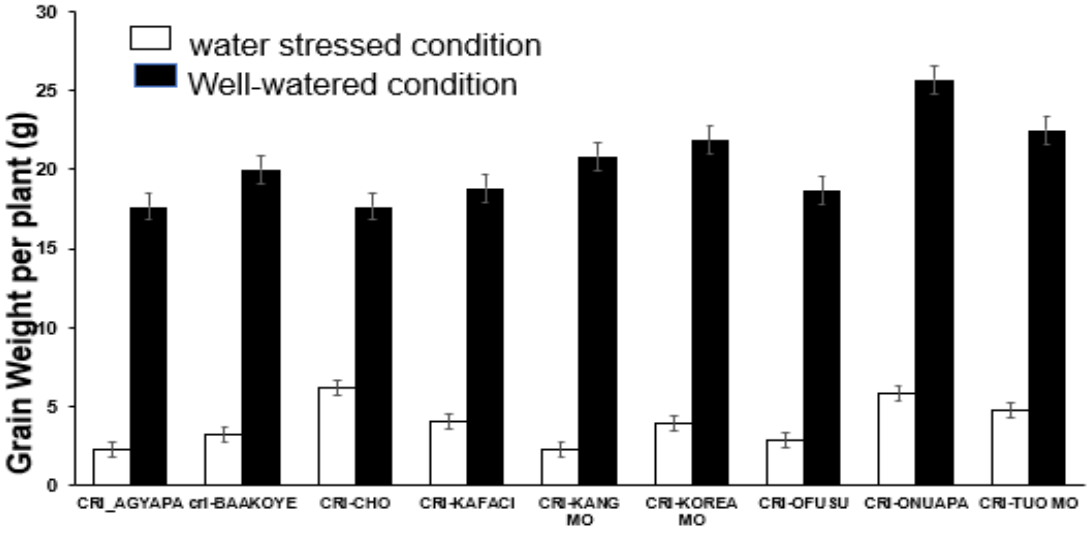

Figure 6: Grain weight per plant (g) for the different genotypes under water stress (plain bars) and well-watered conditions (dark bars) recorded after maturity during the reproductive stage experiment. The error bars indicate the absolute variation in the data around the mean

Physiological and yield-related response of rice to water stress

The average leaf chlorophyll content under well-watered conditions during the seedling phase was 4733.09, with a minimum of 2519 and a maximum of 6626 (Figure 5A). Conversely, the identical genotypes subjected to water stress during the seedling

phase exhibited an average chlorophyll content of 1995, with minimum and maximum values of 488 and 5254, respectively (Figure 5A). The mean chlorophyll content of the reproductive stage control condition was 5906.64, ranging from 7486 to 4277 (Figure 5A). Conversely, a mean chlorophyll content of 4944.06, with minimum and maximum values of 488 and 9093, characterized the reproductive water stress stage (Figure 5A). The mean quantum yield of photosystem II at the seedling stage under water stress was 0.275, ranging from 0 to 0.69 (Figure 5B). In contrast, the mean quantum yield for photosystem II under the seedling control condition was 0.61, ranging from 0.47 to 0.73 (Figure 5B). In the controlled reproductive stage, the mean quantum yield for photosystem II was 0.65, ranging from 0.47 to 0.73 (Figure 5B). In contrast, the reproductive stage under water stress exhibited an average quantum yield of 0.60, with minimum and maximum values of 0.07 and 0.79, respectively (Figure 5B).

Generally, there was a significant difference in the effects of well-watered and managed drought-stress conditions on the grain yield of the genotypes. Genotypes under well-watered conditions tend to have higher grain weight per plant than those under managed water stress, which is not by chance (Figure 6). Though a significant difference existed between the treatments, there was no significant difference among genotypes under similar treatment (Figure 6). Under well water conditions, CRI-ONUAPA had the highest grain yield (25. 67g/plant), and this was followed by CRI-TUO MO (22.5 g/plant), CRI-KOREA MO (21.83 g/plant), CRI-KANG MO (20.83 g/plant), CRI-BAAKOYE (20 g/plant), CRI-KAFACI (18.83 g/plant), CRI-OFOSU (18.67 g/plant) and finally, CRI-CHO or CRI-AGYAPA (17.67 g/plant) in descending order of performance (Figure 6). Under reproductive-stage water stress, the variety with the highest performance was CRI-CHO (6.167 g/plant). It was followed by CRI-ONUAPA 5.83 (g/plant), CRI-TUO MO (4.83 g/plant), CRI-KAFACI (4.05 g/plant), CRI-KOREA MO (3.95g/plant), CRI-BAAKOYE (3.27 g/plant), CRI-OFUSU (2.90 g/plant), CRI-AGYAPA (2.33 g/plant), and CRI-KANG MO (2.30g/plant), respectively (Figure 6).

