

Rapid Rhizometric Screening and Selection of Upland Rice Landraces for Drought Tolerance

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ABSTRACT

In line with a progressive plant breeding program, the current study attempted to identify prospective parent materials for drought tolerance breeding using rhizometric and morphometric variables. Twelve upland rice genotypes (URLs) as subplots were subjected to 0, 5, 10, 15 and 20-days duration of water withdrawal (DWW) as main plots in a Split-plot experiment of a modified adaptation of the PVC Tube method in RCBD. The ANOVA revealed that DWW affected drought sensitivity-leaf rolling and drought recovery score. Drought susceptibility index determined that Rinara was tolerant, and the rest were found to be highly tolerant. Principal Component Analysis (PCA) revealed that 84.34% of the variation observed in this experiment can be accounted by three principal components. Standardized Shannon-Weaver Diversity Index (H') of URLs under 20 days DWW ranged from $H'=0.71$ to $H'=0.98$ and were highly diverse ($H'=0.83$) confirming PCA results. Pearson Product-Moment Correlation showed that maximum root length had medium positive linear relationship with plant height ($r = 0.63^{**}$) whereas root surface area was highly correlated with network length ($r = 0.91^{**}$) and volume ($r = 0.93^{**}$).

Keywords: Phenomics, Genetic Diversity, Stress Memory

INTRODUCTION

Studies dealing with the characterization, observation, and quantification of plant root growth and root systems (rhizometric) have been and remain a critical area of research in all disciplines of plant science. The Asian cultivated rice (*Oryza sativa* L.) is one of the most important crops and a major food source for more than half of the global population. Furthermore, it also serves as a model crop for the plant science community especially on genetic studies. On the other hand, rice farming is even dubbed as the “most important economic activity on earth” (Maclean et al., 2002). Rice production is undeniably essential to both the food supply and the economy. In the Philippines, rice is regarded as the most important food crop, being the staple food throughout the archipelago. Rice is life for the Filipinos, not only because it is the staple food, but also because it is tightly woven into the Filipino culture (Romero, 2008).

Being the less popular rice cultivation practice due to its low yield and investment returns, research and breeding efforts for upland rice have not received much attention. However, the prevailing climatic and socio-economic tensions proved to be also vulnerable to climate change, thus the great need to divert to upland rice cultivation. With the prospects offered by upland rice cultivation, breeding efforts to further improve upland rice cultivars must be undertaken, hence this study. Rice has the evolutionary peculiarity of being semiaquatic. As a result, rice has few adaptations to water-limited conditions and is extremely sensitive to drought stress (Lafitte et al., 2004). Drought is considered as the single most devastating environmental stress, which decreases crop productivity more than any other environmental stress (Lambers et al., 1997). Drought severely affects plant growth and development with substantial reductions in crop growth rate and biomass accumulation.

Traditional upland rice landraces had long been used by farmers. However, little is known about the responses of these upland rice landraces to drought stress. This study was conducted to evaluate the response of various upland rice landraces to drought stress at the early vegetative stage in hopes of harnessing the potential of the Mindanao Island region in upland rice cultivation with its vast rainfed areas. Specifically, the study intended to generate baseline information on the quantitative root characteristics of upland rice; quantify the phenotypic diversity among upland rice landraces; determine associations and inter-relationships among drought related components with different morphometric and rhizometric traits; and identify drought tolerant and susceptible landraces.

METHODOLOGY

The experiment was conducted at the Agricultural Experiment Center, Central Mindanao University, Musuan, Maramag, Bukidnon from October to December 2016. Germplasm materials: seeds of Azucena upland rice variety and ten upland rice landraces namely: Domodao, Dinorado, Baysilanon, Rinara, Dumalengan, Pinalawan, Ginilingan Puti, Chayong, Kalinayan, and Panilisa were sourced from the Northern Mindanao Agricultural Crops and Livestock Research Center (NMACLRC) of the Philippine Department of Agriculture – Regional Field Office 10. The susceptible check UPL Ri-5 was sourced from the Genetic Resources Division of the Central Experiment Station of the Philippine Rice Research Institute in Muñoz, Nueva Ecija. Data on number of roots, total plant length and maximum root length were measured at the date of extraction. Extracted and cleaned root systems were then imaged and processed through the GiaRoots Image Analysis software to estimate the following parameters: root surface area, root length density and daily root length gain, network length and network volume. Visual evaluation of leaf rolling score, leaf drying score and drought recovery score were also performed.

Experimental plants were planted in 7.62 cm x 40.64 GI tubes. Soil medium was obtained from the field and was mixed thoroughly to homogenize the soil medium (Figure 1). A conservative fertilization rate of 60-60-60 NPK (kg/ha) was thoroughly mixed on the soil medium prior to filling. After which, a tube was filled until the tube was optimally full, the soil was extracted and weighed. The rest of the remaining tubes were then filled with 750.00 g of soil (Figure 1).



Figure 1. Thoroughly mixed soil medium, GI sheet, tie wire ring, digital weighing scale and fabricated GI tube

Three grams of seeds for every experimental genotype were placed in small cloth bags. These bags were secured by tying and were labeled properly. Seeds were soaked in water for 24 hours and were incubated for the next 36 hours in a mound of rice straw. Each tube was sown with one pre-germinated rice seedling based on the experimental layout. The seedlings were taken-care for uniformly and were protected from insect pests and diseases until termination of the experiment at 30 days after sowing (DAS) in a rain-out shed. Agrometeorological factors such as temperature and relative humidity were not controlled. Adtuyon clay

(Ultisol) was the prevalent soil type in the area which were gathered from corn fields and homogenized prior to filling into GI tubes. Soils in tubes were watered daily to field capacity from the date of sowing until seven days after sowing (DAS) to ensure successful seedling emergence and growth. The amount of water applied was based on the water holding capacity of the soil media. Beyond the 7 DAS period, the experimental tubes were watered following the different re-watering schedules assigned as main-plot factors. The area was kept free from weeds throughout the growing period. This was done by hand weeding. Subsequent hand weeding was done as often as the need arises. The experiment was laid out in a Split-plot arrangement in Randomized Complete Block Design (RCBD), with three replications. The treatments are presented in Table 1.

