



RESEARCH ARTICLE

Genetic analysis for yield and drought tolerance traits in rice (*Oryza sativa* L.)

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Abstract

The experimental material consisted of six generations (P₁, P₂, F₁, F₂, BC₁ and BC₂), which resulted from two crosses, viz. ADT 45 × IR 64 Drt and MDU 6 × IR 64 Drt of rice using three parents. The experiment was carried out in a randomized block design with two replications to study the generation mean analysis. Correlation and path analysis were carried out using F₂ generation. Thirteen traits, viz. days to 50 % flowering, plant height, number of productive tillers/plant, panicle length, number of filled grains / panicle, hundred grain weight, single plant yield, root length, root volume, root thickness, dry root weight, dry shoot weight and root/shoot ratio were studied for above analysis. In generation mean analysis, existence of dominance gene action along with one or more interaction effects, viz. additive x additive (i), additive x dominance (j) and dominance x dominance was observed for all the traits except grain yield and dry root weight which registered both additive and dominance gene action and epistatic components. Correlation analysis showed positive and significant association of grain yield with most of the yield and drought tolerant traits viz. productive tillers per plant, panicle length, filled grains per panicle, 100 grain weight, dry root weight, root length, root volume, root thickness and root/shoot ratio. Path analysis showed that many root characters viz. root thickness, root length, root volume and dry root weight exhibited positive direct effect on grain yield indicating their greater influence on yield under drought stress conditions. Number of filled grains also recorded positive direct effect on grain yield.

Keywords: Correlation and path analysis; drought; generation mean analysis; rice

Introduction

Rice (*Oryza sativa* L.) is the most widely consumed staple food for a large part of the world's human population, especially in Asia (1). Rice is grown in different ecosystems ranging from irrigated to rainfed lowland, rainfed upland and flood-prone conditions (2). Nearly 640 million tons of rice are grown in Asia, representing 90 % of global production. India has the production of 127.93 million tones (3). Rice production and growth of the human population in the past decade suggested the urgent need to increase rice production by 70 % to fulfill upcoming demand by 2050 (3, 4). The production of rice is limited by both biotic (bacterial and fungal) and abiotic (drought, flooding etc.) stress which causes yield loss (5). Among the above stresses, most important constraint for rice production is inconsistent water supply. The production of rice had decreased by about 25.4 % due to the effect of drought (6). In India, about 33 % of area where drastic yield reduction occurs. To overcome these constraints, more attention should be given towards the development of rice varieties with drought tolerance. To develop varieties under drought prone environment, there should be a detailed evaluation of nature and magnitude of gene action governing traits, effect of drought on yield at various crop growth stages. The information on generation mean analysis is important to

determine the nature and magnitude of gene action for quantitative traits.

Generation mean analysis is used for the analysis of various gene effects (7). It is also used for the estimation and interpretation of epistatic interactions. The information about dominance and epistatic gene effects is valuable for development of hybrids. Hence, a study was conducted to decode the nature of gene action and epistatic gene interaction governing grain yield parameters and drought tolerant traits.

Grain yield is a complex trait influenced by a number of yield attributes. These yield contributing traits are interrelated with each other showing a complex relationship (8). Success of rice breeding relies on the degree of association between yield and its contributing traits. Path analysis is an important statistical technique used to assess the interrelation of different component traits and their direct and indirect effects on grain yield (9). With this background, the present investigation was taken up on "Genetic studies of drought tolerant traits in rice" with the following objectives. To estimate the nature of gene action involved in the inheritance of yield and drought tolerant traits. To study the nature of relationship between yield and drought tolerant characters.

Materials and Methods

The present investigation was carried out at Agricultural College and Research Institute, Madurai using six generation viz. P₁ (Female parent used for a cross), P₂ (Male parent used for a cross), F₁ (F₁ generation of a cross), F₂ (F₂ generation of a cross), B₁ (F₁-Backcross with female parent) and B₂ (F₁-Backcross with male parent), involving two cross combinations viz. ADT (R) 45 × IR 64 Drt (Cross 1), MDU 6 × IR 64 Drt (Cross 2) and their respective parents viz. ADT (R) 45, MDU 6 and IR 64 Drt, for developing various generations. IR 64 Drt is a Marker Assisted Selection (MAS) derived drought tolerant rice variety developed in the genetic background of popular mega rice variety IR64. It possesses qDTY 2.2 and qDTY 4.1 QTLs associated with high yield under drought at reproductive and grain filling stages. The parents were crossed to get fresh F₁ and parents seeds were selfed. The F₁ hybrid seeds were selfed to obtain F₂ generation. F₂ generations of following two cross combinations were selected based on the single plant yield and drought tolerant traits. The segregating population seeds were sown during *Rabi*, 2019 along with their parents. B₁ were obtained by backcrossing the F₁ with the female parent P₁, while F₁ was backcrossed to male parent P₂ to result in B₂. As a result of this, six generations, P₁, P₂, F₁, F₂, B₁ and B₂ for two crosses were established. 10 plants each in P₁, P₂ and F₁; 200 plants in F₂; 50 plants each in B₁ and B₂ for each cross were maintained for the study. The stress was imposed on 70th day after sowing and continued for a period of 15 days. The most damaging impact of drought stress on grain yield appears to be during the reproductive growth stage. It has been reported that drought stress during flowering has a detrimental impact on pollination, resulting in poor seed setting, reduced grain size and grain number. In severe drought cases, flower abortion takes place, leading to a 100 % yield decline (10-12). It is therefore established that any intensity of drought stress (mild or severe) during the reproductive growth phase lowers the final grain production; this is because the translocation of assimilates from leaves to reproductive organs (panicle, kernel) are interrupted (13). Observations were recorded individually to assess the association between traits. Yield attributing traits such as days to 50 % flowering, plant height, number of productive tillers / plants, panicle length, number of filled grains / panicle, 100 grain weight, single plant yield and root traits viz. root length, root volume, root thickness, dry root weight, dry shoot weight and root/shoot ratio were recorded. Correlation and path

analysis were calculated using the previously known method (14, 15). Statistical analysis for generation mean analysis was carried out using the method (16).