The correlation matrix of the morpho-physiological parameters showed both significant and non-significant associations among them during the seedling-stage experiment (Figure 7). A substantial and robust positive relationship was observed between the fresh shoot weight and the percentage relative water content of the shoot (% RWC_shoot) ($r = 0.7$, Figure 7). A highly significant yet weak positive correlation was identified between the fresh and shoot dry weights ($r = 0.4$; see Figure 7). A moderately substantial and weak correlation was present between the root length and the fresh shoot weight ($r = 0.3$). In contrast, significant and weak associations were found between the fresh shoot weight and the chlorophyll content ($r = 0.2$) and between the fresh shoot weight and the fresh root weight ($r = 0.2$). Nevertheless, the root length exhibited a significant negative correlation with the root-to-shoot ratio ($r = -0.2$).

A highly significant and strong association ($r = 0.7$) existed between shoot length and plant height. A highly substantial and moderate association existed between shoot length, shoot dry weight ($r = 0.5$), and estimated leaf area ($r = 0.6$). There was also a highly significant but weak correlation between shoot length and root dry weight ($r = 0.3$) and shoot length and fresh root weight ($r = 0.3$). Fresh root weight exhibited a highly significant correlation with shoot dry weight and root dry weight; however, it strongly correlated with root dry weight ($r = 0.7$) while moderately correlated with shoot dry weight ($r = 0.6$, Figure 7). A moderately significant correlation was identified between root length and shoot dry weight. At the same time, there was a substantial correlation

between root length and root dry weight, as well as between root length and estimated leaf area (Figure 7). There was a weak correlation between root length and shoot dry weight (r = 0.3), a very weak correlation between root length and root dry weight (r = 0.2) and between root length and estimated leaf area (r = 0.2). Plant height significantly correlated with shoot dry weight (Figure 7). However, there was a moderately significant association between plant height and root-to-shoot ratio and between plant height and root dry weight (Figure 7). There was a moderate correlation between plant height and shoot dry weight (r = 0.6). The correlation between plant height and the root-to-shoot ratio was weak (r = 0.3). Nonetheless, the association between plant height and dry root weight was weak (r = 0.3, Figure 7). Plant height also exhibited a significant but weakly negative correlation with the percentage relative water content (r = -0.21; Figure 7).

A highly significant, moderate correlation was observed between estimated leaf area and shoot dry weight (r = 0.6; Figure 7). A weak correlation was observed between estimated leaf area and root dry weight (r = 0.3; Figure 13). The estimated leaf area showed a highly significant yet weak correlation with the root-to-shoot ratio (r = -0.3) and a moderately significant yet weak correlation with the shoot relative water content (r = -0.25; Figure 7). Chlorophyll content exhibited a highly substantial and strong correlation with quantum yield (r =0.7). At the same time, there was a moderately substantial and weak correlation (r = 0.3) between chlorophyll content and the percentage relative water content of the shoot (Figure 7). Quantum yield showed a highly significant but weak correlation (r = 0.3) with the shoot's relative water content (Figure 7).

Root dry weight showed a highly significant, moderate correlation (r = 0.5) with both the root-to-shoot ratio and shoot dry weight. However, it showed a weak but essential negative correlation (r = 0.2) with the shoot relative water content (Figure 7). A highly substantial yet weak negative association (r = 0.4) existed between shoot dry weight and root-to-shoot ratio (Figure 7).

