



Generation Mean Analysis for Yield and Drought Tolerant Traits under Rainfed and Irrigated Conditions in Rice (*Oryza sativa* L.)

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Generation mean analysis was carried out using two crosses, involving a high yielding drought susceptible variety NDR 359 and drought tolerant rainfed cultivars Nagina 22 and Vandana. Six generations namely P₁, P₂, F₁, F₂, BC₁ and BC₂ were grown under both rainfed and irrigated environment to study the gene action for various yield and drought tolerance traits. Scaling test revealed the presence of epistasis for most of the yield and drought tolerance traits in both the crosses. Hence, six parameter model was adopted for these traits and for few traits where epistasis was absent, three parameter model was used. The results revealed that dominance gene effect along with non-allelic interactions had profound effect on the genetic control of majority of the yield traits. Therefore, early generation selection will be misleading for these traits. However, the drought tolerance related traits like proline content and stomatal conductance were governed by additive component as well. Duplicate epistasis was observed for majority of the traits. Hence, present study indicates that, epistasis has a key role in the expression of almost all the traits in both the environment.

Keywords: *Generation mean analysis; gene action; rice; epistasis; drought tolerance.*

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1. INTRODUCTION

Rice (*Oryza sativa* L.) is the staple food for more than fifty percent of the world's population. It is also the major energy source for majority of people in countries like India, Bangladesh, Cambodia, Indonesia, Myanmar, Vietnam, and China [1]. Increasing human population and rapid climate change necessitates the improvement of grain yield in rice. To begin a systematic plant breeding program, knowledge of the gene action is inevitable for the trait of interest. Combining ability analysis itself indicates the extent to which trait improvement is possible through selection. However, it does not consider the nature and magnitude of gene action. Internal cancellation of different components of gene effects, therefore, remains undetected in combining ability analysis. Besides estimating additive and dominance components, generation mean analysis also provides the information about the epistasis which is not possible through Line \times Tester analysis. It is imperative to detect and estimate non-allelic interactions which could otherwise exaggerate the measures of additive and dominance components. Among different biometrical techniques employed in gene action studies, generation mean analysis is one of most suitable methods studying the gene action of quantitative traits. It provides appropriate information about the relative importance of various gene effects viz., the average effects of the genes, additive gene effects, dominance gene effects and effects due to non-allelic interactions in ascertaining the genotypic values of the individuals and also mean genotypic values of families and generations.

Mean values of all six-generation viz., P_1 (Parent 1), P_2 (Parent 2), F_1 (first-filial generation), F_2 (second-filial generation), BC_1 ($F_1 \times P_1$) and BC_2 ($F_1 \times P_2$) were subjected to scaling test. Generation mean analysis is one such biometrical technique, which provides information about the relative importance of the average effect of genes, dominance effects and non-allelic interaction. If scaling test implies the presence of epistasis, six parameter models of generation mean analysis give trustworthy estimates of main gene effects as well as epistatic (non-allelic) interactions.

In general, among the various abiotic stress encountered in India, drought is a major constraint which leads to 30 to 70 % yield loss [2]. It is estimated that, globally 13 % of the rice area is under upland condition and around 28 % is under rainfed lowlands [3] which are highly prone to water stress condition. Success of plant

breeding depends mainly on the knowledge of the gene action and selection of suitable breeding method for the improvement of the target traits. But most of the gene action studies were restricted to irrigated condition in rice, and there are very few studies under rainfed condition, which is the need of the hour. So, to estimate the gene action for various traits, generation mean analysis was carried out for two crosses namely, NDR 359 \times Nagina 22 and NDR 359 \times Vandana under both rainfed and irrigated conditions.