Results

Correlation analysis

The phenotypic correlation among the drought tolerant and yield component traits of F₂ are presented in Table 1 & 2.

Days to 50 % flowering (-0.967) had negatively significant association with single plant yield. Plant height (0.238), Panicle length (0.493), Number of productive tillers per plant (0.695), Number of filled grains (0.839), 100 grain weight (0.455), root length, root volume (0.816) and root/shoot ratio (0.570) registered positive and significant association with single plant yield. Dry shoot weight showed negative association with single plant yield (-0.444).

Intercorrelation of yield and drought tolerant traits of cross 1

Days to 50 % flowering also had negative significant association with plant height (-0.217), number of productive tillers per plant (-0.682), panicle length (-0.456), number of filled grains per panicle (-0.803), 100 grain weight (-0.426), root length (-0.837), root volume (-0.818), root thickness (-0.725), dry root weight (-0.655) and root/shoot ratio (-0.574). Plant height exhibited significantly negative association with dry shoot weight (-0.202) in cross 1. Plant height exhibited a positive and significant association with panicle length (0.535), Number of productive tillers per plant (0.288), 100 grain weight (0.226), root length (0.198), root volume (0.191), dry root weight (0.185) and root/shoot ratio (0.194). In cross 1, characters namely number of total filled grains per panicle (0.623), 100 grain weight (0.224), root length (0.622), root volume (0.612), root thickness (0.544), dry root weight (0.457) and root/shoot ratio (0.410) had positive relation with number of productive tillers per plant. Panicle length also had significant positive association with number of filled grains (0.438), 100 grain weight (0.269), root length (0.378), root volume (0.364), root thickness (0.340), root weight (0.286) and root/shoot ratio (0.273), where it had negative and significant relation with dry shoot weight (-0.245). Number of filled grains per panicle registered positive correlation with other traits except dry shoot weight. All other traits have positive relations to 100 grain weight, except dry shoot weight had negative and significant association. In cross 1, root length

Table 1. Phenotypic correlation coefficient between different traits in F₂ generation of ADT (R) 45 × IR 64 Drt (cross 1)

Characters	DFF	PH	NPT	PL	NFG	HGW	RL	RV	RT	DRW	DSW	R/S Ratio	SPY
DFF	1.000												
PH	-0.217**	1.000											
NPT	-0.682**	-0.116	1.000										
PL	-0.456**	0.535**	0.004	1.000									
NGP	-0.803**	0.288**	0.623**	0.438**	1.000								
HGW	-0.426**	0.226**	0.224**	0.269**	0.441**	1.000							
RL	-0.837**	0.198**	0.622**	0.378**	0.727**	0.501**	1.000						
RV	-0.818**	0.191**	0.612**	0.364**	0.698**	0.518**	0.981**	1.000					
RT	-0.725**	0.197	0.544**	0.340**	0.640**	0.533**	0.905**	0.901**	1.000				
DRW	-0.655**	0.185**	0.457**	0.286**	0.563**	0.483**	0.851**	0.863**	0.824**	1.000			
DSW	0.429**	-0.202**	-0.313**	-0.245**	-0.443**	-0.337**	-0.641**	-0.650**	-0.562**	-0.731**	1.000		
R/S	-0.574**	0.194**	0.410**	0.273**	0.529**	0.446**	0.802**	0.816**	0.765**	0.9368**	-0.914**	1.000	
SPY	-0.967**	0.238**	0.695**	0.493**	0.839**	0.455**	0.832**	0.816**	0.715**	0.6372**	-0.444**	0.570**	1.000

Note: DFF- days to 50 % flowering; PH- plant height; NPT-number of productive tillers per plant; PL-panicle length; NFG-number of filled grains per panicle; HGW-hundred grain weight; SPY-single plant yield; RL-root length; RV-root volume; RT-root thickness; DRW-dry root weight; DSW-dry shoot weight; R/S ratio- root/shoot ratio.

Table 2. Phenotypic correlation coefficient between different traits in F₂ generation of MDU 6 × IR 64 DRT (cross 2)

Characters	DFF	PH	NPT	PL	NFG	HGW	RL	RV	RT	DRW	DSW	R/S Ratio	SPY
DFF	1.000												
PH	-0.535	1.000											
NPT	-0.798	0.574**	1.000										
PL	-0.763	0.489**	0.665**	1.000									
NGP	-0.786	0.481**	0.827**	0.722**	1.000								
HGW	0.009	0.030	-0.212**	0.020	0.019	1.000							
RL	-0.813**	0.437**	0.684**	0.744**	0.652**	0.021	1.000						
RV	-0.818**	0.435**	0.694**	0.742**	0.657**	0.071	0.960**	1.000					
RT	-0.866**	0.518**	0.684**	0.739**	0.695**	0.035	0.854**	0.866**	1.000				
DRW	-0.782**	0.448**	0.671**	0.703**	0.667**	0.014	0.885**	0.850**	0.784**	1.000			
DSW	0.791**	-0.462	-0.693**	-0.686**	-0.691**	0.000	-0.812**	-0.790**	-0.760**	-0.963**	1.000		
R/S	-0.786**	0.455**	0.676**	0.705**	0.675**	0.000	0.863**	0.831**	0.776**	0.991**	-0.984**	1.000	
SPY	-0.953**	0.567**	0.844**	0.772**	0.844**	-0.006	0.786**	0.791**	0.855**	0.775**	-0.800**	0.782**	1.000