The analysis of morpho-physiological parameters during the reproductive stage experiment revealed a range of correlations, with some parameters exhibiting significant associations and others showing no significant associations (Figure 8). Plant height was significantly correlated with grain weight per plant, root length, estimated leaf area, quantum yield, tiller number, leaf length and leaf width (Figure 8). At the same time, plant height exhibited a strong positive association (r = 0.8) with tiller number and leaf width, moderate correlation (r = 0.6) with leaf length and estimated leaf area, weak association (r = 0.3) with root length and quantum yield, and a significant and weak correlation (r = 1.2) with dry root weight (Figure 8). Leaf length also significantly correlated with dry root weight, quantum yield, leaf width and plant height (r = 0.7***, 0.3**, 0.4***, 0,6***, Figure 8). Leaf width had a significant and positive correlation with dry root weight, grain weight, dry shoot weight (biomass dry weight), root length, estimated leaf area, and quantum yield, but a negative significant correlation with tiller number (r = 0.4***, 0,5***, 0.2*, 0.3**, 0.3**, 0.3**, -0.5***, respectively, Figure 8). Tiller number correlated negatively and significantly with root dry weight, dry shoot weight, root length, chlorophyll content, and quantum yield and chlorophyll content but associated significantly and positively with grain weight (r = - 0.4***, - 0.3**, - 0.3**, - 0.3**, - 0.2*, - 0.3***, 0.6***, respectively, Figure 8). Chlorophyll content was associated positively and significantly with grain weight, dry shoot weight and quantum yield (r = 0.4***, 0,3***, 0.5***, Figure 8). The quantum yield at the reproductive stage is associated positively and significantly with

grain weight, dry shoot weight and estimated leaf area (r = 0.2*, 0.3**, 0.3**, Figure 8). Chlorophyll content correlates significantly but negatively with dry shoot weight (r = 0.2*) and estimated leaf area (r = 0.2*, Figure 8). Leaf length only correlated with estimated leaf area (r = 0.4***, Figure 8). Root length positively and significantly correlated with dry root weight, grain weight and dry shoot weight (Figure 8). Dry shoot weight was also significantly and positively correlated with dry root and grain weight (r = 0.4***, 0.6***). Grain weight is positively and significantly related to dry root weight (r = 0.5***, Figure 8).

