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Genetic effects of yield and root parameters in rice (*Oryza sativa* L.) at reproductive stage drought stress as apportioned by generation mean analysis

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ABSTRACT

The nature of gene action governing important quantitative traits viz.yield and drought tolerance in rice were studied through six parameter model of generation means analysis using six generations (viz., P_1, P_2, F_1, F_2, BC_1 and BC_2) of five crosses by imposing drought stress at reproductive stage. Additive gene action was noticed for the traits like days to flowering, panicle length, 100 grain weight and root thickness in majority of the crosses while the yield characters like productive tillers / plant, filled grains / panicle, harvest index and grain yield / plant and the drought tolerant characters like spikelet fertility, root length and root / shoot ratio were governed by dominance gene action. Both additive and dominance effects were found in panicle length in the cross Kallurundaikar / Moroberekan; spikelet fertility, dry root weight, root/shoot ratio and grain yield / plant in the cross Norungan / Moroberekan and 100 grain weight and root thickness in the cross PMK 2 / Moroberekan. Interaction effects mainly of additive x additive was noticed in panicle length, filled grains /panicle, dry root weight and root/shoot ratio in most of the crosses while dominance x dominance gene action was predominant in 100 grain weight and both additive x dominance and dominance x dominance in days to flowering and plant height.

Key words: *Drought, epistasis, gene action, generation mean, reproductive stage, rice*

INTRODUCTION

Rice is the most important and widely grown cereal in India and World and accounts for 35 to 75% of calories consumed by more than three billion Asians (FAO, 2003). Rice, probably being the most diverse crop cultivated over a broad range of environmental conditions in terms of topography, soil type, water regime and climate (Babu et al., 2003). About half of the world's rice area and 48 per cent of India's rice area is under rainfed situation, where unprecedented drought causes severe yield reduction which also reflects in the total rice production and productivity (Siddhiq, 1996). With the productivity in irrigated area almost reaching a plateau, there is vast scope for increasing the productivity in rainfed uplands and lowlands. However, little progress has been made in characterizing the genetic determinants of drought tolerance. Drought is a complex phenomenon comprising a number of physio-biochemical processes at both cellular and organelle levels at different stages of plant development (Tripathy et al., 2000). Development of drought tolerant varieties with inbuilt mechanism of physiological and morphological drought tolerance is the need of the hour. But the progress in development of varieties for drought prone rainfed areas is slow when compared to the irrigated ecosystems and only very few varieties have been released with stable tolerance to drought. This may be attributed to the confounding effect of drought tolerance related characters under water stress situations. Effect of drought on yield under various crop growth stages, the nature and magnitude of gene action governing drought tolerant traits and presence of undesirable linkages if any, needs to be assessed in detail in order to develop varieties for drought prone environments. Although drought may occur at different stage of the crop growth, plants are most susceptible to water stress at the reproductive stage. Dramatic reduction of grain yield occurs when stress coincides with the irreversible reproductive processes, making the genetic analysis of drought resistance at the reproductive stage crucially important (Boonjung and Fukai, 2000); Pantuwan et al.(2002) and Yue et al. (2006). Hence, a study was attempted to elucidate the nature of gene action and epistatic gene interactions governing grain yield parameters and drought tolerant traits under reproductive stage drought stress.

MATERIALS AND METHODS

The present investigation was undertaken at Agricultural College and Research Institute, Madurai using six generations *viz*., P1 (Female parent of a cross), P2 (Male Parent of a cross), F_1 (F_1 generation of a cross), F_2 (F_2 generation of a cross), B_1 (B_1-Backcross with female parent) and B_2 (B_2- Backcross with male parent) involving five cross combinations *viz*., PMK 2 / Moroberekan, MDU 5 / Moroberekan, Norungan / Moroberekan, Nootripathu / Moroberekan and kallurundaikar / Moroberekan and their respective parents *viz*., PMK 2, MDU 5, Norungan, Nootripathu, Kallurundaikar and Moroberekan for building up of various generations. These five cross combinations, all having Moroberekan as the male parent and two established varieties and three land races as female parents were chosen as regards to their wide genetic adaptability for yield and drought tolerance. Using the parents of respective crosses as female and F_1 as male, backcross progenies were derived *viz*., B_1 (F_1 backcrossed to female parent P1) and B2 (F_1 backcrossed to male parent P2). The F_1 hybrids (F_1) were selfed to obtain F_2 generation (F_2). The parents were selfed and were also crossed to obtain fresh F_1 hybrid seeds. Thus, six generations *viz*., P1, P2, F_1, F2, B_1 and B_2 for all the five crosses were constituted.

Six generations of the five selected cross combinations were sown in raised nursery beds. Thirty days old seedlings were transplanted to the main field in a randomized block design with three replications adopting a spacing of 20 cm between rows and 15 cm between plants in rows of 2 m length. Ten plants each in P1, P2 and F_1; 150 plants in F_2 and 75 plants each in B_1 and B_2 for each cross in each replication were maintained for the study. The recommended package of practices and plant protection measures for rice crop were adopted.