Note: DFF- days to 50 % flowering; PH- plant height; NPT-number of productive tillers per plant; PL-panicle length; NFG-number of filled grains per panicle; HGW-hundred grain weight; SPY-single plant yield; RL-root length; RV-root volume; RT-root thickness; DRW-dry root weight; DSW-dry shoot weight; R/S ratio- root/shoot ratio.

showed a positive significant association with root volume (0.981), root thickness (0.905), root dry weight (0.851) and root/shoot ratio (0.802). The traits viz. root thickness (0.901), dry root weight (0.863) and root/shoot ratio (0.816) exhibited highly positive and significant relation root volume. Root thickness showed highly positive significant association with dry root weight (0.824), root/shoot ratio (0.765). In cross 1, root/shoot ratio (0.936) had highly significant and positive association with dry root weight. Dry shoot weight showed negative association with root/shoot ratio (-0.914).

In cross 2, single plant yield (-0.953) and days to 50 % flowering had negative significant correlation among themselves. Positive significant association was exhibited between plant height (0.567), number of productive tillers per plant (0.844), panicle length (0.772), number of filled grains (0.844), root length (0.855), root thickness (0.855), dry root weight, root/shoot ratio (0.782) and single plant yield. Dry shoot weight showed a significant negative correlation with single plant yield (-0.800). Root/shoot ratio had a significant positive association with single plant yield in cross 2 (0.782).

Intercorrelation of yield and drought tolerant traits of cross 2

Days to 50 % flowering had negative significant association with most of the traits except 100 grain weight (0.009) and dry shoot weight (0.791), which had a positive association. Among the

interrelations, plant height showed a negative association with dry shoot weight (-0.462) in cross 2 and revealed significant positive association with all other traits. Among the yield and drought tolerant related traits, number of productive tillers per plant also had significant positive association with panicle length (0.665), number of filled grains per panicle (0.827), root length (0.684), root volume (0.694), root thickness (0.684), dry root weight (0.671) and root/shoot ratio (0.676). The traits viz. root length (0.021), root volume (0.071), root thickness (0.035) and dry root weight (0.014) had positive association with 100 grain weight in cross 2. Root length exhibited positive and significant correlation with the traits namely root volume, root thickness, dry root weight and root/shoot ratio. Root volume recorded significant and positive relation with root thickness, dry root weight and root/shoot weight. Root thickness also had positive correlation with dry root weight and root/shoot ratio.

Path analysis

A brief account of direct and indirect effects on different component traits on grain yield is presented in Table 3 & 4.

Direct effects

In cross 1 positive low direct effect was recorded by root volume (0.153) and number of filled grains per panicle (0.123). Number of productive tillers per plant (0.096), panicle length (0.089), 100 grain

Table 3. Direct and indirect effects of different traits on grain yield per plant in F₂ generation of ADT (R) 45 × IR 64 Drt

Characters	DFF	PH	NPT	PL	NFG	HGW	RL	RV	RT	DRW	DSW	R/S Ratio
DFF	-0.714	0.0008	-0.0659	-0.0408	-0.0993	-0.0164	0.0231	-0.1253	0.0343	-0.0192	-0.0406	0.0957
PH	0.1554	-0.0036	-0.0113	0.0479	0.0356	0.0087	-0.0055	0.0293	-0.0093	0.0054	0.0192	-0.0332
NPT	0.487	0.0004	0.0966	0.0004	0.077	0.0086	-0.0172	0.0938	-0.0257	0.0134	0.0297	-0.0683
PL	0.3257	-0.0019	0.0004	0.0895	0.0542	0.0103	-0.0104	0.0558	-0.0161	0.0084	0.0233	-0.0456
NGP	0.574	-0.001	0.0602	0.0393	0.1236	0.0169	-0.02	0.107	-0.0303	0.0165	0.042	-0.0881
100	0.3047	-0.0008	0.0217	0.0241	0.0545	0.0383	-0.0138	0.0794	-0.0252	0.0142	0.0319	-0.0744
RL	0.5982	-0.0007	0.0602	0.0338	0.0898	0.0192	-0.0276	0.1502	-0.0428	0.0249	0.0607	-0.1337
RV	0.5846	-0.0007	0.0592	0.0326	0.0863	0.0199	-0.027	0.1531	-0.0427	0.0253	0.0615	-0.136
RT	0.5176	-0.0007	0.0525	0.0304	0.0792	0.0205	-0.025	0.1381	-0.0473	0.0242	0.0532	-0.1274
DRW	0.4678	-0.0007	0.0442	0.0256	0.0696	0.0185	-0.0235	0.1321	-0.039	0.0293	0.0692	-0.156
DSW	-0.3066	0.0007	-0.0303	-0.022	-0.0548	-0.0129	0.0177	-0.0995	0.0266	-0.0214	-0.0946	0.1523
R/S	0.4101	-0.0007	0.0396	0.0245	0.0654	0.0171	-0.0221	0.125	-0.0362	0.0274	0.0865	-0.1665