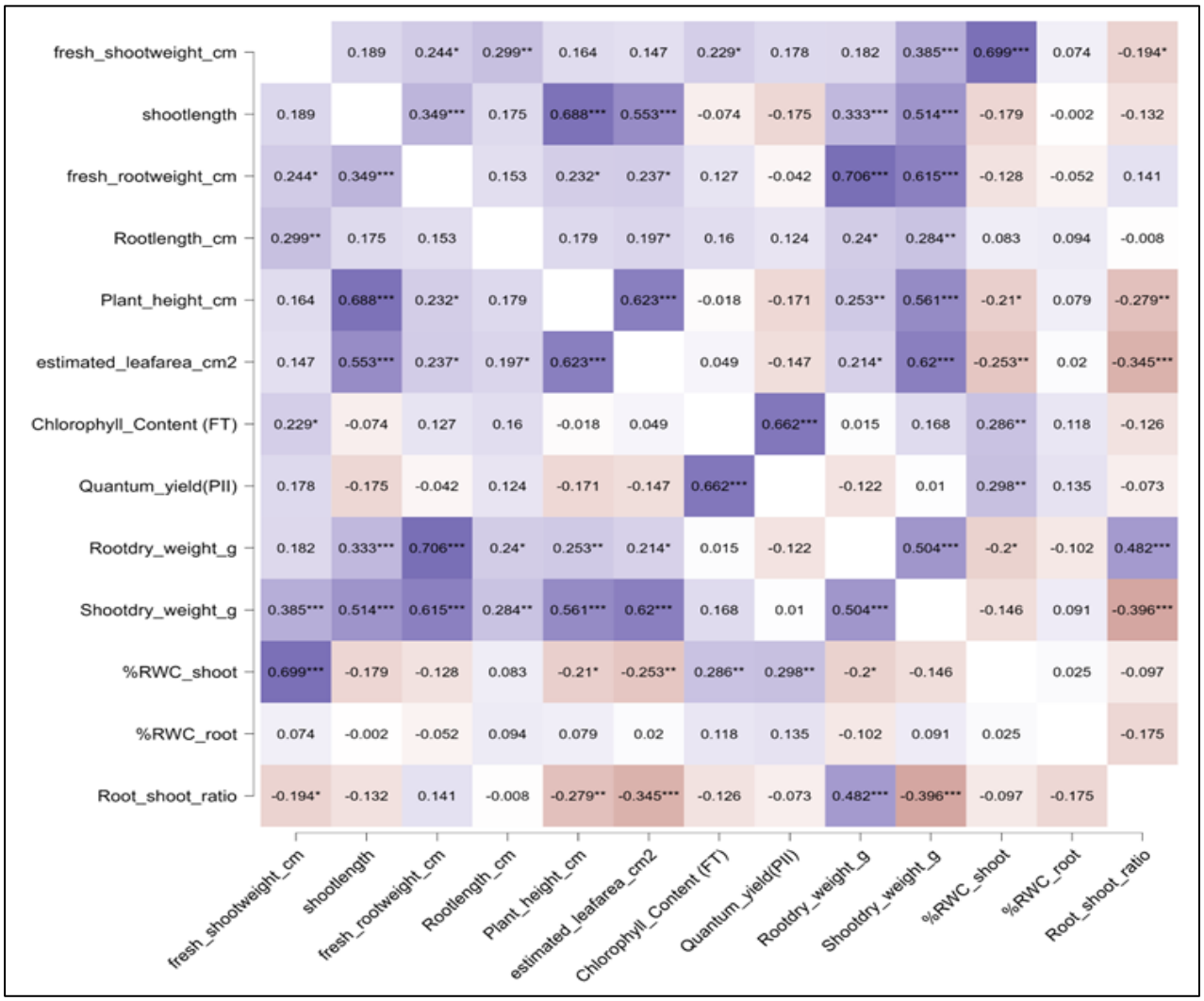

*Figure 7: Correlation matrix for morphophysiological attributes of nine rice genotypes under well-watered and terminal water-stressed conditions at the seedling stage. The vertical and horizontal axes indicate the parameters studied. Values of correlations and significance are indicated with stars. *: significant ($p < 0.05$), **: moderately significant ($p < 0.01$), ***: highly significant ($p < 0.001$).*