Moisture stress was imposed at reproductive stage of the crop by withholding irrigation at about 86 days after sowing till maturity. Observations were recorded on randomly selected five plants for parents and F_1; 50 plants for F_2 and 25 plants for B_1 and B_2. Yield contributing characters such as days to first flowering, plant height, productive tillers / plant, panicle length, filled grains / panicle, spikelet fertility, harvest index and grain yield / plant and root characters *viz*., root length, root dry weight, root thickness and root / shoot ratio were recorded as per standard procedures. Observations on root characters were recorded by carefully uplifting the plants after overnight soaking of the field and by giving a deep dig near the root surface and ensuring least damage caused to the rootlets.

Days to flowering

The number of days taken from sowing to panicle emergence of individual plants in each row was taken as days to flowering in generation mean analysis.

Plant height

Plant height was measured from the ground to the tip of the tallest panicle at the time of maturity and expressed in centimetre.

Productive tillers/plant

In each plant, number of ear bearing tillers with uniformly matured grains were counted at the time of harvest and expressed in number.

Panicle length

The length of the primary panicle was measured from the base to the tip and expressed in centimetre.

Filled grains/panicle

The number of fully developed and well filled grains in the primary panicle of the selected plants was counted and expressed in number.

100 grain weight

From each selected plant, one hundred well filled grains selected at random were weighed and expressed in gram.

Spikelet fertility

The number ofthe fertile spikelets (filled grains) in the panicle of the selected plants werecounted and recorded as percentage to total spikelets.

$$\text{Spikelet fertility} = \frac{\text{Number of fertile spikelets per panicle}}{\text{Total number of spikelets per panicle}} \times 100$$

Root length

At the time of harvest, selected plants were uprooted by giving a deep dig near the base after watering and the length of the longest root was recorded in centimetre.

Dry root weight

Roots of the selected plants at the time of harvest were cut from the stem, dried moisture free in a hot air oven at 80ºC for 48 hours (till attaining constant weight), weighed and recorded in gram.

Root thickness

Thickness of root was measured using screw gauge in top, middle and bottom portions of five randomly selected roots per genotype, averaged and expressed in millimetre

Root/shoot ratio

The root weight of selected plants was recorded as mentioned above. The shoot weight was recorded separately after drying the shoot portion including grains in hot air oven at 80ºC for 48 hours till reaching constant weight. Root/shoot ratio was worked out as follows,

$$\text{Root/shoot ratio} = \frac{\text{Root dry weight (g)}}{\text{Shoot dry weight (g)}}$$

Harvest index (HI)

The selected plants were uprooted and shade dried until attaining 14 per cent moisture content and weighed as biological yield. The grains were then separated and weighed as economic yield. Harvest index was computed as follows,

$$\text{HI} = \frac{\text{Economic yield (g)}}{\text{Biological yield (g)}}$$

Grain yield/plant

All the grains extracted from selected single plants were cleaned, dried, processed, weighed at 14 per cent moisture content and expressed in gram.

Statistical analysis

The mean values and the variance of mean were computed for all six generations *viz*., P_1, P_2, F_1, F_2, B_1 and B_2 for each cross.

Study of means

The adequacy of the data for a simple additive - dominance model was tested utilizing the A, B and C scaling tests of Mather (1949) and Hayman and Mather (1955). The significance of the scales A, B and C was determined by comparing the calculated and table 't' values. The simple additive-dominance model is inadequate if any one of the three scales was found to deviate significantly from zero.

Estimation of genetic effects

The inadequacy of the data to fit in with a simple additive - dominance model requires the extension of analysis for estimating the parameters describing epistasis. Using the six generation means, the estimates of mid parent (m), additive effect (d), dominance effect (h), additive x additive interaction (i), additive x dominance interaction (j) and dominance x dominance interaction (l) were obtained by a perfect fit method from the equations formulated by Mather and Jinks, (1971).

RESULTS AND DISCUSSION

The scaling tests (Table 1) revealed the presence of epistasis in all the characters except for productive tillers / plant and 100 grain weight in the cross MDU 5 / Moroberekan and productive tillers / plant and root length in the cross Kallurundaikar / Moroberekan. Hence, a simple additive - dominance model proved insufficient to explain the gene action and therefore the six parameter model suggested by Mather and Jinks (1971) was applied for all other characters in the 5 crosses to estimate the various gene actions and interactions (Table 2).

Among the characters exhibiting absence of epistasis, the residual effect 'm' was found to be positive and significant and was greater than both dominance

Table 1. Scaling Tests for Yield and Root characters.