Note: DFF- days to 50 % flowering; PH- plant height; NPT-number of productive tillers per plant; PL-panicle length; NFG-number of filled grains per panicle; HGW-hundred grain weight; SPY-single plant yield; RL-root length; RV-root volume; RT-root thickness; DRW-dry root weight; DSW-dry shoot weight; R/S ratio- root/shoot ratio

Table 4. Direct and indirect effects of different traits on grain yield per plant in F₂ generation of MDU 6 × IR 64 DRT

Characters	DFF	PH	NPT	PL	NFG	HGW	RL	RV	RT	DRW	DSW	R/S
DFF	-0.4537	-0.0153	-0.1117	-0.0378	-0.1285	-0.0001	-0.0536	0.0531	-0.1527	-0.081	-0.4106	0.4566
PH	0.2428	0.0286	0.0798	0.0242	0.0787	-0.0003	0.0289	-0.0283	0.0913	0.0464	0.2401	-0.2644
NPT	0.3625	0.0163	0.1399	0.0329	0.1353	0.0002	0.0451	-0.0451	0.1207	0.0696	0.3598	-0.3928
PL	0.3464	0.014	0.093	0.0495	0.1181	-0.0002	0.0491	-0.0482	0.1303	0.0729	0.3563	-0.4092
NGP	0.3569	0.0138	0.1158	0.0358	0.1634	-0.0002	0.043	-0.0427	0.1226	0.0691	0.3586	-0.3922
100	-0.0043	0.0009	-0.003	0.001	0.0032	-0.0086	0.0014	-0.0046	0.0062	0.0015	-0.0001	-0.0003
RL	0.3691	0.0125	0.0957	0.0368	0.1066	-0.0002	0.0659	-0.0624	0.1506	0.0917	0.4212	-0.5009
RV	0.3713	0.0124	0.0971	0.0367	0.1074	-0.0006	0.0633	-0.0649	0.1526	0.088	0.4101	-0.4823
RT	0.3932	0.0148	0.0958	0.0366	0.1137	-0.0003	0.0563	-0.0562	0.1762	0.0813	0.3945	-0.4504
DRW	0.3549	0.0128	0.094	0.0348	0.109	-0.0001	0.0584	-0.0552	0.1383	0.1036	0.5	-0.5752
DSW	-0.3591	-0.0132	-0.097	-0.034	-0.1129	0	-0.0535	0.0513	-0.134	-0.0998	-0.5187	0.5711
R/S	0.357	0.013	0.0947	0.0349	0.1104	0	0.0569	-0.054	0.1368	0.1026	0.5105	-0.5803

Note: DFF- days to 50 % flowering; PH- plant height; NPT-number of productive tillers per plant; PL-panicle length; NFG-number of filled grains per panicle; HGW-hundred grain weight; SPY-single plant yield; RL-root length; RV-root volume; RT-root thickness; DRW-dry root weight; DSW-dry shoot weight; R/S ratio- root/shoot ratio.

weight (0.038) and dry root weight (0.029) registered positive and negligible direct effect on single plant yield. In cross 2, root thickness (0.176), number of filled grains per panicle (0.163), number of productive tillers per plant (0.139) and dry root weight (0.1036) showed positive and low direct effect, while the traits viz. root length (0.065), panicle length (0.04) and plant height (0.028) exhibited positive and negligible direct effect on single plant yield.

Indirect effect for cross 1

Days to 50 % flowering recorded positive and indirect effect on single plant yield through root/shoot ratio (0.095) whereas, it registered negative indirect effect through root volume (-0.125). Plant height registered positive effect through days to 50 % flowering (0.155) and negative effect through root/shoot ratio (-0.033). Number of productive tillers per plant had high positive indirect effect on single plant yield through days to 50 % flowering (0.487), while negative indirect effect through root/shoot ratio (-0.068). Panicle length exhibited positive indirect effect through days to 50 % flowering (0.325) and negative indirect effect through root/shoot ratio. Number of filled grains per panicle registered positive indirect effect through days to 50 % flowering (0.574) and it had negative indirect effect through root/shoot ratio (-0.088) on plant yield per plant. 100 grain weight recorded positive and high indirect effect through days to 50 % flowering (0.304) on single plant yield. Positive indirect effect on single plant yield was recorded by root length through days to 50 % flowering (0.598) and root volume (0.150). Root volume exhibited negative indirect effect on grain yield through root/shoot ratio (-0.136). Root thickness showed positive indirect effect through days to 50 % flowering (0.517) and number of filled grains per panicle (0.079) and negative effect through root/shoot ratio (-0.127). Dry root weight had positive high indirect effect through days to 50 % flowering (0.467) and dry shoot weight (0.500) on grain yield. Dry shoot weight registered positive and negligible indirect effect on grain yield through root thickness (0.026) whereas, it had negative high indirect effect through days to 50 % flowering (-0.306). Positive and high indirect effect was registered by this trait on single plant yield through days to 50 % flowering (0.410).

Indirect effect for cross 2

Days to 50 % flowering had indirect positive effect on root/shoot ratio (0.456). High indirect negative effect was registered by this trait through dry shoot weight (-0.410). Positive indirect effect observed on single plant yield by plant height through the characters viz. days

to 50 % flowering (0.242) and dry shoot weight (0.240). Number of productive tillers per plant observed positive high indirect effect through days to 50 % flowering (0.362) and dry shoot weight (0.359) on grain yield. Panicle length revealed positive indirect effect through dry shoot ratio (0.356), root thickness (0.130) and number of filled grains per panicle (0.118) on grain yield. NFG observed positive and high indirect effect on grain yield through dry shoot weight (0.358). Positive indirect effect on single plant yield was registered by 100 grain weight through root thickness (0.006) negative indirect effect through root volume (-0.0046). Root length expressed positive indirect effect through dry shoot weight (0.421) and days to 50 % flowering (0.295). Root volume registered positive indirect effect through dry shoot weight (0.410) and positive moderate indirect effect through days to 50 % flowering (0.295) on single plant yield. Dry root weight had a positive high indirect effect through dry shoot weight (0.500) on grain yield. It showed positive indirect effect through root/shoot ratio (0.57) for the dry root weight.