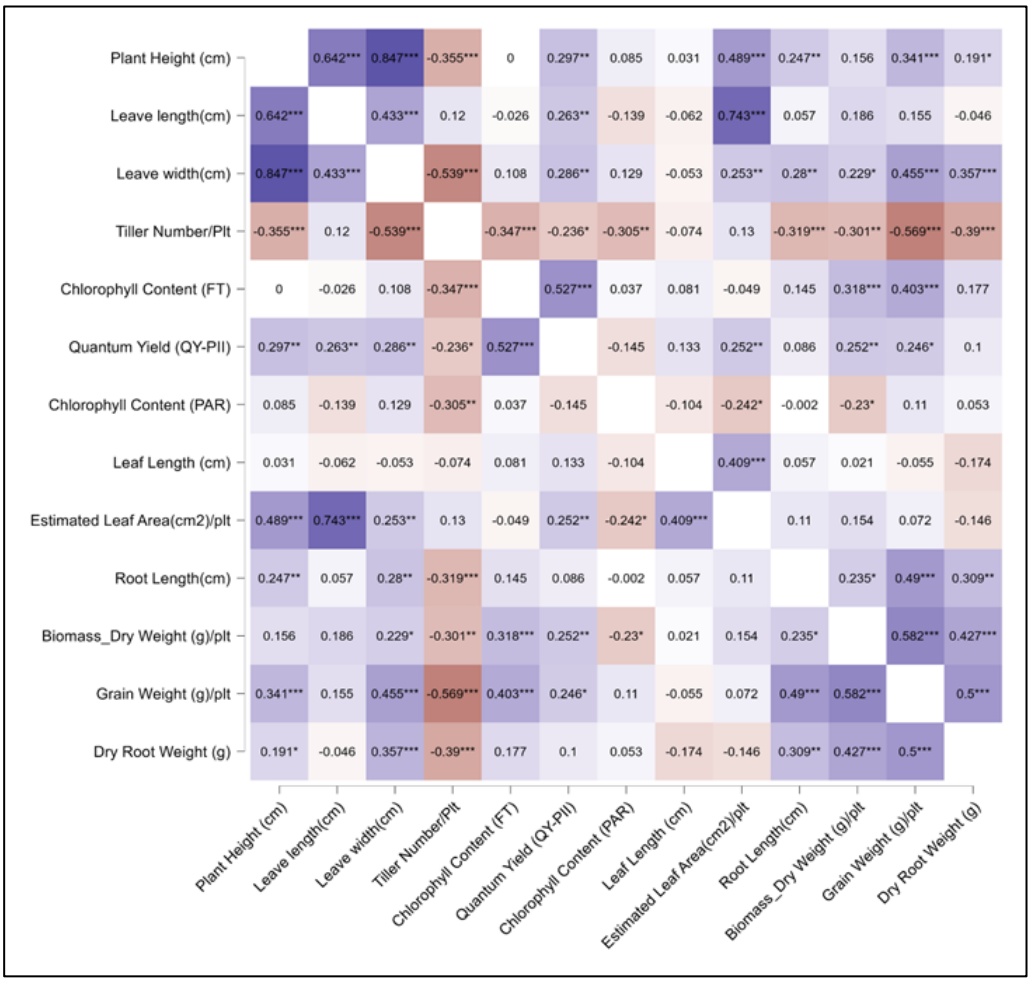

*Figure 8: Correlation matrix for morphophysiological attributes of nine rice genotypes under well-watered and terminal water-stressed conditions at the reproductive stage. Vertical and horizontal axes indicate the parameters studied. Values of correlations and significance are indicated with stars. *: significant (P < 0.05), **: moderately significant (P < 0.01), ***: highly significant (P < 0.001).*

Discussions

The study investigated the morphological and physiological responses of improved rice varieties to water stress at both the seedling and reproductive stages. The varieties under scrutiny were developed using advanced breeding techniques to enhance their resilience to water-deficient conditions. Understanding how these varieties respond to water stress is crucial for informing breeding programs and agronomic practices aimed at sustainable rice cultivation in water-limited environments. The response of improved rice varieties to reduced water availability at both the seedling and reproductive stages is a critical topic in rice cultivation, especially in water-scarce regions (Kang et al., 2021; Larkhunthod et al., 2018; Sahebi et al., 2018). Rice, a water-intensive crop, is highly sensitive to water availability across its growth stages (Sandhu et al., 2013; Zhu et al., 2019).

Variation among genotypes across treatments at both seedling and reproductive stages

The significant treatment effect across all traits in the seedling-stage experiment suggested that the water treatment was sufficient to explain variation in the genotypes' performance in response to drought and that the imposed treatment could induce alterations in the genotypes' performance on the traits studied. Similar findings were reported by Warioba et al. (2026) in their study of 40 genotypes screened for drought at the seedling stage. However, the absence of significant genotypic effects on all traits at the seedling stage suggested that, despite significant treatment effects, there was no genetic variability among genotypes in their responses to drought for the estimated traits across treatments. This further suggested that the genotypes responded similarly across the treatment levels. At the reproductive stage, the significance of genotypic effects on plant height, fresh root weight, dry root weight, and tiller number indicated genetic variability among the genotypes in their responses to drought for these traits, as revealed by the treatment effects. The presence of genotypic variation also suggested the possibility of selection for the traits. The significant treatment effects for all traits except root-shoot ratio also suggested that the treatment effects were sufficient to explain and induce variation in the genotype's performance for the estimated traits. At both seedling and reproductive stages, the presence of significant genotype-by-treatment interaction effects for plant height at both reproductive and seedling stage experiments and for dry biomass, tiller number, fresh root weight, dry root weight and root-shoot ratio suggested that the performance of the genotype for the traits varied in response to changes in the treatment condition.

Morphological changes of rice to water stress

Rice plants respond to drought stress through various mechanisms, including morphological and structural alterations, activation of drought-resistant genes, and synthesis of osmotic regulatory substances and hormones. They manage the negative impacts of stress by implementing mechanisms that induce metabolic and physiological changes. Various defence mechanisms enable plants to cope with drought stress, generally through morphological, physiological, and biochemical alterations driven by several molecular mechanisms (Yang et al., 2021; Oguz et al., 2022). Rice plants utilize three main strategies to cope with drought stress across all developmental stages: tolerance, escape, and avoidance. The capacity of a rice plant to respond to drought conditions varies across multiple levels, from the molecular to the morphological. Under drought escape, plants exhibit remobilization of photosynthates, plasticity, and early maturity, thereby shortening the maturity period. Early-maturing rice varieties may utilize these drought escape mechanisms to combat terminal drought. Additionally, rice plants adapt by altering root architecture, closing stomata, and modifying leaf epidermal structures to enhance water use efficiency and maintain relative water content, thereby avoiding drought. To induce drought tolerance, rice plants may also increase the concentration of compatible solutes in their cells, perform osmotic adjustment, and produce desiccation-tolerance enzymes, thereby enabling them to survive during drought (Yang et al., 2021; Oguz et al., 2022).