Table 1. List of main plot and subplot factors of the Split-plot experiment

MAIN PLOT FACTOR (Duration of water withdrawal)	SUBPLOT FACTOR (Upland rice genotypes)
D1 – daily watering	V1 - Azucena (Tolerant check)
D2 – 5 days withdrawal prior to re-watering	V2 - UPL Ri-5 (Susceptible check)
D3 – 10 days withdrawal prior to re-watering	V3 - Domodao
D4 – 15 days withdrawal prior to re-watering	V4 - Dinorado
D5 – 20 days withdrawal prior to re-watering	V5 - Baysilanon
	V6 - Rinara
	V7 - Dumalengan
	V8 - Pinalawan
	V9 - Ginilingan Puti
	V10 - Chayong
	V11 - Kalinayan
	V12 - Panilisa

Statistical Analysis. Data gathered for drought sensitivity scores, drought recovery score and drought tolerance index were analyzed following the Analysis of Variance (ANOVA) in Split-plot for RCBD. Drought sensitivity and recovery scores were subjected to arc sine transformation. The Honestly Significant Difference (HSD) or Tukey's Test was used to determine significant differences between genotype means. These procedures were performed using SAS v.9.1.2. Principal Component Analysis (PCA) was performed. The variables identified by PCA were subjected to Standardized Shannon-Weaver Diversity Index (SSWDI) or simple H' which was computed to determine the phenotypic diversity of the upland rice varieties. The following rating scale adopted from Jamago and Cortes (2012) was used. Cluster analysis was performed to assess germplasm for their genetic variation and to discover patterns of genetic diversity by grouping genetically similar genotypes. Clustering was based on agglomerative hierarchical clustering using Euclidean distance of dissimilarity and Ward's agglomeration method in XLStat.

RESULTS AND DISCUSSION

Baseline Morphometric and Rhizometric Traits

Among the 22 morphometric and rhizometric traits observed in this experiment only eight variables were found to have varied significantly either among different durations of water withdrawal (DWW) or among the

different upland rice landraces (URLs). The rest of the variables were found to be non-variable indicating that upland rice landraces had similar responses to the DWW. Furthermore, no significant interaction between upland rice varieties and durations of water withdrawal was detected in the ANOVA of all the traits.

Total Plant Length

Data on total plant length of the 12 experimental genotypes (Table 2) were analyzed statistically and revealed highly significant differences among means. Domodao recorded the longest plant length of 524.40 mm. Tukey's test further revealed that Domodao had a total plant length that was statistically comparable to nine other experimental upland rice genotypes. On the other hand, Dinorado (333.27 mm) recorded the shortest plant length. This implies that the total plant length of this experiment's set of upland rice landraces exhibits phenotypic diversity in terms of total plant length, consistent with findings on the genetic variability and phenotypic diversity of upland rice genotypes (Tefera et al., 2023; Sohrabi et al., 2012). Mean plant lengths attributed to the effects of the different DWW implemented were not statistically comparable. This suggests that the different DWW implemented did not affect the total plant length of upland rice genotypes, aligning with studies indicating limited environmental influence on certain morphological traits in upland rice (Lyu et al., 2014).

Table 2. Total plant length, number of roots and maximum root length of upland rice genotypes at different DWW

TREATMENT COMBINATIONS	TOTAL PLANT LENGTH (mm)	NUMBER OF ROOTS	MAXIMUM ROOT LENGTH (mm)
<i>Different Duration of Water Withdrawal</i>			
Daily Watering	412.81	9.36	191.94
5 Days of Water Withdrawal	398.83	6.94	179.61
10 Days of Water Withdrawal	413.50	7.64	196.36
15 Days of Water Withdrawal	403.06	7.69	196.81
20 Days of Water Withdrawal	463.08	9.11	223.94
F-test	NS	NS	NS
<i>Upland Rice Genotypes</i>			
Azucena	420.67 ^{abc}	8.93 ^{ab}	193.60 ^{ab}
UPL Ri-5	367.93 ^{abc}	9.27 ^{ab}	157.47 ^{ab}
Domodao	524.40 ^a	8.40 ^{ab}	275.67 ^a
Dinorado	333.27 ^c	5.87 ^b	140.40 ^b
Baysilanon	423.53 ^{abc}	6.87 ^{ab}	206.40 ^{ab}
Rinara	451.13 ^{abc}	8.80 ^{ab}	220.47 ^{ab}
Dumalengan	514.27 ^{ab}	9.07 ^{ab}	269.40 ^{ab}
Pinalawan	409.00 ^{abc}	7.87 ^{ab}	188.40 ^{ab}

Ginilingan Puti	346.07 ^{bc}	8.60 ^{ab}	143.40 ^b
Chayong	371.07 ^{abc}	7.07 ^{ab}	170.93 ^{ab}
Kalinayan	455.07 ^{abc}	9.67 ^a	224.53 ^{ab}
Panilisa	402.67 ^{abc}	7.40 ^{ab}	182.13 ^{ab}
Ftest b	**	*	**
Ftest a*b	NS	NS	NS
CV _a (%)	28.28	25.93	21.47
CV _b (%)	24.53	26.45	23.88
HSD (a)	-	-	-
HSD (b)	176.13	3.62	129.92
HSD (a*b)	-	-	-

Means on the same column that show at least one common letter are not significantly different at $\alpha=0.05$ (HSD).

- ** - Means are significantly different based on $\alpha=0.01$
- * - Means are significantly different based on $\alpha=0.05$
- NS - Means are not significantly different based on $\alpha=0.05$

Number of Roots

Results of ANOVA reveal that upland rice genotypes had statistically variable mean number of roots. The analysis identified Kalinayan to have the greatest mean number of roots (9.67), which was statistically comparable with nine other experimental upland rice genotypes. The mean analysis also revealed that Dinorado recorded the least number of roots, having developed only 5.87 roots. The number of roots of any crop is crucial for their respective drought response; however, results in this experiment imply that these upland rice genotypes have comparable numbers of roots. This finding aligns with previous studies that highlight the adaptability of root traits in upland rice under varying environmental conditions, including drought stress (Tuhina-Khatun et al., 2015; Gonzalez et al., 2021). However, it can be noted that while Dinorado is popular with consumers because of the aroma it exudes when cooked, it has the least number of roots. On the other hand, the mean number of roots attributed to the effect of the DWW implemented was not statistically variable. The interaction of the DWW and the different upland rice genotypes was found to be statistically non-significant, consistent with findings that root traits often exhibit limited variability under controlled drought conditions (Shoaib et al., 2022).

Maximum Root Length

F-test (ANOVA) revealed that the 12 experimental genotypes varied significantly ($P<0.01$) in terms of maximum root length (Figure 2). The upland rice landrace Domodao recorded the longest root, having a mean root length of 275.67 mm. In contrast, Ginilingan Puti and Dinorado recorded the shortest maximum root lengths of 143.40 mm and 140.40 mm, respectively. These results imply that most upland rice genotypes, which are popular landraces, have significant root reach potential, a trait often associated with adaptation to drought conditions (Wang et al., 2023; Gonzalez et al., 2021). Additionally, it can be concluded that the smaller the number of roots an upland rice genotype has, the shorter the root length, as exhibited by Dinorado. The mean maximum root length attributed to the effect of DWW implementation was not statistically variable. The interaction of the DWW and the different upland rice genotypes was found to be statistically non-

significant, consistent with findings that environmental factors often have limited influence on maximum root traits in drought-adapted rice genotypes (Xu et al., 2020).