Generation mean analysis

Generation mean analysis is a first order statistics which explains about the estimation of genetic component of variation (16). It also useful to determine presence or absence of non-allelic interaction. The most important advantage of generation mean analysis is that it helps in the estimation of epistatic gene effect namely additive × additive (i), additive × dominance (j) and dominance × dominance (l).

The A, B, C and D scaling test for almost all the traits in the two crosses expressed that at least one of the four scaling were found significant indicating the presence of non-allelic interaction.

Additive gene effect (d) was significant in cross 1 for the traits viz. Days to 50 % flowering, plant height, panicle length, number of filled grains per panicle, hundred grain weight, dry shoot weight, root/shoot ratio (Table 5, 6 & 7) whereas in the case of cross 2 it was observed significant for plant height, number of filled grains per panicle, single plant yield, root length and root/shoot ratio (Table 5, 6 & 7). The results were in parallel to the previous findings for days to 50 % flowering, panicle length, 100 grain weight and root thickness (17, 18). Pedigree breeding method or simple selection procedure is reliable method to control additive gene action for given characters.

Dominant gene effect was significant for the traits viz. plant height, panicle length, number of productive tillers per plant, number of filled grains per panicle, 100 grain weight, single plant

Table 5. Generation means, scaling test and gene effects for number of days to 50 % flowering and plant height, panicle length and number of productive tillers per plant

Generation/cross	Days to 50 % flowering		Plant height		Panicle length		Number of productive tillers per plant	
	Crosses		Crosses		Crosses		Crosses	
	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2
P ₁	84.00 ± 0.28	76 ± 0.56	106.78 ± 0.60	108.55 ± 0.54	22.97 ± 0.32	25.10 ± 0.32	22.97 ± 0.32	25.10 ± 0.32
P ₂	81.00 ± 0.31	81 ± 0.31	97.15 ± 0.33	96.55 ± 0.40	23.25 ± 0.31	23.25 ± 0.31	23.25 ± 0.31	23.25 ± 0.31
F ₁	72.5 ± 0.45	72.50 ± 0.43	105.40 ± 0.45	106.85 ± 0.51	23.82 ± 0.28	25.20 ± 0.24	23.82 ± 0.28	25.20 ± 0.24
F ₂	82.00 ± 0.22	80.00 ± 0.17	99.67 ± 1.03	98.58 ± 1.11	23.72 ± 0.15	24.02 ± 0.15	23.72 ± 0.15	24.02 ± 0.15
B ₁	83.00 ± 0.50	78.00 ± 0.53	95.98 ± 0.35	95.89 ± 0.33	23.84 ± 0.15	25.10 ± 0.18	23.84 ± 0.15	25.10 ± 0.18
B ₂	79.74 ± 0.51	80.00 ± 0.70	118.42 ± 0.46	116.52 ± 0.41	28.27 ± 3.83	24.59 ± 0.22	28.27 ± 3.83	24.59 ± 0.22
Scales								
A	9.5* ± 1.78	7.50* ± 1.36	-20.22* ± 1.05	-23.62* ± 1.09	0.89 ± 1.65	-0.10 ± 0.50	0.89 ± 1.65	-0.10 ± 0.50
B	5.9* ± 1.70	6.50* ± 1.50	34.29* ± 1.07	29.64* ± 1.05	9.47* ± 1.24	0.73 ± 0.70	9.47* ± 1.24	0.73 ± 0.70
C	18* ± 1.94	18.00* ± 1.37	-15.06* ± 4.34	-15.25* ± 4.31	1.02 ± 0.98	-2.67* ± 0.15	1.02 ± 0.98	-2.67* ± 0.15
D	1.26 ± 1.13	2.00 ± 0.94	0.44 ± 0.45	2.28* ± 0.20	-4.67* ± 1.01	-1.65 ± 0.20	-4.67* ± 1.01	-1.65 ± 0.20
Parameters								
m	82 ± 0.20	80.00 ± 0.17	99.67* ± 1.03	98.58* ± 1.11	23.72 ± 0.15*	24.02 ± 0.15*	23.72 ± 0.15*	24.02 ± 0.15*
d	3.26* ± 0.22	-2.00 ± 0.87	-22.44* ± 0.60	-20.63* ± 0.59	-4.43 ± 0.24*	0.51 ± 0.30	-4.43 ± 0.24*	0.51 ± 0.30
h	-12.52 ± 0.74	-10.00* ± 1.97	33.55* ± 1.77	34.80* ± 1.76	10.05 ± 1.05*	4.32 ± 0.70*	10.05 ± 1.05*	4.32 ± 0.70*
i	-2.52 ± 0.76	-4.00 ± 1.88	30.12* ± 1.69	30.50* ± 1.68	9.34 ± 1.04*	3.30 ± 0.80*	9.34 ± 1.04*	3.30 ± 0.80*
j	1.76 ± 1.67	0.50 ± 0.96	-27.25* ± 0.74	-26.63* ± 0.73	-4.29 ± 0.24*	-0.42 ± 0.30	-4.29 ± 0.24*	-0.42 ± 0.30
l	-12.96* ± 1.88	-10.00 ± 3.76	-44.19* ± 4.88	-36.52* ± 2.88	-19.7 ± 1.12*	-3.93 ± 1.11*	-19.7 ± 1.12*	-3.93 ± 1.11*

Cross 1 - ADT (R) 45 × IR 64 Drt, Cross 2 - MDU 6 × IR 64 Drt, *Significant at 5 % level.