Characters	PMK 2 / Moroberekan			MDU 5 / Moroberekan			Norungan / Moroberekan			Nootripathu / Moroberekan			Kallurundaikar / Moroberekan		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
Days to flowering	-15.48* ± 0.97	5.16* ± 1.33	-37.44* ± 2.26	2.92* ± 0.64	-3.54* ± 1.19	-47.38* ± 1.46	-40.13*± 0.99	8.48* ± 1.05	-114.06* ± 1.61	-51.02* ± 1.04	-8.60* ± 1.02	-91.64* ± 1.81	-24.24* ± 1.08	-6.20* ± 1.21	-66.88* ± 2.32
Plant Height	3.57 ± 2.47	19.50* ± 2.46	-15.87* ± 6.42	23.01* ± 2.30	6.30* ± 1.95	3.96 ± 3.96	-15.36* ± 2.95	-4.36* ± 2.19	9.15 ± 6.16	-24.51* ± 4.02	51.11* ± 22.51	5.69 ± 7.35	-6.47 ± 3.38	14.27* ± 2.90	-14.51* ± 7.12
Productive tillers / plant	-2.40* ± 1.17	-4.70* ± 1.10	-9.28* ± 2.15	-0.66 ± 1.13	0.76 ± 1.35	0.30 ± 2.04	7.27* ± 1.27	3.72* ± 1.06	-1.86 ± 1.96	-1.34 ± 1.13	-1.06 ± 1.13	-7.06* ± 1.69	-2.12 ± 1.11	-2.14 ± 1.13	-3.14 ± 1.95
Panicle length	-1.91* ± 0.59	2.15* ± 0.49	-7.43* ± 1.03	7.00* ± 0.50	4.05* ± 0.46	1.66 ± 0.96	-6.40* ± 0.81	2.67* ± 0.76	-4.79* ± 1.36	-2.14* ± 0.86	-0.66 ± 0.56	0.85 ± 1.19	-1.19 ± 0.64	-0.88* ± 0.45	-8.29* ± 1.04
Filled grains/ panicle	-7.40 ± 6.09	8.50 ± 5.87	-63.16* ± 11.65	77.2* ± 7.10	42.62* ± 6.42	1.56 ± 10.51	-49.48* ± 7.76	14.76* ± 6.62	-134.40* ± 10.47	-14.44 ± 7.49	-34.54* ± 7.53	7.36 ± 12.97	-30.40* ± 9.82	-40.86* ± 7.33	-119.94* ± 13.82
Spikelet fertility	3.94 ± 2.34	-26.26* ± 3.19	-40.32* ± 5.71	15.09* ± 3.66	-5.33 ± 2.83	3.96 ± 4.99	-11.65* ± 3.49	16.85* ± 2.92	-33.79* ± 5.48	5.69 ± 3.12	-10.71* ± 4.46	8.79 ± 5.55	-18.15* ± 3.58	-20.12* ± 4.14	-29.47* ± 6.56
100 grain weight	-0.15* ± 0.03	-0.41* ± 0.03	-1.50* ± 0.05	0.01 ± 0.05	0.001 ± 0.06	-0.10 ± 0.07	-0.96* ± 0.04	-0.63* ± 0.04	-0.63* ± 0.04	-0.95* ± 0.05	-0.66* ± 0.06	-1.49* ± 0.11	-0.15* ± 0.06	-0.62* ± 0.05	0.003 ± 0.11
Root length	1.15 ± 1.03	-3.80* ± 0.98	-5.17* ± 1.96	-1.83 ± 0.97	4.89* ± 1.34	-0.05 ± 1.92	1.87 ± 1.35	13.57* ± 0.97	-5.68* ± 1.92	0.33 ± 0.99	1.80* ± 0.89	14.94* ± 2.30	-0.25 ± 1.16	1.18 ± 1.15	2.03 ± 1.97
Dry root weight	1.31* ± 0.21	0.52* ± 0.20	-0.42 ± 0.47	2.74* ± 0.18	4.02* ± 0.23	5.14* ± 0.34	0.81* ± 0.29	2.56* ± 0.14	0.47 ± 0.49	-0.14 ± 0.17	1.38* ± 0.13	4.92* ± 0.42	2.18* ± 0.23	-0.60* ± 0.19	2.28* ± 0.37
Root thickness	0.68* ± 0.05	0.15* ± 0.05	0.39* ± 0.12	0.81* ± 0.07	0.34* ± 0.05	1.23* ± 0.12	0.94* ± 0.06	-0.38* ± 0.04	0.91* ± 0.12	-0.21* ± 0.09	-0.43* ± 0.07	0.26 ± 0.14	0.69* ± 0.11	0.69* ± 0.07	2.12* ± 0.16
Root/shoot ratio	0.02* ± 0.01	0.09* ± 0.01	0.07* ± 0.01	0.08* ± 0.01	0.11* ± 0.01	0.14* ± 0.01	0.06* ± 0.01	0.13* ± 0.01	0.04* ± 0.01	0.01* ± 0.01	0.05* ± 0.01	0.15* ± 0.01	0.11* ± 0.01	0.02* ± 0.01	0.13* ± 0.01
Harvest index	-0.01 ± 0.01	0.01 ± 0.01	-0.16* ± 0.03	0.23* ± 0.01	0.04* ± 0.01	0.25* ± 0.02	0.08* ± 0.03	0.17* ± 0.01	-0.26* ± 0.04	-0.04 ± 0.02	-0.01 ± 0.02	-0.08* ± 0.03	0.05* ± 0.02	-0.08* ± 0.02	-0.07* ± 0.03
Grain yield /plant	-0.19 ± 1.55	-7.21* ± 1.04	-13.04* ± 2.83	9.94* ± 1.26	7.09* ± 1.79	7.36* ± 2.50	0.03 ± 2.43	7.05* ± 1.85	-12.83* ± 3.51	-1.92 ± 2.29	-5.39* ± 1.86	-6.00 ± 3.29	0.45 ± 1.82	-7.04* ± 1.66	-6.93* ± 3.19

* denotes significant at 5% level.