2. MATERIALS AND METHODS

In the present study, three rice varieties namely NDR 359 (a high yielding variety under irrigated condition), Nagina 22 and Vandana (drought tolerant rainfed cultivars) were used to generate two crosses namely, NDR 359 \times N22 and NDR 359 \times Vandana to estimate the gene action of various traits. The present investigation was carried out in two locations namely Agricultural Research Farm, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi and National Rice Research Institute (NRRRI), Cuttack, Odisha. The material advancement was done by shuttling between two locations to save time, and the final evaluation was done at NRRRI, Cuttack in dry season, 2018. The annual rainfall at Cuttack is 1200 mm to 1500 mm, received mostly during June to October (*kharif* or *wet* season) from the southwest monsoon. Minimal rainfall is received from November to May (*rabi* or *dry* season). Six generations viz., P_1 (Parent 1), P_2 (Parent 2), F_1 (first-filial generation), F_2 (second-filial generation), BC_1 ($F_1 \times P_1$) and BC_2 ($F_1 \times P_2$) of two crosses were grown in Compact Family Randomized Block Design in two environments (under rainfed and normal condition) adopting standard package of practices. Observations on plant height, days to fifty percent flowering, days to maturity, panicle length, flag leaf length, flag leaf width, number of effective tillers per plant, chlorophyll content, proline content, stomatal conductance, number of panicles per plant, number of grains in main panicle, number of chaff grains in main panicle, hundred grain weight and grain yield per plant were recorded. Chlorophyll content was measured using SPAD (Soil Plant Analysis Development) chlorophyll meter. The free proline content based on fresh weight of leaves was estimated at anthesis stage according to the method given by [4].

Scaling test was done as suggested by Mather and Hayman and Mather [5,6] to determine the presence or absence of epistasis. The scales

significantly deviating from zero indicates the presence of non-allelic interaction, which showed inadequacy of additive dominance model. In such condition six parameter model was used to estimate gene effects (\hat{m}, \hat{d} and \hat{h}) and their interaction (\hat{i}, \hat{j} and \hat{l}) following Hayman and Jinks and Jones [7, 8]. In the absence of non-allelic interaction (adequacy of additive dominance model), three parameter model was used to estimate gene effects (\hat{m}, \hat{d} and \hat{h}) following the method suggested by Jinks and Jones [8]. The test of significance of gene effects were carried out by 't' test. The calculated values were compared with tabulated values of 't' at respective degree of freedom at 5% and 1% level of significance, respectively.

3. RESULTS AND DISCUSSION

The results obtained from the scaling test for rainfed and irrigated conditions were presented in Table 1. Significance of scale A or B indicates the presence of all three types of epistasis viz., *i* (additive × additive), *j* (additive × dominance) and *l* (dominance × dominance) non-allelic interaction. Significance of only C scale revealed dominance × dominance type of epistasis (*l*) and significance of only D scale revealed additive × additive (*i*) epistasis.

In the present study, significant deviation of scales (A, B, C, D) from zero for both the crosses (NDR 359 × N22 and NDR 359 × Vandana) in rainfed and irrigated condition revealed the presence of epistasis for most of the characters studied indicating the complex nature of the traits studied. There are plenty of reports to support the presence of epistasis for yield traits in rice [9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19 and 20]. This indicates the complex nature of inheritance for yield and drought tolerance traits in rice. Hence in all such crosses where epistasis was found, six parameter model was used for examining their gene action. However, epistatic interaction was absent in the cross NDR 359 × N22 under rainfed condition for the trait's days to maturity and number of panicles per plant and in NDR 359 × Vandana under rainfed condition for hundred grain weight.

The estimates of gene effect for fifteen traits under irrigated and rainfed condition is presented in Table 2. Among the main gene effect, dominance gene effects [h] was evident in majority of the crosses in both the environment for almost all the traits studied. Dominance gene effect was positive for majority of the traits except flag leaf width and hundred grain weight. The

relative contribution of dominance gene effect [h] was much higher as compared to additive gene effect [d], indicating the predominance of dominance gene effects in the inheritance of these traits. These observations agree with the earlier findings by Singh and Singh [21], Ramana and Singh [22], Thirumeni et al. [23], Renata et al. [24] and Srivastava et al. [25]. However, Kumar et al. [26] reported additive effect for number of tillers per plant and predominance of dominance × dominance interaction for grain yield in rice. In our study, additive gene effect showed significance for only few traits in either rainfed or irrigated environment. For certain drought tolerant traits like proline content and stomatal conductance, additive gene effect showed significance. In addition, duplicate epistasis was found in higher frequency for majority of the traits, which further confirms the prevalence of dominant gene effects for the expression of traits studied. This agrees with the findings of Awasthi and Lal, [27].