In our study, the improved rice varieties were developed to be more resilient to water stress using rapid generation advance (RGA) technology (https://rbi.irri.org/ or https://www.irri.org/news-and-events/news/speedbreed-crop-breeding-center-built-speed). However, their

response to reduced water availability may vary at different growth stages. Our findings illustrate substantial morphological plasticity in response to water stress among the rice genotypes studied. Water stress during the seedling stage reduced plant height and altered root growth patterns, with significant decreases in fresh and dry root weights compared to well-watered conditions. The observed morphological responses of rice genotypes to water stress align closely with findings from previous studies. Consistent with our results, studies by Kadam et al. (2017) and Hassan et al. (2023) reported reduced plant height and compromised root growth under water-stress conditions in rice genotypes engineered for drought tolerance. These results underscore the universal challenge of maintaining growth and productivity in water-limited environments, a crucial requirement for sustainable rice production (Ahmed et al., 2017). They further emphasize the adaptive responses of specific rice genotypes to manage water scarcity, which is critical for breeding programs to enhance drought resilience. In the era of unpredictable climate change, where droughts can severely impact yields, and in countries like Ghana, where access to irrigation facilities is limited (Laube et al., 2012), selecting genotypes with robust root systems and efficient water-use traits is pivotal. Water management practices such as alternate wetting and drying (AWD) help reduce water use while maintaining yields. Other management practices, such as mulching, conservation agriculture, and precision irrigation, can enhance water use efficiency. Integrated crop management practices, including optimal fertilizer and pest management, can help mitigate the effects of water stress. Integrating these findings into breeding strategies could expedite the development of varieties better suited to thrive under erratic rainfall patterns and contribute to food security initiatives.

Physiological responses of rice to water stress

Understanding the physiological responses of rice varieties to water stress provides insights into their adaptive mechanisms and their potential to maintain yield under adverse conditions (Salgotra & Chauhan, 2023). Our study corroborates the existing literature on the physiological responses of rice to water stress, particularly regarding chlorophyll content and photosystem II quantum yield. Consistent with studies by (Jin et al., 2023) and (Ali et al., 2023), we found decreased chlorophyll content and photosynthetic efficiency under water stress, indicative of reduced photosynthetic activity and stress-induced leaf senescence (Figure 5A, 5B), and further highlights the vulnerability of rice reproductive development to water deficit and underscoring the need for strategies to mitigate yield losses during this critical growth stage (Figure 6). Thus, enhancing photosynthetic efficiency and maintaining reproductive vigour under water stress conditions are imperative. Figures 7 and 8 also revealed intricate relationships among morpho-physiological parameters, echoing findings from studies on rice stress responses, as reported by Tang et al. (2023) and which demonstrated strong correlations between root traits and shoot biomass, indicative of coordinated resource allocation strategies under stress. Therefore, identifying specific correlations that optimize water-use efficiency and growth resilience in rice genotypes is worth exploring. For instance, the positive associations among root dry weight, shoot biomass, and grain yield underscore potential breeding targets to enhance overall crop performance under water-limited conditions (Figures 7 and 8). This study provides a roadmap for selecting and breeding rice varieties resilient to water stress in Ghana. Farmers can mitigate yield losses and enhance agricultural sustainability in a changing climate scenario by prioritizing genotypes with

strong root-shoot relationships and efficient resource utilization.

Similar drought tolerance response observed for lowland and upland rice varieties

The comparison between lowland and upland rice varieties under water stress provides insights into their adaptive strategies and potential for cultivation in diverse agroecological zones. Our study revealed similar responses to water stress in lowland and upland rice varieties, with upland varieties exhibiting water-stress tolerance comparable to that of lowland varieties, as reflected in reduced tillering, leaf area, photosynthesis, and grain yield. The results indicate that all the improved lowland rice varieties used in the study responded similarly to the upland rice varieties during the drought's seedling and reproductive stages. One potential contributing factor for such a response could be the rapid generation of advanced technology from IRRI using a single-seed descent breeding approach by CSIR-CRI, Ghana, during the development of the lowland lines, which might impose physiological stress on the plants. Consequently, the stress memory of the lowland rice progenies may become inherent and carried along in their character. Such arguments and research are grounded in studies of acquired tolerance. The insignificant differences in the performance of upland and lowland rice varieties under water-deficit conditions in the current study suggested the development of acquired drought-tolerance mechanisms in these lines, as they were all developed through a rapid generation approach that gradually exposed them to mild levels of drought stress. Plants exhibited acquired tolerance to severe stress following continual exposure to mild stress conditions (Ramu et al., 2016; Sreeman et al., 2018; Sung et al., 2003). Vijayaraghavareddy et al. (2020) reported similar findings when Apo and IR64 were subjected to mild, progressive stress prior to exposure to severe stress. However, further research is needed to substantiate this claim, and a confirmatory field assessment is necessary to validate these observations.