Figure 2. Scanned root images subjected to GiaRoots Image Analysis

Root Surface Area

Data on the root surface area was obtained by subjecting scanned images of rice roots to GiaRoots image analysis software. GiaRoots-generated data was found to be statistically variable among different upland rice genotypes. With this, the mean analysis identified Rinara to have the highest root surface area of 143494.85 mm³. However, Tukey's test also found that Rinara had a mean root surface area that was statistically comparable to 10 other experimental upland rice landraces. On the other hand, Domodao was found to have the least root surface area among all the experimental upland rice landraces, with only 178373.21 mm³ root surface area. These results suggest that most of the experimental genotypes possess large root surface areas, which are advantageous for nutrient and water uptake in soils with poor fertility (Pang et al., 2020). However, ANOVA declared these mean values to be statistically comparable. Furthermore, the interaction between DWW and URLs was found to be non-significant.

Root Length Density

A total of 10 URLs were found to have statistically similar mean root length density with Domodao, which recorded the highest root length density of 0.57 mm/mm³. On the other hand, Dinorado and Ginilingan Puti had the lowest root length densities of 0.29 mm/mm³. Root length density of a crop's root system shows the relative presence of roots in every unit length of the soil profile, a critical trait for nutrient and water uptake efficiency (Wang et al., 2023; Sandhu et al., 2016). In this variable, Dinorado has consistently shown inferior performance despite its popularity among upland rice farmers.

Table 3. Root surface area, root length density and daily root length gain of upland rice genotypes at different DWW

TREATMENT COMBINATIONS	ROOT SURFACE AREA (mm ³)	ROOT LENGTH DENSITY (mm/mm ³)	DAILY ROOT LENGTH GAIN (mm/day)
<i>Different Duration of Water Withdrawal</i>			
Daily Watering	148979.33	0.39	6.62
5 Days of Water Withdrawal	108349.36	0.37	6.19
10 Days of Water Withdrawal	124256.02	0.40	6.77

15 Days of Water Withdrawal	132824.83	0.40	6.79
20 Days of Water Withdrawal	163909.63	0.46	7.72
F-test	NS	NS	NS
<i>Upland Rice Genotypes</i>			
Azucena	153240.28 ^{abc}	0.40 ^{ab}	6.68 ^{ab}
UPL Ri-5	133876.79 ^{ab}	0.32 ^{ab}	5.43 ^{ab}
Domodao	178373.21 ^c	0.57 ^a	9.51 ^a
Dinorado	91654.68 ^{bc}	0.29 ^b	4.84 ^b
Baysilanon	97376.96 ^{abc}	0.42 ^{ab}	7.12 ^{ab}
Rinara	143494.85 ^a	0.45 ^{ab}	7.60 ^{ab}
Dumalengan	185417.69 ^{abc}	0.55 ^{ab}	9.29 ^{ab}
Pinalawan	116146.24 ^{abc}	0.39 ^{ab}	6.50 ^{ab}
Ginilingan Puti	112431.82 ^{abc}	0.29 ^b	4.94 ^b
Chayong	116478.24 ^{abc}	0.35 ^{ab}	5.89 ^{ab}
Kalinayan	176191.35 ^{ab}	0.46 ^{ab}	7.74 ^{ab}
Panilisa	123283.89 ^{abc}	0.37 ^{ab}	6.28 ^{ab}
Ftest b	**	**	**
Ftest a*b	NS	NS	NS
CVa (%)	16.30	21.47	31.47
CVb (%)	8.63	23.88	53.88
HSD (a)	-	-	-
HSD (b)	84276.99	0.27	4.48
HSD (a*b)	-	-	-

Means on the same column that show at least one common letter are not significantly different at $\alpha=0.05$ (HSD).

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- NS - Means are not significantly different based on $\alpha=0.05$

This suggests that the trait behind Dinorado's popularity is its grain aroma when cooked rather than its yield or root efficiency, as supported by studies highlighting trade-offs between agronomic traits and consumer preferences in upland rice (Pang et al., 2020). Analysis of the means ruled that Dinorado and Ginilingan Puti were statistically different from the rest of the experimental genotypes in terms of root length density,

consistent with findings that root architecture traits vary significantly among upland rice genotypes under different environmental conditions (Gonzalez et al., 2021).

Daily Root Length Gain

In terms of daily root length gain, Domodao took the lead among the 12 URLs having recorded a mean daily root length gain of 9.51 mm/day. On the other hand, Ginilingan Puti and Dinorado recorded the lowest mean daily root length gain of 5.89 mm/day and 4.84 mm/day, respectively. Being a measure of the speed of a crops root system growth towards the depth of the soil strata, results imply that most of the URLs have similar speed of root penetration and that there is a narrow room for improvement in this variable of URLs. Finally, statistical analysis declared mean daily root length gain attributed to the effect of the implementation of DWW to be non-variable. Furthermore, no significant interaction was detected between the implementation of DWW and the experimental upland rice landraces.

Network Volume and Length

Root network length and volume were obtained using the GiaRoots image analysis software. Statistical analysis of the data revealed that both network variables were non-variable at each of the two levels of comparison possible (Table 4). Mean root network volume and length attributed to the effect of the implementation of DWW were found to have conferred no variability in both variables. Finally, the possible interactions of the two variables were considered in the experiment; however, its accuracy is sacrificed over the accuracy of the measurement of the genotypic effects or the experimental upland rice genotypes. Hence, based on the results, it is recommended that similar experiments should be done until physiological maturity. However, ANOVA revealed that mean root network volume and length were found to be statistically variable. Mean analysis also identified Dinorado to have the lowest root network volume of 116184.68 mm³. In this variable, it was observed that Dumalengan recorded the highest mean root network length of 14118.53 mm together with Domodao, which recorded an average root network length of 14623.80 mm. Dinorado was observed to have the lowest root network length among the twelve experimental upland rice landraces. It should be remembered that Dinorado also recorded a significantly lower root network volume. Hence, it can be concluded that among all the URLs in this experiment, Dinorado recorded poor network volume and length, which might explain its drought susceptibility in farmers' fields (Gonzalez et al., 2021; Pang et al., 2020). However, thanks to its aromatic grains, Dinorado still enjoys a great extent of popularity among upland rice farmers and consumers in Bukidnon (Sandar et al., 2022).