Table 6. Generation means, scaling test and gene effects for number of filled grains per panicle, 100 grain weight, single plant yield and root length

Generation/cross	Number of filled grains per panicle		Hundred grain weight		Single plant yield		Root length	
	Crosses		Crosses		Crosses		Crosses	
	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2
P ₁	142.90 ± 3.35	160.25 ± 1.50	1.85 ± 0.05	2.21 ± 0.06	18.42 ± 0.54	19.5 ± 0.95	13.98 ± 0.30	15.90 ± 0.44
P ₂	182.20 ± 2.90	182.20 ± 2.90	2.14 ± 0.16	2.14 ± 0.16	22.14 ± 0.46	22.14 ± 0.46	14.26 ± 0.33	14.26 ± 0.33
F ₁	181.45 ± 2.95	200.10 ± 2.15	2.03 ± 0.35	2.17 ± 0.39	27.35 ± 0.92	25.10 ± 1.28	14.83 ± 0.30	15.20 ± 0.37
F ₂	197.71 ± 3.01	200.15 ± 2.16	1.93 ± 0.15	2.08 ± 0.12	21.24 ± 0.82	22.15 ± 0.85	14.73 ± 0.19	14.98 ± 0.22
B ₁	166.55 ± 3.20	185.20 ± 1.88	1.82 ± 0.45	1.93 ± 0.12	19.29 ± 0.61	20.15 ± 0.75	14.85 ± 0.16	15.22 ± 0.18
B ₂	198.15 ± 3.35	200.10 ± 2.10	1.73 ± 0.22	1.87 ± 0.13	17.85 ± 0.67	16.75 ± 1.11	16.28 ± 3.55	17.75 ± 0.25
Scales								
A	8.75* ± 0.12	10.05* ± 0.14	-2.35 ± 0.40	-5.20* ± 0.47	-7.19* ± 1.62	-4.30* ± 2.10	0.89 ± 1.63	-0.66 ± 0.64
B	32.65* ± 0.35	-5.00* ± 1.11	-6.06* ± 1.5	-5.65* ± 0.50	-13.79* ± 1.70	-13.74* ± 2.88	3.47* ± 0.50	6.04* ± 0.68
C	101.84* ± 0.90	35.05* ± 0.38	-3.45* ± 0.70	-3.55* ± 0.70	-10.42* ± 3.86	-3.42* ± 0.15	1.02 ± 0.55	-0.64 ± 0.68
D	30.77* ± 0.31	15.00* ± 0.27	-0.88 ± 0.50	3.65* ± 0.40	5.34* ± 3.14	7.40* ± 4.5	-1.67 ± 0.20	-3.01* ± 0.50
Parameters								
m	197.71* ± 3.01	200.15* ± 2.16	1.93 ± 0.15*	2.08 ± 0.12*	21.24* ± 0.82	22.15* ± 0.84	14.73 ± 0.19*	14.98 ± 0.15*
d	-31.60* ± 0.50	-14.90* ± 0.85	-4.43 ± 0.24*	0.51 ± 0.30	1.44 ± 0.88	3.40* ± 1.28	-1.43 ± 0.22	-2.53* ± 0.22
h	-42.54* ± 0.70	-12.57* ± 0.74	10.05 ± 1.05*	4.32 ± 0.70*	-3.61* ± 3.88	-10.52* ± 4.50	4.05 ± 0.29*	6.14* ± 1.10
i	-61.44* ± 0.88	-30.00* ± 0.95	9.34 ± 1.04*	3.30 ± 0.80*	-10.68* ± 3.76	-14.80* ± 4.22	3.34 ± 0.25*	6.02* ± 1.01
j	-11.95* ± 0.30	7.52* ± 2.10	-4.29 ± 0.24*	-0.42 ± 0.30	3.3* ± 0.95	4.72* ± 1.55	-1.29 ± 0.24	-3.35* ± 0.50
l	20.04* ± 0.35	24.95* ± 2.12	-19.7 ± 1.12*	-3.93 ± 1.11*	31.66* ± 5.27	37.00* ± 6.88	-7.7 ± 0.30*	-11.40* ± 4.50

Cross 1 - ADT (R) 45 × IR 64 Drt, Cross 2 - MDU 6 × IR 64 Drt,*Significant at 5 % level.

Table 7. Generation means, scaling test and gene effects for root volume, dry root weight, dry shoot weight and root/shoot ratio