Among the interactions, dominance × dominance gene interaction showed significance for majority of the traits followed by additive × additive and additive × dominance gene interaction. Similar reports were reported by [15]. Additive × dominance interaction showed negative values in higher frequency when compared to additive × additive and dominance × dominance interaction. However, the magnitude of additive × additive interaction and dominance × dominance interaction was much higher than additive × dominance interaction for majority of the traits in both rainfed and irrigated condition (ignoring the sign). Significant and negative values of non-allelic interaction was observed profusely for the traits hundred grain weight and flag leaf width under both rainfed and irrigated condition. This indicates the enhancing (+) and diminishing (-) effects for the expression of these traits in both the environments. This clearly indicates the complex nature of various yield and drought tolerant traits, making early generation selection a difficult process. Predominance of non-additive gene action for majority of the traits in both the environment indicates that selection will be effective in later generations. These findings are similar to the earlier reports of Sharma et al. [28], Choudhary [29], Subbaraman and SreeRangasamy [30], Xu et al. [31] and Malinee et al. [32].

In the presence of epistasis, the dominance gene effects [h] and dominance × dominance gene effect [l] were having opposite sign for majority of the traits indicating the presence of duplicate

Table 1. Scaling test for fifteen traits under irrigated and rainfed condition in rice

Sl. No.	Trait	Environment	Cross	Scaling Test				Non-allelic interaction
				A	B	C	D	
1	Plant Height (cm)	Irrigated	NDR 359 x N22	-0.78	-9.33**	-14.39**	-2.14	Present
			NDR 359 x Vandana	-0.79	-2.70	-15.55*	-6.03	Present
		Rainfed	NDR 359 x N22	-8.13**	-9.32**	-26.21**	-4.38	Present
			NDR 359 x Vandana	3.39	-5.39*	7.68	4.84	Present
2	Days to fifty percent flowering	Irrigated	NDR 359 x N22	0.001	-11.50**	-12.78*	-0.64	Present
			NDR 359 x Vandana	-3.60*	-0.50	-15.38*	-5.64	Present
		Rainfed	NDR 359 x N22	-9.10**	-10.70**	-16.20*	1.8	Present
			NDR 359 x Vandana	-0.90	-7.60	-28.38**	-9.94*	Present
3	Days to maturity	Irrigated	NDR 359 x N22	2.50	-11.90**	-10.32*	-0.46	Present
			NDR 359 x Vandana	-4.80**	-1.40	-5.40	0.40	Present
		Rainfed	NDR 359 x N22	-1.90	0.10	-1.44	0.18	Absent
			NDR 359 x Vandana	4.20	-3.80	-34.36**	-17.38**	Present
4	Panicle Length (cm)	Irrigated	NDR 359 x N22	-2.75*	-0.97	-11.68**	-3.98**	Present
			NDR 359 x Vandana	-5.95**	-4.93**	-15.42**	-2.27	Present
		Rainfed	NDR 359 x N22	-1.02	-2.91*	-2.81	0.56	Present
			NDR 359 x Vandana	0.23	-0.55	-3.88**	-1.78*	Present
5	Flag leaf length (cm)	Irrigated	NDR 359 x N22	-2.27	-0.05	-9.08**	-3.38*	Present
			NDR 359 x Vandana	-5.08**	-2.67	-18.90**	-5.57**	Present
		Rainfed	NDR 359 x N22	-4.36**	-4.90**	-6.14**	1.56	Present
			NDR 359 x Vandana	-2.20*	-4.78**	-17.77**	-5.39**	Present
6	Flag leaf width (cm)	Irrigated	NDR 359 x N22	-0.63**	-0.72**	-1.44**	-0.05	Present
			NDR 359 x Vandana	-0.50**	-0.20*	-1.92**	-0.61**	Present
		Rainfed	NDR 359 x N22	-0.29	-0.20*	-0.31	0.10	Present
			NDR 359 x Vandana	-0.31**	0.03	-0.65**	-0.18*	Present
7	Number of effective tillers per plant	Irrigated	NDR 359 x N22	-0.18	-7.34**	-6.52*	0.50	Present
			NDR 359 x Vandana	-2.48	-7.74*	-14.66**	-2.22	Present
		Rainfed	NDR 359 x N22	-0.40	-0.40	1.92	1.36*	Present
			NDR 359 x Vandana	-2.30**	-2.32**	-7.30**	-1.34**	Present
8	Chlorophyll Content	Irrigated	NDR 359 x N22	3.47	-4.53*	-2.82	-0.88	Present
			NDR 359 x Vandana	-0.49	-9.89**	-21.29**	-5.46**	Present