Table 2. Estimates of genetic effects for yield and root characters under reproductive stage drought stress.

Cross	Gene effects						
	m	d	h	i	j	l	Epistasis
				Days to flowering			
PMK 2 / Moroberekan	67.33* ± 2.36	-6.25* ± 0.35	32.87* ± 5.63	27.12* ± 2.34	-10.32* ± 0.75	-16.8* ± 3.48	Duplicate
MDU 5 / Moroberekan	44.39* ± 1.78	-10.15* ± 0.24	87.05* ± 4.51	46.76* ± 1.77	3.23* ± 0.65	-46.14* ± 2.84	Duplicate
Norungan / Moroberekan	21.65* ± 1.85	3.35* ± 0.30	129.99* ± 4.62	82.40* ± 1.82	-24.31* ± 0.68	-50.74* ± 2.95	Duplicate
Nootripathu / Moroberekan	74.83* ± 1.85	6.15* ± 0.29	-15.33* ± 4.54	32.02* ± 1.82	-21.21* ± 0.64	27.60* ± 2.92	Duplicate
Kallurundaikar / Moroberekan	57.61* ± 2.24	-6.65* ± 0.35	42.59* ± 5.29	36.44* ± 2.22	-9.02* ± 0.70	-6.00 ± 3.34	Duplicate
				Plant Height			
PMK 2 / Moroberekan	55.94* ± 6.03	13.67* ± 1.03	105.94* ± 13.21	38.93* ± 5.94	-7.97* ± 1.5	-61.99* ± 7.75	Duplicate
MDU 5 / Moroberekan	49.16* ± 3.38	-8.36* ± 0.99	84.10* ± 8.11	25.35* ± 3.23	8.36* ± 1.32	-54.66* ± 5.27	Duplicate
Norungan / Moroberekan	126.54* ± 5.76	16.46* ± 1.12	-68.58* ± 12.86	-28.88* ± 5.65	-5.50* ± 1.60	48.61* ± 7.69	Duplicate
Nootripathu / Moroberekan	86.43* ± 23.12	26.15* ± 1.03	62.36 ± 68.40	20.92 ± 23.10	-37.81* ± 11.31	-47.52 ± 45.63	Duplicate
Kallurundaikar / Moroberekan	68.88* ± 6.57	9.99* ± 1.34	66.90* ± 14.83	22.30* ± 6.43	-10.37* ± 1.93	-30.10* ± 9.03	Duplicate
				Productive tillers / plant			
PMK 2 / Moroberekan	9.12* ± 1.63	0.20 ± 0.46	3.26 ± 3.91	2.18 ± 1.56	1.15 ± 0.63	4.92 ± 2.74	Complementary
MDU 5 / Moroberekan	13.00* ± 1.67	0.20 ± 0.47	-0.50 ± 4.29	-	-	-	-
Norungan / Moroberekan	-2.06 ± 1.43	-0.30 ± 0.39	36.52* ± 3.71	12.86* ± 1.37	1.78* ± 0.63	-23.86* ± 2.78	Duplicate
Nootripathu / Moroberekan	6.69* ± 1.66	0.25 ± 0.35	9.67* ± 4.34	4.66* ± 1.62	-0.14 ± 0.70	-2.26 ± 2.94	Duplicate
Kallurundaikar / Moroberekan	11.92* ± 1.53	-0.30 ± 0.43	-4.90 ± 3.84	-	-	-	-
				Panicle length			
PMK 2 / Moroberekan	16.56* ± 0.99	0.42 ± 0.26	16.84* ± 2.36	7.67* ± 0.96	-2.03* ± 0.36	-7.9* ± 1.44	Duplicate
MDU 5 / Moroberekan	12.29* ± 0.84	-2.31* ± 0.22	30.79* ± 1.96	9.39* ± 0.81	1.47* ± 0.29	-20.45* ± 1.24	Duplicate
Norungan / Moroberekan	23.99* ± 1.24	1.24* ± 0.20	-1.18 ± 3.10	1.06 ± 1.22	-4.54* ± 0.45	2.67 ± 2.11	Duplicate
Nootripathu / Moroberekan	28.29* ± 1.12	0.85* ± 0.27	-12.15* ± 2.84	-3.64* ± 1.09	-0.74 ± 0.45	6.44* ± 1.88	Duplicate
Kallurundaikar / Moroberekan	18.81* ± 0.99	1.23* ± 0.20	9.94* ± 2.38	6.21* ± 0.97	-0.16 ± 0.34	-4.14* ± 1.52	Duplicate
				Filled Grains / panicle			
PMK 2 / Moroberekan	46.79* ± 11.95	-3.95 ± 2.41	157.97* ± 28.32	64.26* ± 11.70	-7.95* ± 3.99	-65.36* ± 17.24	Duplicate
MDU 5 / Moroberekan	-25.86* ± 11.02	-28.70* ± 2.84	360.84* ± 27.98	118.26* ± 10.65	17.29* ± 4.57	-238.08* ± 17.77	Duplicate
Norungan / Moroberekan	10.62 ± 11.05	-4.70* ± 2.30	172.44* ± 28.95	99.68* ± 10.81	-32.12* ± 4.63	-64.96* ± 19.19	Duplicate
Nootripathu / Moroberekan	166.74* ± 14.31	-4.60* ± 2.17	-179.16* ± 35.20	-56.34* ± 14.14	10.05* ± 4.96	105.32* ± 22.04	Duplicate
Kallurundaikar / Moroberekan	68.02* ± 13.45	1.70 ± 3.28	41.7 ± 34.22	48.68* ± 13.04	5.23 ± 5.52	22.58 ± 22.5	Complementary
				Spikelet fertility			
PMK 2 / Moroberekan	54.19* ± 5.51	-0.92 ± 1.46	27.14* ± 12.75	17.99* ± 5.31	15.10* ± 1.91	4.33 ± 7.55	Complementary
MDU 5 / Moroberekan	68.37* ± 4.22	-4.22* ± 1.94	32.83* ± 10.87	5.79 ± 3.75	10.21* ± 2.27	-15.55* ± 6.89	Duplicate
Norungan / Moroberekan	34.37* ± 5.96	0.25* ± 1.32	92.61* ± 14.65	38.98* ± 5.81	-14.25* ± 2.22	-44.18* ± 9.00	Duplicate
Nootripathu / Moroberekan	86.52* ± 6.46	-0.39 ± 1.40	-31.69 ± 16.66	-13.81* ± 6.31	8.20* ± 2.65	18.83 ± 10.55	Duplicate
Kallurundaikar / Moroberekan	83.95* ± 6.56	2.05 ± 1.64	-45.86* ± 16.22	-8.80 ± 6.35	0.98 ± 2.56	47.07* ± 10.25	Duplicate