Breeding programs can prioritize traits associated with drought tolerance strategies, such as drought escape mechanisms and efficient water uptake, to enhance resilience in rain-fed agricultural environments prevalent in northern Ghana (Yeleliere et al., 2023). Integrating these insights into varietal selection and crop management strategies can optimize rice production across diverse landscapes, contributing to the region's food security and sustainability efforts. In the current study, the top three performing varieties for grain yield under drought stress conditions included CRI-ONUAPA, CRI-TUO MO and CRI-KOREA MO in descending order.

Implications for rice cultivation in Ghana

The findings from this study have significant implications for rice cultivation in Ghana, particularly in water stress management and climate resilience. The observed morphological and physiological responses of rice genotypes to water stress highlight the critical importance of selecting varieties with robust drought-resilience traits. For instance, reduced plant height, compromised root growth, and decreased chlorophyll content under water stress conditions underscore the need for targeted breeding programs. By focusing on genotypes that exhibit strong root systems and efficient water use, breeders can develop varieties better suited to withstand periods of water scarcity. This is especially crucial for regions in Ghana prone to erratic rainfall and intermittent dry spells. Promoting the cultivation of high-yielding, drought-tolerant rice varieties such as CRI_ONUAPA and CRI_CHO, which demonstrated relatively better performance under water stress, can help stabilize production and minimize the risk of crop failure. This strategy is crucial for enhancing food security and sustaining farmers' livelihoods in drought-prone regions.

Additionally, the significant differences in grain yield between well-watered and water-stressed conditions indicate the vulnerability of rice yields to water deficits, further emphasizing the need for resilient varieties. The detailed analysis of morpho-

physiological parameters provides insights into the critical stages of rice growth most affected by water stress. Understanding the correlation between root and shoot traits under water-deficit conditions can inform the development of more effective irrigation practices. For example, ensuring an adequate water supply during the reproductive stage can mitigate yield losses and optimize resource use. Implementing targeted irrigation strategies that match rice's growth-stage-specific water needs can improve water-use efficiency and enhance crop productivity. This approach is particularly relevant for smallholder farmers in Ghana who rely on rainfed agriculture and have limited access to irrigation infrastructure.

Furthermore, the study's findings can inform Ghana's agricultural policies promoting climate-smart agriculture. By identifying and disseminating drought-tolerant rice varieties, policymakers can support adaptive strategies that enhance the farming sector's resilience to climate change. Additionally, the results can guide investment in research and development to refine drought-resilient traits further and improve overall crop performance. Incorporating research findings into national agricultural policies can drive the adoption of resilient rice varieties and sustainable farming practices. This alignment between research and policy is crucial for achieving Ghana's long-term food security and sustainable development goals.

Conclusion

Our findings reveal that Ghana's released upland and lowland rice varieties exhibit significant reductions in morphophysiological traits under water stress, particularly during the early seedling and reproductive stages. The pronounced physiological adjustments observed during the reproductive stage underscore the susceptibility of rice reproductive development to water deficits, emphasizing the necessity for strategies to mitigate yield losses during this critical period. These results suggest that rice cultivation in Ghana must account for the specific water requirements and tolerance levels of different varieties. Such information is crucial for rice farmers in Ghana, enabling them to make informed decisions about which varieties to cultivate under water-stressed conditions. Understanding the morphophysiological responses of various rice varieties to water stress will enable farmers to select and prioritize varieties better adapted to Ghana's unique environmental conditions. Moreover, this knowledge can inform the development of effective irrigation strategies and water management practices for rice cultivation in Ghana. By understanding how different rice varieties respond to water stress, farmers can optimize water usage and minimize the adverse impacts of water scarcity on rice production. This will ultimately enhance the country's sustainability and rice cultivation productivity. It is important to note that the morphophysiological responses of rice varieties to water stress are relevant to Ghana and can be applied to other regions with similar environmental conditions and water-scarce conditions. This knowledge provides valuable insights into rice cultivation practices in those regions and contributes to the global understanding of crop adaptation to water stress.

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Conflict of interest

The authors wish to declare no conflicts of interest.

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