Table 4. Root network variables of upland rice genotypes at different DWW

TREATMENT COMBINATIONS	NETWORK VOLUME (mm ³)	NETWORK LENGTH (mm)
<i>Different Duration of Water Withdrawal</i>		
Daily Watering	182725.06	11977.44
5 Days of Water Withdrawal	137724.54	8340.94
10 Days of Water Withdrawal	149242.14	10062.28
15 Days of Water Withdrawal	166696.66	10353.22
20 Days of Water Withdrawal	205886.63	12784.06
F-test	NS	NS
<i>Upland Rice Genotypes</i>		
Azucena	180842.85 ^{abc}	12612.47 ^{ab}

UPL Ri-5	169279.27 ^{abc}	10346.53 ^{ab}
Domodao	219833.16 ^{ab}	14118.53 ^a
Dinorado	116184.68 ^c	7012.80 ^b
Baysilanon	118779.85 ^{bc}	7734.60 ^{ab}
Rinara	178577.13 ^{abc}	11257.80 ^{ab}
Dumalengan	229676.60 ^a	14623.80 ^a
Pinalawan	137085.70 ^{abc}	9547.87 ^{ab}
Ginilingan Puti	140182.89 ^{abc}	8811.93 ^{ab}
Chayong	154318.80 ^{abc}	8959.80 ^{ab}
Kalinayan	225320.26 ^a	13627.80 ^{ab}
Panilisa	151378.90 ^{abc}	9789.13 ^{ab}
Ftest b	**	**
Ftest a*b	NS	NS
CV _a (%)	106.39	116.61
CV _b (%)	50.22	53.08
HSD (a)	-	-
HSD (b)	151378.90	6927.73
HSD (a*b)	-	-

Means on the same column that show at least one common letter are not significantly different at $\alpha=0.05$ (HSD).

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Diversity Analysis

Phenotypic diversity was assessed in this experiment using the Standardized Shannon-Weaver Diversity Index (H') and described using the scale of Jamago and Cortes (2012). Variables that were found to have significantly contributed to the variability accounted for the first principal component in the principal component analysis of every duration of water withdrawal implemented were identified and subjected to SSWDI. Furthermore, SSWDI-derived H' obtained from the different contributory variables were presented in Table 5. Interestingly, it was found that the implementation of DWW has significantly affected the phenotypic diversity of upland rice seedlings, consistent with studies emphasizing the impact of water stress on phenotypic traits (Domingo et al., 2023; Wang et al., 2021). This experiment might have been the first attempt to determine the phenotypic diversity dynamics of upland rice seedlings under various levels of drought stress, as previous studies have focused on mature plants or field conditions (Yin et al., 2023; Tuhina-Khatun, 2015). Based on the results, it was found that the SSWDI of the same variables under different DWW can fluctuate

despite being measured on the same genotypes. Moreover, the mean diversity (H') of significant contributory variables at DWW may also fluctuate. In this experiment, it can be noted that the mean diversity of significantly contributory variables of upland rice seedlings subjected to daily watering, five- and 15-day durations of water withdrawal were numerically comparable. However, mean phenotypic diversity dropped when the same upland rice seedlings were subjected to a 10-day duration of water withdrawal. These findings hint at the possibility of genetic plasticity in upland rice landraces to early vegetative stage drought stress induced by water withdrawal alone, aligning with research on drought adaptation mechanisms in traditional upland rice varieties (Domingo et al., 2023; Yin et al., 2023; Rabara et al., 2014).

It should also be noted that subjecting upland rice seedlings in 20 days duration of water withdrawal has increased the mean phenotypic diversity to 0.82 H' . Furthermore, SSWDI values recorded on significantly contributory variables of upland rice seedlings subjected to the 20 duration of water withdrawal mostly rhizometric and shoot biomass variables. The high variability observed in this main plot factor may indicate that the implementation of long duration of water withdrawal on upland rice seedlings is able to induce the expressions of certain rhizometric responses and trigger the expression of new drought stress response genes.

Table 5. Standardized Shannon Index of experimental upland rice varieties in terms of various morphometric and rhizometric variables under different DWW

MORPHOMETRIC AND RHIZOMETRIC VARIABLES	DURATION OF WATER WITHDRAWAL (DAYS)				
	Daily	5	10	15	20
Plant Height	0.66	0.81	0.86	-	-
Maximum Root Length	-	0.79	-	-	-
Root Fresh Weight	0.91	0.63	0.74	0.73	0.81
Root Dry Weight	0.71	0.87	-	0.74	0.79
Shoot Fresh Weight	0.79	0.58	0.67	0.76	0.86
Shoot Dry Weight	-	-	-	0.74	0.76
Root-shoot Weight Ratio	-	-	-	-	-
Root-shoot Length Ratio	-	0.92	-	-	-
Daily Root Weight Gain	0.81	0.69	-	0.80	0.74
Daily Root Length Gain	-	0.81	-	0.74	-
Daily Shoot Weight Gain	0.70	-	-	0.74	0.71
Daily Shoot Length Gain	0.64	0.81	0.74	-	-
Total Plant Length	0.86	0.83	0.81	-	-
Total Plant Biomass	0.67	0.86	-	0.79	0.81
Root Diameter	0.77	-	0.35	-	-

Root Weight Density	-	0.71	0.67	0.76	0.82
Root Length Density	-	0.79	-	-	-
Average Root Width	-	-	-	-	-
Number of Roots	-	0.77	-	0.88	-
Root Surface Area	0.79	0.78	-	0.74	0.97
Network Length	0.83	0.74	-	-	0.79
Network Volume	-	0.74	-	0.88	0.97
Leaf Rolling Score	-	-	-	-	-
Leaf Drying Score	-	-	-	-	-
Drought Recovery Score	-	-	-	-	-
Mean	0.76	0.77	0.69	0.77	0.82

Results show that the diversity of fresh weight decreases when URL seedlings are subjected to increasing DWW. On the other hand, shoot fresh weight was found to have an increasing phenotypic diversity trend in terms of shoot weight. This study deduced that the decrease of the phenotypic diversity observed in root fresh weight may indicate that drought stress in upland rice seedlings tend to approach to a mean root fresh weight as evidenced by observed downward trend of its phenotypic diversity. This is due to the general response of upland rice seedlings under drought where they prioritize root development. For instance, take a scenario where genotypes with high root biomass are subjected to drought, physiologically, plants would compromise below-ground biomass accumulation to give way for longitudinal root development. Other genotypes with poorer root biomass will also do the same but would have to mobilize above-ground biomass to pursue root development. This then results in an increase in the variability of shoot biomass as genotypes with poor root biomass will mobilize shoot biomass while those with greater root biomass can just mobilize photosynthates that are close to the root apex being the priority growing point.