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				100 Grain weight			
PMK 2 / Moroberekan	1.44* ± 0.06	0.08* ± 0.01	1.38* ± 0.16	0.94* ± 0.06	0.13* ± 0.02	-0.38* ± 0.09	Duplicate
MDU 5 / Moroberekan	2.10* ± 0.09	-0.10* ± 0.01	0.62* ± 0.23	-	-	-	Duplicate
Norungan / Moroberekan	4.91 ± 0.11	0.35* ± 0.01	-6.09* ± 0.26	-2.25* ± 0.11	-0.17* ± 0.03	3.83* ± 0.15	Duplicate
Nootripathu / Moroberekan	2.55* ± 0.09	0.13* ± 0.01	-1.39* ± 0.22	-0.11 ± 0.09	-0.15* ± 0.03	1.72* ± 0.15	Duplicate
Kallurundaikar / Moroberekan	3.33* ± 0.10	0.25* ± 0.02	-2.23* ± 0.25	-0.77* ± 0.10	0.23* ± 0.03	1.54* ± 0.16	Duplicate
				Root length			
PMK 2 / Moroberekan	16.38* ± 2.13	-0.62* ± 0.29	5.27 ± 5.07	2.52 ± 2.11	2.47* ± 0.67	0.13 ± 3.10	Duplicate
MDU 5 / Moroberekan	13.26* ± 1.99	-1.70* ± 0.20	14.58* ± 5.03	3.11 ± 1.98	-3.36* ± 0.71	-6.18 ± 3.33	Duplicate
Norungan / Moroberekan	-1.75 ± 1.99	-0.15 ± 0.31	63.81* ± 5.01	21.13* ± 1.96	-5.85* ± 0.73	-36.58* ± 3.27	Duplicate
Nootripathu / Moroberekan	33.95* ± 2.31	1.62* ± 0.36	-23.59* ± 5.18	-12.81* ± 2.28	-0.73 ± 0.61	10.69* ± 3.04	Duplicate
Kallurundaikar / Moroberekan	22.54* ± 2.34	1.92* ± 0.33	6.01 ± 5.75	-	-	-	-
				Dry root weight			
PMK 2 / Moroberekan	0.26 ± 0.45	-0.16* ± 0.05	8.14* ± 1.02	2.25* ± 0.45	0.39* ± 0.12	-4.08* ± 0.63	Duplicate
MDU 5 / Moroberekan	0.27 ± 0.38	-0.63* ± 0.04	11.12* ± 0.96	1.63* ± 0.38	-0.64* ± 0.13	-8.39* ± 0.61	Duplicate
Norungan / Moroberekan	0.24 ± 0.52	0.46* ± 0.06	10.28* ± 1.23	2.90* ± 0.52	-0.88* ± 0.15	-6.26* ± 0.74	Duplicate
Nootripathu / Moroberekan	7.15* ± 0.41	0.79* ± 0.06	-5.31* ± 0.89	-3.68* ± 0.41	-0.76* ± 0.10	2.45* ± 0.51	Duplicate
Kallurundaikar / Moroberekan	4.28* ± 0.39	0.90* ± 0.05	1.69 ± 0.95	-0.71 ± 0.38	1.39* ± 0.13	-0.86 ± 0.61	Duplicate
				Root thickness			
PMK 2 / Moroberekan	0.68* ± 0.11	0.05* ± 0.01	1.87* ± 0.26	0.43* ± 0.11	0.26* ± 0.03	-1.26* ± 0.16	Duplicate
MDU 5 / Moroberekan	1.14* ± 0.11	0.03 ± 0.02	0.99* ± 0.25	-0.09 ± 0.10	0.23* ± 0.03	-1.06* ± 0.17	Duplicate
Norungan / Moroberekan	1.54* ± 0.12	0.13* ± 0.02	0.11 ± 0.26	-0.34* ± 0.11	0.66* ± 0.03	-0.22 ± 0.15	Duplicate