Generation/cross	Root volume		Dry root weight		Dry shoot weight		Root/Shoot ratio	
	Crosses		Crosses		Crosses		Crosses	
	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2
P ₁	13.40 ± 0.37	14.40 ± 0.32	14.15 ± 0.05	15.25 ± 0.06	41.50 ± 0.08	34.75 ± 0.15	0.80 ± 0.07	0.34 ± 0.03
P ₂	17.30 ± 0.45	17.30 ± 0.45	18.85 ± 0.16	18.85 ± 0.16	34.80 ± 0.20	34.80 ± 0.20	1.14 ± 0.02	0.54 ± 0.04
F ₁	15.56 ± 0.30	16.13 ± 0.36	16.76 ± 0.35	17.85 ± 0.40	37.75 ± 0.45	35.83 ± 0.42	1.08 ± 0.05	0.53 ± 0.05
F ₂	14.77 ± 0.15	15.65 ± 0.22	15.35 ± 0.18	16.66 ± 0.15	36.88 ± 0.16	34.70 ± 0.17	1.00 ± 0.04	0.50 ± 0.04
B ₁	14.55 ± 0.22	15.20 ± 0.17	15.10 ± 0.47	16.25 ± 0.16	35.89 ± 0.16	34.25 ± 0.15	0.90 ± 0.06	0.46 ± 0.03
B ₂	15.35 ± 0.24	14.45 ± 0.25	14.88 ± 0.23	14.39 ± 0.14	39.46 ± 0.15	36.85 ± 0.14	1.05 ± 0.04	0.50 ± 0.04
Scales								
A	0.14 ± 0.64	-0.13 ± 0.50	-0.71 ± 0.20	-0.6 ± 0.12	-7.47* ± 0.57	-2.08 ± 0.20	-0.08* ± 0.04	0.05 ± 0.01*
B	-2.16 ± 0.14	-4.53* ± 0.88	-5.85* ± 0.49	-7.92* ± 0.45	6.37* ± 0.11	-2.13 ± 0.40	-0.12 ± 0.01	-0.07 ± 0.02
C	-2.74* ± 0.15	-1.36 ± 0.51	-5.12* ± 0.51	-3.16* ± 0.40	-4.28* ± 0.22	-2.41 ± 0.50	-0.10* ± 0.01	0.06 ± 0.01*
D	-0.36 ± 0.55	1.65 ± 0.30	0.72 ± 0.70	2.68* ± 0.30	-1.59 ± 0.20	-1.70 ± 0.30	0.05* ± 0.02	0.04 ± 0.01*
Parameters								
m	14.77* ± 0.15	15.65* ± 0.22	15.35* ± 0.18	16.66* ± 0.15	36.88* ± 0.16	34.70* ± 0.17	0.50 ± 0.04	0.58 ± 0.03
d	-0.8 ± 0.50	0.75 ± 0.56	0.22 ± 0.50	1.86 ± 0.70	-3.57* ± 0.16	-2.60 ± 0.60	-0.4 ± 0.01*	-0.04 ± 0.004*
h	2.23* ± 0.10	-3.02* ± 0.60	-1.18 ± 0.19	-4.56* ± 0.55	2.78* ± 0.66	4.45* ± 0.72	-1.83 ± 0.05	-0.21 ± 0.02
i	0.72 ± 0.70	-3.30* ± 0.65	-1.44 ± 0.50	-5.36* ± 0.53	3.18* ± 0.71	3.40* ± 0.65	-0.08 ± 0.008	-0.32 ± 0.02
j	1.15 ± 0.50	2.25* ± 0.17	2.57* ± 0.40	3.66* ± 0.20	-6.92* ± 0.15	2.57* ± 0.10	-0.06 ± 0.006	0.01 ± 0.01*
l	1.3 ± 0.60	7.96* ± 1.76	8.00* ± 4.8	13.88* ± 5.8	-2.08 ± 0.10	-4.39* ± 0.16	0.10 ± 0.01*	0.50 ± 0.03*

Cross 1 - ADT (R) 45 x IR 64 Drt, Cross 2 - MDU 6 x IR 64 Drt, *Significant at 5 % level.

yield, root length, root volume, dry shoot weight in the cross 1 (Table 5, 6 & 7). In cross 2 significant dominant gene effect was registered for Days to 50 % flowering, plant height, panicle length, number of productive tillers per plant, number of filled grains per panicle, hundred grain weight, single plant yield, root length, root volume, root thickness, dry root weight, dry shoot weight (Table 5, 6 & 7).

The additive × additive (i) had significant effect in cross 1 for the traits viz. plant height, panicle length, number of productive tillers per plant, number of filled grains per panicle, 100 grain weight, single plant yield, root length, root volume, root thickness and dry shoot weight whereas in the cross 2 the traits viz. plant height, panicle length, number of productive tillers per plant, number of filled grains per panicle, 100 grain weight, single plant yield, root length, root volume, root thickness, dry root weight, dry shoot weight (Table 5, 6 & 7).

The additive × dominance gene effect observed significant in cross 1 for the traits viz. plant height, panicle length, number of productive tillers per plant, number of filled grains per panicle, 100 grain weight, single plant yield, root thickness, dry root weight and dry shoot weight. In cross 2, the traits viz., plant height, panicle length, number of productive tillers per plant, number of filled grains per panicle, single plant yield, root length, root volume, root thickness, dry root weight, dry shoot weight, root/shoot ratio (Table 5, 6 & 7).

The dominance × dominance gene effect (l) was significant in cross 1 for the traits viz. days to 50 % flowering, plant height, panicle length, number of productive tillers per plant, number of filled grains per panicle, hundred grain weight, single plant yield, root length, root volume, dry root weight and root/shoot ratio (Table 5, 6 & 7). In cross 2, it was significant for plant height, panicle length, number of productive tillers per plant, number of filled grains per panicle, 100 grain weight, single plant yield, root length, root volume, root thickness, dry root weight, dry shoot weight and root/shoot ratio.

The two components viz. *h* and *l* showed opposite signs for most of the traits in both the crosses. This indicates presence of duplicate epistasis. This results in the postponement of selection to future generations.