Relationship of Drought Related Components

Principal Component Analysis (PCA) of various morphometric and rhizometric data of upland rice seedlings under five days of water withdrawal was performed. The procedure aimed to determine variables responsible for the variability observed in upland rice seedlings subjected to five days of recurring drought stress. The biplot generated in this analysis is illustrated in Figure 2. PCA results suggest that total plant length (TPL), daily root length gain (DRLG), daily shoot weight gain (DSWG), and shoot dry weight (SDW) contributed the most to the variability observed in upland rice seedlings subjected to five days of recurring drought, consistent with findings that morphometric traits are key indicators of drought tolerance (Verma et al., 2019; Yin et al., 2023). It was further noted that drought sensitivity traits such as leaf rolling and leaf drying scores, along with drought recovery score and average root width, improved their contribution to variability under drought conditions, as these traits are expressed more prominently during stress periods (Pang et al., 2020; Yin et al., 2023). The prioritization of cellular activity in root apices to enhance root penetration aligns with studies on adaptive mechanisms in upland rice genotypes under limited water availability (Da Mata et al., 2023; Sandar et al., 2022). This postulate also makes sense as physiological activity under stress is limited to photosynthate partitioning due to leaf rolling or drying out, a phenomenon widely observed in drought-stressed rice varieties (Ding et al., 2013; Verma et al., 2019).

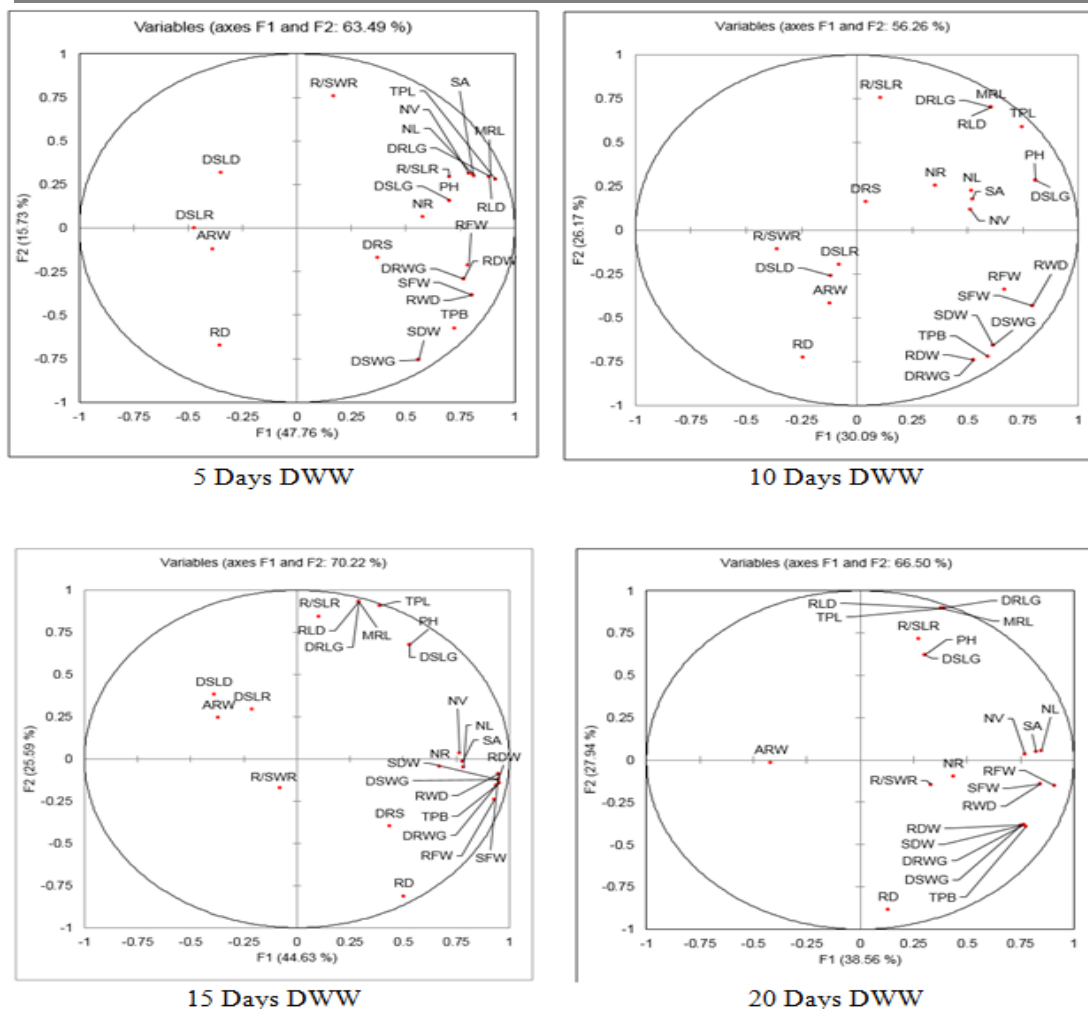


Figure 2. Bi-plot of factor loadings of 25 qualitative and quantitative morphometric and rhizometric variables from principal component analysis of twelve upland rice genotypes under different DWW

Identification of Drought Tolerant Genotypes

Drought Sensitivity and Recovery

Rice plants that were watered daily showed healthy leaves. Presented in Table 5 are the drought-induced leaf rolling sensitivity values of the different upland rice genotypes at DWW implemented. Statistical analysis revealed that the mean leaf rolling score of URLs attributed to the effect of the implementation of DWW varied significantly. Mean analysis revealed that upland rice seedlings subjected to 15 days duration of water withdrawal resulted in the highest mean leaf rolling score of 31.34 percent. On the other hand, seedlings of URLs subjected to five, 10- and 20-days durations of water withdrawal recorded statistically similar mean leaf rolling scores. Finally, seedlings of upland rice genotypes which were watered daily recorded the lowest leaf rolling score of 0.25 percent.

Earlier experiments have shown proof of plant seedlings to survive drought due to the expression of early vigor. Richards et al., (2006, 2007) and Rebetzke et al., (2016) agreed that early vigor under conditions of low evapotranspiration may allow annual crops to optimize water use efficiency (WUE) and limit the loss of water due to direct evaporation from the soil surface. This leaves stored more water available for later developmental stages when soil moisture becomes progressively exhausted and increasingly limiting for survival. Absciscic acid (ABA) has been shown to affect many of the traits that influence the water balance of the plant through both dehydration avoidance and dehydration tolerance (Thompson et al., 2007). However, the sudden introduction of moisture to plants by the early vigor expressed in seedlings may prove to be detrimental as the sudden influx of water may have diluted ABA concentrations in rice leaves. The dilution and transpiration of ABA may have been the reason drought symptoms were aggravated in seedlings subjected to 15 days of water

withdrawal (Yan et al., 2023; Wang et al., 2023b). The same may also have been the reason upland rice seedlings have survived, as traits like leaf rolling and ABA modulation have been linked to drought tolerance (Yan et al., 2023). Additionally, studies have identified that phenotypic traits such as reduced vegetative growth and improved root systems contribute significantly to drought adaptation in upland rice genotypes (Shruthi et al., 2024; Lanna et al., 2021).