Nootripathu / Moroberekan	2.09* ± 0.14	0.13* ± 0.02	-1.71* ± 0.35	-0.89* ± 0.14	0.11* ± 0.05	1.53* ± 0.23	Duplicate
Kallurundaikar / Moroberekan	2.02* ± 0.15	0.20* ± 0.04	-0.37 ± 0.37	-0.75* ± 0.14	0.001 ± 0.06	-0.63* ± 0.24	Complementary
				Root / Shoot Ratio			
PMK 2 / Moroberekan	0.01 ± 0.01	-0.01 ± 0.002	0.22* ± 0.03	0.04* ± 0.01	-0.04* ± 0.004	-0.14* ± 0.02	Duplicate
MDU 5 / Moroberekan	0.001 ± 0.01	-0.01* ± 0.002	0.29* ± 0.02	0.04* ± 0.01	-0.02* ± 0.004	-0.22* ± 0.02	Duplicate
Norungan / Moroberekan	-0.10* ± 0.02	0.01* ± 0.002	0.51* ± 0.04	0.16* ± 0.01	-0.03* ± 0.01	-0.35* ± 0.02	Duplicate
Nootripathu / Moroberekan	0.15* ± 0.02	0.003 ± 0.002	-0.09* ± 0.04	-0.09* ± 0.02	-0.02* ± 0.01	-0.04 ± 0.03	Complementary
Kallurundaikar / Moroberekan	0.06* ± 0.01	0.001 ± 0.002	0.17* ± 0.02	-0.004 ± 0.01	0.04* ± 0.003	-0.13* ± 0.02	Duplicate
				Harvest Index			
PMK 2 / Moroberekan	0.16* ± 0.03	-0.002 ± 0.003	0.45* ± 0.06	0.17* ± 0.03	-0.01 ± 0.01	-0.17* ± 0.04	Duplicate
MDU 5 / Moroberekan	0.24* ± 0.02	-0.06* ± 0.003	0.42* ± 0.06	0.02 ± 0.02	0.09* ± 0.01	-0.29* ± 0.04	Duplicate
Norungan / Moroberekan	-0.2* ± 0.05	-0.03* ± 0.003	1.34* ± 0.11	0.51* ± 0.05	-0.04* ± 0.01	-0.76* ± 0.07	Duplicate
Nootripathu / Moroberekan	0.28* ± 0.04	-0.02* ± 0.01	0.05 ± 0.10	0.02 ± 0.04	-0.01 ± 0.01	0.03 ± 0.06	Complementary
Kallurundaikar / Moroberekan	0.25* ± 0.03	-0.05* ± 0.001	0.17* ± 0.08	0.04 ± 0.03	0.07* ± 0.01	-0.001 ± 0.05	Duplicate
				Grain Yield / Plant			
PMK 2 / Moroberekan	9.57* ± 3.00	-0.86 ± 0.47	15.58* ± 6.96	5.65 ± 2.96	3.51* ± 0.89	1.75 ± 4.14	Complementary
MDU 5 / Moroberekan	1.21 ± 2.70	-4.08* ± 0.30	46.97* ± 6.81	9.66* ± 2.68	1.43 ± 0.97	-26.69* ± 4.44	Duplicate
Norungan / Moroberekan	-3.28 ± 3.68	0.56* ± 0.23	55.52* ± 9.33	19.92* ± 3.67	-3.51* ± 1.30	-27.00* ± 6.21	Duplicate
Nootripathu / Moroberekan	17.41* ± 3.46	0.06 ± 0.31	-3.01 ± 3.45	-1.27 ± 3.45	1.74 ± 1.27	8.59 ± 5.91	Duplicate
Kallurundaikar / Moroberekan	14.7* ± 2.92	-1.04* ± 0.39	2.36 ± 7.14	0.34 ± 2.89	3.75* ± 0.98	6.26 ± 4.81	Complementary