Discussion

Inheritance of grain yield and drought tolerant traits is complex because of polygenic control of these traits. Hence, knowledge of association among yields contributes to morphological and physiological traits is necessary for the selection of desirable genotypes. Correlation analysis is performed to assess the nature of association between different component characters and grain yield. Selection for grain yield will be effective only if the selection relies on yield and other yield components (19). When selection pressure is applied for the selection of a trait, it will lead to the improvement of other traits also if both characters are positively related. Hence correlation analysis assists in the improvement of two or more characters simultaneously.

Single plant yield exhibited significant and positive association with yield contributing characters, viz. productive tillers per plant, panicle length, filled grains per panicle, 100 grain weight and drought tolerant traits, viz. root length, root volume, root thickness, dry root weight and root/shoot ratio. This is in conformity with the similar findings for hundred grain weight (20), root length and root volume (21) 100 grain weight (22), productive tillers per plant, spikelets per panicle (23), root length, root/shoot weight ratio, root thickness and root weight (24), panicle length and filled grains per panicle (25), productive tillers per plant, filled grains per panicle and panicle length (26), root length (27) and R/S ratio. The negative and significant association of days to 50 % flowering with grain yield registered in the present study corroborates with the earlier findings (18, 28). Days to 50 % flowering had negative and significant intercorrelation with all drought tolerant traits except root/shoot ratio and many yield traits. Studies reported significant negative correlation between days to flowering and number of productive tillers (24).

Plant height registered significant intercorrelation with dry shoot weight only. Number of productive tillers, panicle length, filled grains per panicle and 100 grain weight showed significant and positive intercorrelation with all drought tolerant traits except dry shoot weight.

Positive association of root traits viz. root length, root volume, root thickness, dry root weight, root/shoot ratio were observed among themselves. There also established positive correlation among root traits (20). Significant intercorrelation between panicle length and filled grains per panicle was given (24, 29). Positive intercorrelation of spikelet fertility with root length, dry shoot weight and root/shoot ratio was reported (26). Studies established negative relation between plant height and grain yield, which is contrasting to the present research findings (22). Positive intercorrelation between yield traits was observed (30).

Path analysis

Path analysis is used to partition the genotypic correlation coefficient into direct and indirect effects. It is also used to assess the cause-and-effect relationship between them (15). It helps the breeders to concentrate on the variable that shows a high direct effect on grain yield.

Hence, selection can be restricted to one or few traits, which ultimately reduces the time needed for selection. Yield traits viz. productive tillers and filled grains per panicle and root characters viz. root length, root volume, root thickness and dry root weight had positive and direct effect on grain yield. The indirect effect of all characters through root/shoot ratio in cross 1 (ADT (R) 45 x IR 64 Drt) and through dry shoot weight in cross 2 (MDU 6 x IR 64 Drt) indicates their major role in influencing grain yield under drought conditions.

These results coincide with the published results for root length (31); root/shoot ratio (32); filled grains per panicle and spikelet fertility (34); root length, root volume and root thickness (20); root length (23); hundred grain weight (30) and productive tillers per panicle (25). Hence, the characters which registered both direct and indirect effects on grain yield should be given more weightage during selection for improving drought tolerance along with yield under water stress conditions.

Epistatic gene action cannot be studied in Line x Tester analysis. Hence, generation mean analysis was also performed with six generations viz. P₁, P₂, F₁, F₂, B₁ and B₂ of three selected crosses viz. MDU 6 x IR 64 Drt and ADT (R) 45 x IR 64 Drt, to study the epistatic interaction effects in governing the yield and drought tolerant traits.

It could be noted that the presence of additive, dominance, additive x additive and dominance x dominance interaction effects were present along with either duplicate dominant epistasis or complementary recessive epistasis for grain yield and most of its contributing traits. Hence, selection in the early segregating generations may not give desirable recombinants. Therefore, selection may be delayed to later segregating generations when the dominance and epistasis disappear and resorting to intermating of segregants followed by recurrent selection. Similar results were earlier reported for 100 grain weight and number of grains per panicle (34).

Both additive and dominance gene actions play major roles in several characters. In such circumstances, biparental mating design or reciprocal recurrent selection can be followed for further recombination of alleles to produce desirable segregants. These methods can also be well adopted in order to harness the epistatic interactions by way of breaking the undesirable linkages. Diallel selective mating system proposed could also be followed to break such undesirable linkages between two or more genes and to produce desirable recombinants (35).

Conclusion

Present investigation revealed that characters such as productive tillers per plant, panicle length, filled grains per panicle, 100 grain weight, dry root weight, root length, root volume, root thickness and root/shoot ratio are the important yield and drought tolerant related characters which showed significant and positive association with grain yield. However, path analysis concluded that characters such as root thickness, root length, root volume and dry root weight exhibited positive direct effect on grain yield. Number of filled grains also recorded positive direct effect on grain yield. These characteristics should be given priority for the improvement of grain yield under moisture stress. Generation mean analysis resulted that interaction effects viz. additive x additive (i), additive x dominant (j) and dominance x dominance was observed for all the traits except grain yield and dry root weight, which registered both additive and dominance gene action and epistatic components. Simple breeding methods followed by selection in early segregating generations can be adopted to harness additive gene action. To exploit dominance gene action, hybridization followed by selection in advanced generations can be practiced.

Authors' contributions

AA conducted the research. SB supervised the study. RPG assisted with fieldwork and thesis revision. PA performed and corrected the statistical analyses. PJ provided the African rice lines for screening under the Nigra project and conducted one season of screening under rainout shelter conditions at the Paddy Breeding Station, Coimbatore. Physiological analyses were carried out under the guidance of RA. NSV oversaw all aspects of the research. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors declare no competing interests.

Ethical issues: None

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