9	Proline content	Rainfed	NDR 359 x N22	5.06**	-1.10	4.80*	0.42	Present
		Irrigated	NDR 359 x Vandana	-5.68**	-8.20**	-10.42**	1.73	Present
10	Stomatal conductance	Rainfed	NDR 359 x N22	-9.23**	-18.16**	-18.07**	4.66	Present
		Irrigated	NDR 359 x Vandana	2.48	-14.42**	-23.98**	-6.02**	Present
11	Number of panicles per plant	Rainfed	NDR 359 x N22	-7.28**	-3.06*	-2.62	3.86**	Present
		Irrigated	NDR 359 x Vandana	-1.92	-8.19**	-11.09**	-0.49	Present
12	Number of filled grains in main panicle	Rainfed	NDR 359 x N22	-39.35	-60.74**	-41.77	29.16	Present
		Irrigated	NDR 359 x Vandana	-27.79	-40.34*	-45.81	11.16	Present
13	Number of chaff grains in main panicle	Rainfed	NDR 359 x N22	-63.06**	-37.02*	-139.32**	-19.62	Present
		Irrigated	NDR 359 x Vandana	-81.19**	-140.60**	-117.71**	52.04**	Present
14	100 grain weight (g)	Rainfed	NDR 359 x N22	2.09	-6.53**	-7.92	-1.74	Present
		Irrigated	NDR 359 x Vandana	-1.46	-2.22*	-5.24**	-0.78	Present
15	Total grain yield per plant (g)	Rainfed	NDR 359 x N22	-0.50	-0.20	-0.14	0.28	Absent
		Irrigated	NDR 359 x Vandana	-0.83	-1.03*	-4.22**	-1.18**	Present
16	Number of filled grains in main panicle	Rainfed	NDR 359 x N22	-7.04	1.66	-31.74**	-13.18*	Present
		Irrigated	NDR 359 x Vandana	-0.64	2.64	-28.80*	-15.40*	Present
17	Number of chaff grains in main panicle	Rainfed	NDR 359 x N22	-8.70*	-16.60**	-19.26**	3.02	Present
		Irrigated	NDR 359 x Vandana	-20.51**	-20.43**	-75.94**	-17.50**	Present
18	100 grain weight (g)	Rainfed	NDR 359 x N22	-8.16	15.08**	59.80**	26.44**	Present
		Irrigated	NDR 359 x Vandana	5.34	16.36**	21.18**	-0.26	Present
19	Total grain yield per plant (g)	Rainfed	NDR 359 x N22	2.80	3.00	17.84**	6.02**	Present
		Irrigated	NDR 359 x Vandana	2.75	9.59**	25.98**	6.82*	Present
20	Number of filled grains in main panicle	Rainfed	NDR 359 x N22	-0.51**	-0.39**	-0.87**	0.02	Present
		Irrigated	NDR 359 x Vandana	-0.07**	-0.26**	-0.02	0.15**	Present
21	100 grain weight (g)	Rainfed	NDR 359 x N22	-0.30**	-0.19**	-0.50**	-0.01	Present
		Irrigated	NDR 359 x Vandana	0.05	-0.02	-0.02	-0.03	Absent
22	Total grain yield per plant (g)	Rainfed	NDR 359 x N22	0.22	-5.05*	-22.86**	-9.02**	Present
		Irrigated	NDR 359 x Vandana	-5.08	-2.11	-29.81**	-11.31**	Present
23	Number of filled grains in main panicle	Rainfed	NDR 359 x N22	-2.42*	-3.82**	-5.45**	0.40	Present
		Irrigated	NDR 359 x Vandana	-0.94	-1.07**	-5.45**	-1.72**	Present