* denotes significant at 5% level

'h' and additive 'd' effects for the trait productive tillers / plant in the cross MDU 5 / Moroberekan and Kallurundaikar / Moroberekan. Both 'd' and 'h' were non-significant for productive tillers / plant in these crosses. However, additive gene action'd' was predominant over dominance gene action. Additive gene action was predominant for root length in the cross Kallurundaikar / Moroberekan whereas, dominance gene action was prevalent for 100 grain weight in the cross MDU 5 / Moroberekan.

The results indicate the presence of additive gene action for the traits *viz*., days to flowering in the crosses PMK 2 / Moroberekan, MDU 5 / Moroberekan and Kallurundaikar / Moroberekan; for plant height in the cross MDU 5 / Moroberekan; 100 grain weight and root thickness in the crosses Norungan / Moroberekan and Nootripathu / Moroberekan; for root length and dry root weight in the crosses Nootripathu / Moroberekan and Kallurundaikar / Moroberekan and for root/shoot ratio in the cross Norungan / Moroberekan.

Dominance genetic effects were significant for the traits days to flowering and plant height in the crosses Nootripathu / Moroberekan and Norungan / Moroberekan respectively and for productive tillers / plant in both the crosses. Dominance gene action was significantly predominant for panicle length, spikelet fertility, filled grains/ panicle, dry root weight, root / shoot ratio and grain yield / plant in crosses PMK 2 / Moroberekan and MDU 5 / Moroberekan and for 100 grain weight and root thickness in the cross MDU 5 / Moroberekan. Dominance gene action was also found to be significant for filled grains / panicle in the cross Norungan / Moroberekan; root/shoot ratio in the cross Kallurundaikar / Moroberekan and harvest index in the crosses Norungan / Moroberekan and Kallurundaikar / Moroberekan. Though not found to be significant, dominance gene action was predominant for productive tillers / plant in the cross PMK 2 / Moroberekan; for filled grains / panicle in the cross Kallurundaikar / Moroberekan; for root length in crosses PMK 2 / Moroberekan and Kallurundaikar / Moroberekan and for grain yield / plant in Kallurundaikar / Moroberekan. Both additive (d) and dominance (h) gene effects were important in controlling the traits *viz*., panicle length in the cross Kallurundaikar / Moroberekan; spikelet fertility, dry root weight, root/shoot ratio and grain yield / plant in the cross Norungan / Moroberekan and 100 grain weight and root thickness in the cross PMK 2 / Moroberekan.

Study of epistasis indicated the prevalence of additive x additive interaction for productive tillers / plant in Nootripathu / Moroberekan; panicle length in PMK 2 / Moroberekan and Kallurundaikar / Moroberekan; filled grains / panicle in PMK 2 / Moroberekan, Norungan / Moroberekan and Kallurundaikar / Moroberekan; for spikelet fertility and root length in the cross Norungan / Moroberekan; dry root weight in MDU 5 / Moroberekkan; root / shoot ratio in crosses PMK 2 / Moroberekan, MDU 5 / Moroberekan and Norungan / Moroberekan; harvest index in the crosses PMK 2 / Moroberekan and Norungan / Moroberekan and grain yield / plant in crosses MDU 5 / Moroberekan and Norungan / Moroberekan.

Additive x dominance interaction alone was prevalent for days to flowering and filled grains / panicle in Nootripathu / Moroberekan and Kallurundaikar / Moroberekan; plant height and root length in PMK 2 / Moroberekan; spikelet fertility in MDU 5 / Moroberekan and Nootripathu / Moroberekan; dry root weight and root / shoot ratio in Kallurundaikar / Moroberekan; root thickness in MDU 5 / Moroberekan; harvest index in the cross MDU 5 / Moroberekan and Kallurundaikar / Moroberekan and grain yield / plant in PMK 2 / Moroberekan and Kallurundaikar / Moroberekan.

Epistasis mainly of dominance x dominance was prevalent for dry root weight, root length and panicle length in Nootripathu / Moroberekan; 100 grain weight in Norungan / Moroberekan and Nootripathu / Moroberekan; spikelet fertility in Kallurundaikar / Moroberekan; plant height and days to flowering in MDU 5 / Moroberekan.

The results clearly indicate that all the three types of epistasis were not prevalent for any of the characters under study. However, presence of both additive x additive and additive x dominance interaction effects were noticed for plant height and productive tillers / plant in Norungan / Moroberekan; panicle length and filled grains / panicle in MDU 5 / Moroberekan and spikelet fertility, 100 grain weight, dry root weight and root thickness in the cross PMK 2 / Moroberekan. Both additive x dominance and dominance x dominance interaction effects were prevalent for days to flowering in crosses PMK 2 / Moroberekan and Norungan / Moroberekkan; plant height in PMK 2 / Moroberekan, Nootripathu / Moroberekan and Kallurundaikar / Moroberekan; filled grains / panicle and root thickness in Nootripathu / Moroberekan and 100 grain weight in Kallurundaikar / Moroberekan.