Table 5. Drought sensitivity and recovery of upland rice genotypes at different DWW

TREATMENT COMBINATIONS	LEAF ROLLING SCORE (%)	LEAF DRYING SCORE (%)	DROUGHT RECOVERY SCORE
<i>Different Duration of Water Withdrawal</i>			
Daily Watering	0.25 ^c	0.25	99.75 ^a
5 Days of Water Withdrawal	14.60 ^b	9.04	68.64 ^b
10 Days of Water Withdrawal	13.99 ^b	9.86	70.48 ^b
15 Days of Water Withdrawal	31.34 ^a	19.89	61.73 ^b
20 Days of Water Withdrawal	7.37 ^{bc}	7.14	68.23 ^b
F-test	**	NS	**
<i>Upland Rice Genotypes</i>			
Azucena	15.59	8.88	72.31
UPL Ri-5	14.53	14.51	75.69
Domodao	12.08	7.60	69.68
Dinorado	13.11	5.25	74.96
Baysilanon	9.00	3.44	81.07
Rinara	12.68	7.04	76.37
Dumalengan	18.89	14.28	67.09
Pinalawan	15.44	9.36	72.48
Ginilingan Puti	14.46	10.29	74.70
Chayong	9.52	8.03	75.49
Kalinayan	12.30	8.56	73.95
Panilisa	14.53	13.61	71.46
Ftest b	NS	NS	NS
Ftest a*b	NS	NS	NS
CVa (%)	24.64	27.04	24.85
CVb (%)	16.92	23.96	24.12
HSD (a)	12.17	-	26.94
HSD (b)	-	-	-
HSD (a*b)	-	-	-

Means on the same column that show at least one common letter are not significantly different at $\alpha=0.05$ (HSD).

- ** - Means are significantly different based on $\alpha=0.01$
- * - Means are significantly different based on $\alpha=0.05$
- NS - Means are not significantly different based on $\alpha=0.05$

With most rice plants exhibiting drought-induced leaf rolling sensitivity reactions after the implementation of only 15 days of water withdrawal, it is recommended that the optimal number of days of water withdrawal that will enable rice breeders to screen upland rice genotypes for drought tolerance/sensitivity using leaf rolling is 15 days. However, this is still subject to verification, hence the research moves for further verification. Nevertheless the 15 days of drought implementation together with the daily watering of the experimental units in their first 7 days from sowing proves to be short enough that even with limited space and resources, rice breeders can still conduct rapid drought screening since this study was able to prove that 15 days of water withdrawal on rice seedlings is enough to weed out drought susceptible genotypes. Finally, statistical analysis detected no significant interaction between duration of water withdrawal and upland rice genotypes.

Leaf drying is also one of the drought sensitivity variables that was measured in this experiment (Table 5). Leaf drying is a drought sensitivity variable being worse than the leaf rolling. The same with leaf rolling score, data on drought sensitivity by leaf drying for the five days main plot factor was based on four repeated ratings, while the 10- and 15-days main plot factor were based on two repeated ratings and the twenty days main plot factor was only taken once.

In general, it was observed that the implementation of 15 days of water withdrawal caused the drought recovery of the URLs to go even lower. However, it should also be noted that compared to the plants which experienced only 10 and 15 days of water withdrawal, more upland rice genotypes exhibited higher drought recovery even after being subjected to 20 days of water withdrawal. This observation aligns with findings that upland rice genotypes possess unique drought tolerance mechanisms, such as sugar-mediated osmotic acclimation and antioxidative responses, which contribute to their ability to recover under prolonged drought conditions (Melandri et al., 2021; Dwivedi et al., 2023). Finally, the researcher recommends the conduct of further experimentation on the drought recovery of upland rice cultivars to better understand the drought recovery performance of upland rice seedlings in response to water withdrawal. ANOVA detected no significant interaction between the main plot and subplot factors of this experiment in terms of drought recovery scores. This implies that the total variation observed in this variable can be due to the implementation of different water withdrawal durations. These findings are consistent with studies highlighting that transcriptomic divergence in upland rice contributes significantly to its drought adaptation and recovery (Lou et al., 2020;).

Drought Susceptibility

Biomass yield has been considered an important variable in varietal selection for drought stress tolerance (Kondhia et al., 2015). Drought Susceptibility Index (DSI) was computed using the Fischer and Maurer formula (1978). Fischer and Maurer (1978) reported that DSI is based on a reduction in yield adjusted for drought intensity of experiment. DSI values are interpreted based on the direction of desirability and were ranked following the scale of (Kumar et al., 2014) as highly drought-tolerant (DSI <0.50), drought-tolerant (DSI: 0.51-0.75), moderately tolerant (DSI: 0.76-1.00) and drought susceptible (DSI >1.00). In general, lower DSI values indicate lower differences in biomass yield across stress and non-stress conditions which translate to more resistance to drought (Table 6). In general, the DSI analysis was successful in determining the degree of tolerance and susceptibility to drought of seedlings of experimental upland rice genotypes. The implementation of five days of recurring drought was found to be most effective in screening for drought susceptibility. This proves that the repetitive exposure to drought of upland rice seedlings is more detrimental than longer exposure to drought stress. Furthermore, based on DSI analysis, seedlings of UPL Ri-5, Domodao, Baysilanon, Dumalengan, Ginilingan Puti, Chayong, Kalinayan and Panilisa are considered highly drought tolerant after consistently exhibiting high drought tolerance across all DWW.