Further, the signs of (h) and (l) were not same in all the crosses for days to flowering, which predicted the presence of duplicate dominance epistasis in governing this trait. Duplicate type of epistasis was also witnessed in the characters plant height, panicle length, 100 grain weight, root length, dry root weight. Similar signs of (h) and (l) were noticed in PMK 2 / Moroberekan for the characters productive tillers / plant, spikelet fertility and grain yield / plant; in Kallurundaikar / Moroberekan for the traits filled grains / panicle, root thickness and grain yield / plant and in the cross Nootripathu / Moroberekan for root/shoot ratio and harvest index. This indicates the presence of complimentary type of epistasis in controlling these traits.

Upon carefully analyzing the gene action through generation means analysis, additive gene action was noticed for the traits days to flowering, panicle length, 100 grain weight and root thickness in majority of the crosses. The results were in akin to the findings of Kalita and Upadhaya (2001) for root weight per plant and root/shoot ratio; Robin (1997) and Anbumalarmathi (2005) for days to first flowering and plant height. To harness additive gene action in these characters simple selection procedures or pedigree breeding method is sufficient.

The yield characters like productive tillers / plant, filled grains / panicle, harvest index and grain yield / plant and the drought tolerant characters like spikelet fertility, root length and root / shoot ratio were governed by dominance gene effects. Predominance of dominance gene effects for panicle length and filled grains/panicle was already reported by Sharma et al. (2005). Similar gene effects were reported by Lavanya (2000) for spikelet fertility; Muthuvijayaraghavan and Murugan (2017) for filled grains / panicle; Kalita and Upadhaya (2001) for root thickness; Banumathy et al. (2003) for 100 grain weight and Kalita and Upadhaya (2000) for root length. The presence of dominance gene action in most of the characters warrants postponement of selection to later generations after effecting crosses. Heterosis breeding procedures are effective in harnessing dominance gene action to the full extent. However, this requires a suitable male sterile line conversion since rice is a self pollinated crop and rigourous efforts are required in varietal crossing programme.

Both additive and dominance genetic effects were found in panicle length in the cross Kallurundaikar / Moroberekan; spikelet fertility, dry root weight, root/ shoot ratio and grain yield / plant in the cross Norungan / Moroberekan and 100 grain weight and root thickness in the cross PMK 2 / Moroberekan. Kalita and Upadhaya (2001) reported the presence of both additive and dominance gene action for root thickness and root / shoot ratio in the crosses Nilajee / Annada and Hasakumra/Annada and for root weight in the cross Nilajee/Annada. In such circumstances biparental mating design or reciprocal recurrent selection can be followed which allows further recombination of alleles to produce desirable segregants.

Interaction effects mainly of additive x additive was noticed in panicle length, filled grains /panicle, dry root weight and root/shoot ratio in most of the crosses while dominance x dominance was predominant in 100 grain weight and both additive x dand dominance x dominance in days to flowering and plant height. additive x additive interaction was reported already for productive tillers/plant and filled grains /panicle by Kumar et al. (2010) while Geetha et al. (2006) reported additive x dominance interaction effects for days to first flowering and grain yield/plant. Interaction mainly of additive x dominance was reported by Muthuvijayaraghavan and Murugan (2017) for plant height and spikelet fertility.

Duplicate type of epistasis was witnessed in all characters, while complementary epistasis was also noticed in certain crosses for productive tillers / plant, spikelet fertility, root length, root thickness, root/shoot ratio, harvest index and grain yield / plant. Duplicate type of epistasis was reported for plant height, filled grains per panicle and grain yield /plant by Saumya Aswathi, 2013.

As regards to additive x additive interaction effects which is easily fixable, selection may be done in early segregating generations as that witnessed for panicle length, filled grains/panicle, dry root weight and root/shoot ratio. But for all other characters one or more type of epistasis is noticed which necessitates other mating designs like biparental mating in F_2 or recurrent selection. These methods can also be well adopted in order to harness the epistatic interactions by way of breaking the undesirable linkages. Since gene expression varies from environment to environment, multi environmental approach is suggested for such studies (Kalita and Upadhaya, 2001). Diallel selective mating system proposed by Jensen (1970) could also be followed to break such undesirable linkages between two or more genes and to produce desirable recombinants.

CONCLUSION

The present investigation on genetic effects of yield and root parameters in rice under reproductive stage drought stress elucidated the nature of gene action governing yield and root characters. The traits like days to flowering, panicle length, 100 grain weight and root thickness were governed by additive gene action; while the yield characters like productive tillers / plant, filled grains / panicle, harvest index and grain yield / plant and the drought tolerance related characters like spikelet fertility, root length and root / shoot ratio were governed by dominance gene effects. Both additive and dominance genetic effects were found to control characters like plant height and dry root weight. Almost all yield and drought tolerance related characters showed duplicate epistasis in majority of crosses. Simple selection procedures and pedigree breeding are adequate for exploiting additive gene actions while hybridization followed by selection in later generations was suggested to harness dominance gene action. In order to explore additive, dominance gene action and epistatic interactions; reciprocal recurrent selection, bi parental mating and diallel selective mating schemes were proposed to break the undesirable linkages and to obtain suitable segregants. Multi environmental approach is also suggested in further studies as gene expression varies with environments.

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