Table 6. Drought susceptibility index of upland rice varieties at different DWW s for total plant biomass

VARIABLES	DWW			
	5 DAYS	10 DAYS	15 DAYS	20 DAYS
Azucena	0.25 ^{HT}	0.18 ^{HT}	0.65 ^T	0.21 ^{HT}
UPL Ri-5	0.19 ^{HT}	0.03 ^{HT}	0.40 ^{HT}	0.33 ^{HT}
Domodao	0.26 ^{HT}	0.02 ^{HT}	0.09 ^{HT}	0.43 ^{HT}
Dinorado	1.22 ^S	0.13 ^{HT}	0.19 ^{HT}	0.78 ^{MT}
Baysilanon	0.32 ^{HT}	0.37 ^{HT}	0.20 ^{HT}	0.35 ^{HT}

Rinara	1.20 ^S	0.35 ^{HT}	0.21 ^{HT}	0.61 ^T
Dumalengan	0.02 ^{HT}	0.20 ^{HT}	0.39 ^{HT}	0.14 ^{HT}
Pinalawan	0.52 ^T	0.60 ^T	0.19 ^{HT}	0.45 ^{HT}
Ginilingan Puti	0.10 ^{HT}	0.09 ^{HT}	0.49 ^{HT}	0.03 ^{HT}
Chayong	0.29 ^{HT}	0.08 ^{HT}	0.37 ^{HT}	0.43 ^{HT}
Kalinayan	0.12 ^{HT}	0.33 ^{HT}	0.30 ^{HT}	0.28 ^{HT}
Panilisa	0.26 ^{HT}	0.27 ^{HT}	0.49 ^{HT}	0.08 ^{HT}

HT	=	Highly tolerant
T	=	Tolerant
MT	=	Moderately tolerant
S	=	Susceptible

CONCLUSIONS AND RECOMMENDATIONS

The current study was able to report the quantitative morphometric and rhizometric traits of the experimental upland rice landraces thereby establishing baseline information of the experimental genotypes in terms of their morphometric and rhizometric traits. Phenotypic diversity of the experimental genotypes was slightly influenced by the implementation of different DWW wherein the 20 DWW induced the highest level of phenotypic diversity on the upland rice genotypes. Based on PCA, it can be concluded that shoot and root length variables of upland rice genotypes are inversely related while all biomass variables as closely related with one another. This indicates that genotypes that develop the most biomass can still yield the most. Through the drought susceptibility index equation, it has been found that 5 days DWW is enough to identify susceptible upland rice genotypes which were Dinorado and Rinara. It can also be concluded that repeated exposure to drought improves upland rice seedlings tolerance to drought thereby ensuring its survival on the long run. However, it should be expected that optimal yield could not be attained by upland rice subjected to drought stress at seedling stage. Hence, further studies are recommended on the quantification of yield reduction of upland rice subjected to different DWW at seedling stage.

DECLARATIONS

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

The datasets during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests

No competing interests.

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REFERENCES

1. Da Mata, C. R., De Castro, A. P., Lanna, A. C., Bortolini, J. C., & De Moraes, M. G. (2023). Physiological and yield responses of contrasting upland rice genotypes towards induced drought. *Physiology and Molecular Biology of Plants*, 29(2), 305-317. <https://doi.org/10.1007/s12298-023-01287-8>.
2. Ding, X., Li, X., & Xiong, L. (2013). Insight into differential responses of upland and Paddy rice to drought stress by comparative expression profiling analysis. *International Journal of Molecular Sciences*, 14(3), 5214-5238. <https://doi.org/10.3390/ijms14035214>.
3. Domingo, K.-L. B., Suralta, R. R., Dalusong, V.G., Baldo, N. B., dela Cruz, R. Y., Abellera, J. C., & Jamago, J. M. (2023). Morphological and molecular diversity of traditional upland rice (*Oryza sativa* L.) varieties for drought tolerance at seedling stage. *Philippine Journal of Science*, 152(5), 1623–1630.
4. Dwivedi, S. K., Kumar, S., Natividad, M. A., Quintana, M. R., Chinnusamy, V., & Henry, A. (2023). Disentangling the roles of plant water status and stem carbohydrate Remobilization on rice harvest index under drought. *Rice*, 16(1). <https://doi.org/10.1186/s12284-023-00631-6>.
5. Fischer, R.A. & Maurer, R. (1978). Drought resistance in spring wheat cultivar: I- Grain yield response. *Aust. J. Agric. Res.* (29).
6. Gonzalez D, Postma J and Wissuwa M (2021) Cost-Benefit Analysis of the Upland-Rice Root Architecture in Relation to Phosphate: 3D Simulations Highlight the Importance of S-Type Lateral Roots for Reducing the Pay-Off Time. *Front. Plant Sci.* 12:641835. doi: 10.3389/fpls.2021.641835.
7. Jamago, J.M. & Cortes, R.V. (2012). Seed diversity and utilization of the upland rice landraces and traditional varieties from selected areas in Bukidnon, Philippines. *International Peer Reviewed Journal*. doi: <http://dx.doi.org/10.7718/ijec.v4i1.366>.
8. Khush, G.S. & P.S. Virk. (2005). IR varieties and their impact. Los Baños (Philippines): International Rice Research Institute.
9. Kondhia, A., Tabien, R.E., & Ibrahim, A. (2015). Evaluation and Selection of High Biomass Rice (*Oryza sativa* L.) for Drought Tolerance. *American Journal of Plant Sciences*, 6, 1962-1972. <http://dx.doi.org/10.4236/ajps.2015.612197>.
10. Lafitte, H.R., Ismail, A., & Bennett, J. (2004). Abiotic stress tolerance in rice for Asia: progress and the future. *Agronomy Australia Proceedings*. Australian Society of Agronomy.
11. Lambers, H., Chapin, F.S., & Pons, T.L. (1997). *Plant physiological ecology*. 2nd Ed. Springer.
12. Lanna, A. C., Coelho, G. R., Moreira, A. S., Terra, T. G., Brondani, C., Saraiva, G. R., Lemos, F. D., Guimarães, P. H., Morais Júnior, O. P., & Vianello, R. P. (2021). Upland rice: Phenotypic diversity for drought tolerance. *Scientia Agricola*, 78(5). <https://doi.org/10.1590/1678-992x-2019-0338>.
13. Luo, Z., Xiong, J., Xia, H., Ma, X., Gao, M., Wang, L., Liu, G., Yu, X., & Luo, L. (2020). Transcriptomic divergence between upland and lowland ecotypes contributes to rice adaptation to a drought-prone agroecosystem. *Evolutionary Applications*, 13(9), 2484-2496. <https://doi.org/10.1111/eva.13054>.
14. Lyu, J., Li, B., He, W., Zhang, S., Gou, Z., Zhang, J., Meng, L., Li, X., Tao, D., Huang, W., Hu, F., & Wang, W. (2014). A genomic perspective on the important genetic mechanisms of upland adaptation of rice. *BMC Plant Biology*, 14(1), 160. <https://doi.org/10.1186/1471-2229-14-160>.
15. Maclean, J.L., Dawe, D.C., Hardy, B., & Hettel, G.P. (eds). (2002). *Rice Almanac. Source Book for the Most Important Economic Activity on Earth*. 3RD Ed. IRRI, Los Baños, Philippines.
16. Melandri, G., AbdElgawad, H., Floková, K., Jamar, D. C., Asard, H., Beemster, G. T., Ruyter-Spira, C., & Bouwmeester, H. J. (2021). Drought tolerance in selected aerobic and upland rice varieties is driven by different metabolic and antioxidative responses. *Planta*, 254(1). <https://doi.org/10.1007/s00425-021-03659-4>.

17. Pang, Z., Zhao, Y., Xu, P., & Yu, D. (2020). Microbial diversity of upland rice roots and their influence on rice growth and drought tolerance. *Microorganisms*, 8(9), 1329. <https://doi.org/10.3390/microorganisms8091329>.
18. Rabara, R., Ferrer, M., Diaz, C., Newingham, M., & Romero, G. (2014). Phenotypic diversity of farmers' traditional rice varieties in the Philippines. *Agronomy*, 4(2), 217-241. <https://doi.org/10.3390/agronomy4020217>.
19. Rebetzke G.J., Jimenez-Berni, J.A., Bovill, W.D., Deery, D.M., & James, R.A. (2016). High-throughput phenotyping technologies allow accurate selection of stay-green. *J. Exp. Bot.* 2016; 67:4919–4924. doi: 10.1093/job/erw301.
20. Richards, R.A. & Passioura, J.B. (1981). Seminal root morphology and water use of wheat. I. Environmental effects. *Crop Sci.* (21).
21. Romero, M.V. (2008). Value-added products of rice and entrepreneurship in the Philippines. *Proceedings: Asia Rice Foundation's Annual Rice Forum*.
22. Sandar, M. M., Ruangsiri, M., Chutteang, C., Arunyanark, A., Toojinda, T., & Siangliw, J. L. (2022). Root characterization of Myanmar upland and lowland rice in relation to agronomic and physiological traits under drought stress condition. *Agronomy*, 12(5), 1230. <https://doi.org/10.3390/agronomy12051230>.
23. Sandhu, N., Raman, K. A., Torres, R. O., Audebert, A., Dardou, A., Kumar, A., & Henry, A. (2016). Rice root architectural plasticity traits and genetic regions for adaptability to variable cultivation and stress conditions. *Plant Physiology*, 171(4), 2562-2576. <https://doi.org/10.1104/pp.16.00705>.
24. Shoaib, M., Banerjee, B. P., Hayden, M., & Kant, S. (2022). Roots' Drought Adaptive Traits in Crop Improvement. *Plants*, 11(17), 2256. <https://doi.org/10.3390/plants11172256>.
25. Sohrabi M, Rafii MY, Hanafi MM, Siti Nor Akmar A, Latif MA. Genetic diversity of upland rice germplasm in Malaysia based on quantitative traits. *ScientificWorldJournal*. 2012;2012:416291. doi: 10.1100/2012/416291. Epub 2012 Apr 30. PMID: 22654604; PMCID: PMC3361239.
26. Sruthi, P., Surendran, U., Siddiqui, M. H., & Alamri, S. (2024). Understanding the leaf rolling of Paddy and exploring its management options under aerobic rice. *Scientific Reports*, 14(1). <https://doi.org/10.1038/s41598-024-68244-7>.
27. Tefera, S., Aragaw, M., & Molla, T. (2023). Agro-morphological and physiochemical studies of upland rice (*Oryza sativa* L.) varieties for variability with yield and quality related parameters in south Gondar district, Ethiopia. *Heliyon*, 9(4), e15186. <https://doi.org/10.1016/j.heliyon.2023.e15186>.
28. Thompson A.J., Andrews, J., Mulholland, B.J., Mckee, J.M.T., Hilton, H.W., Black, C.R., & Taylor, I.B. (2007). Overproduction of abscisic acid in tomato increases transpiration efficiency and root hydraulic conductivity and influences leaf expansion. *Plant Physiol.* 2007; 143:1905–1917. doi: 10.1104/pp.106.093559.
29. Tuhina-Khatun M, Hanafi MM, Rafii Yusop M, Wong MY, Salleh FM, Ferdous J. (2015). Genetic Variation, Heritability, and Diversity Analysis of Upland Rice (*Oryza sativa* L.) Genotypes Based on Quantitative Traits. *Biomed Res Int.* 2015;2015:290861. doi: 10.1155/2015/290861. Epub 2015 Jul 15. PMID: 26258135; PMCID: PMC4518168.
30. United States Department of Agriculture-Foreign Agricultural Service (USDA-FAS). (2016). *PHILIPPINES: Drought in Mindanao Causes Corn Production Decline*. Retrieved May, 2017 from the World Wide Web site: <https://pecad.fas.usda.gov/highlights/2016/03/Philippines/Index.htm>.
31. Verma, H., Borah, J. L., & Sarma, R. N. (2019). Variability assessment for root and drought tolerance traits and genetic diversity analysis of rice Germplasm using SSR markers. *Scientific Reports*, 9(1). <https://doi.org/10.1038/s41598-019-52884-1>.
32. Wang, Y., Jiang, C., Zhang, X., Yan, H., Yin, Z., Sun, X., Gao, F., Zhao, Y., Liu, W., Han, S., Zhang, J., Zhang, Y., Zhang, Z., Zhang, H., Li, J., Xie, X., Zhao, Q., Wang, X., Ye, G., ... Li, Z. (2023). Upland rice genomic signatures of adaptation to drought resistance and navigation to molecular design breeding. *Plant Biotechnology Journal*, 22(3), 662-677. <https://doi.org/10.1111/pbi.14215>.
33. Wang, X., Huang, J., Peng, S., & Xiong, D. (2023b). Leaf rolling precedes stomatal closure in rice (*Oryza sativa*) under drought conditions. *Journal of Experimental Botany*, 74(21), 6650-6661. <https://doi.org/10.1093/jxb/erad316>.

34. Xu, X., Ye, J., Yang, Y., Zhang, M., Xu, Q., Feng, Y., Yuan, X., Yu, H., Wang, Y., Yang, Y., & Wei, X. (2020). Genome-wide association study of rice rooting ability at the seedling stage. *Rice*, 13(1). <https://doi.org/10.1186/s12284-020-00420-5>.
35. Yan, J., Ninkuu, V., Fu, Z., Yang, T., Ren, J., Li, G., Yang, X., & Zeng, H. (2023). OsOLP1 contributes to drought tolerance in rice by regulating ABA biosynthesis and lignin accumulation. *Frontiers in Plant Science*, 14. <https://doi.org/10.3389/fpls.2023.1163939>.
36. Yin J, Zhao H, Wu X, Ma Y, Zhang J, Li Y, Shao G, Chen H, Han R and Xu Z (2023). SSR marker-based analysis for identification and of genetic diversity of non-heading Chinese cabbage varieties. *Front. Plant Sci.* 14:1112748. doi: 10.3389/fpls.2023.1112748.
37. Yoshida, S. & Hasegawa, S. (1982). The rice root system: its development and function. In: *Drought Resistance in Crops, with Emphasis on Rice*. International Rice Research Institute, Manila, Philippines.