** - Significant at $P = 0.01$, * - Significant at $P = 0.05$

Table 2. Estimates of gene effect for fifteen traits under irrigated and rainfed condition in rice

Sl. No.	Trait	Environment	Cross	Estimation of Genetic factors						Epistais
				[5̄]	[5]	[5]	[5]	[5]	[I]	
1	Plant Height (cm)	Irrigated	NDR 359 x N22	85.44**	1.02	5.77**	4.28**	4.28**	5.83**	Complementary
			NDR 359 x Vandana	75.98**	2.7	47.36*	12.06**	0.96**	-8.57	Duplicate
		Rainfed	NDR 359 x N22	42.62**	8.31	9.35**	8.76**	0.6**	8.69**	Complementary
			NDR 359 x Vandana	70.35**	-0.99*	-1.7	-9.68	4.39**	11.68**	Duplicate
2	Days to fifty percent flowering	Irrigated	NDR 359 x N22	90.77*	13.45	-2.49	1.28**	5.75**	10.22**	Duplicate
			NDR 359 x Vandana	79.27*	14.95	26.61**	11.28**	-1.55	-7.18	Duplicate
		Rainfed	NDR 359 x N22	93.3*	14.8	-21.9	-3.6	0.8**	23.4**	Duplicate
			NDR 359 x Vandana	68.27*	16.35	38.11**	19.88**	3.35**	-11.38	Duplicate
3	Days to maturity	Irrigated	NDR 359 x N22	121.68*	13.7	-1.36	0.92**	7.2**	8.48**	Duplicate
			NDR 359 x Vandana	122*	15.1	0.1**	-0.8	-1.7	7**	Complementary
		Rainfed	NDR 359 x N22	115.36*	17.1	7.88**	-	-	-	-
			NDR 359 x Vandana	80.64*	16.7	79.42*	34.76*	4**	-35.16	Duplicate
4	Panicle Length (cm)	Irrigated	NDR 359 x N22	11.01*	4.69	15.52**	7.96*	-0.89**	-4.24	Duplicate
			NDR 359 x Vandana	15.09*	4.04	3.6**	4.53**	-0.51**	6.36**	Complementary
		Rainfed	NDR 359 x N22	16.97*	3.26	-5.5	-1.12	0.94	5.05**	Duplicate
			NDR 359 x Vandana	14.5*	1.04	4.26**	3.56**	0.39	-3.25	Duplicate
5	Flag leaf length (cm)	Irrigated	NDR 359 x N22	25.63*	4.31	7.78**	6.76**	-1.11**	-4.44	Duplicate
			NDR 359 x Vandana	19.55*	6.01	11**	11.14*	-1.2	-3.4	Duplicate
		Rainfed	NDR 359 x N22	19.36*	4.33	-12.94	-3.12	0.27	12.38*	Duplicate
			NDR 359 x Vandana	7.51*	2.27	17.85*	10.78*	1.29	-3.8	Duplicate
6	Flag leaf width (cm)	Irrigated	NDR 359 x N22	1.15	0.35	-0.95**	0.1	0.04	1.25	Duplicate
			NDR 359 x Vandana	0.36	0.01	1.79	1.23	-0.15**	-0.54**	Duplicate
		Rainfed	NDR 359 x N22	1.09	0.58	-0.85**	-0.19**	-0.05**	0.69	Duplicate
			NDR 359 x Vandana	0.69	0.42	0.45	0.37	-0.17**	-0.09**	Duplicate
7	Number of effective tillers per plant	Irrigated	NDR 359 x N22	10.16*	2.72	1.82**	-1	3.58	8.52**	Complementary
			NDR 359 x Vandana	4.77**	2.67	13.45**	4.44**	2.63**	5.78**	Complementary
		Rainfed	NDR 359 x N22	6.22*	1	-6.04	-2.72	-1.59	3.52**	Duplicate
			NDR 359 x Vandana	0.93	0.89	1.73**	2.68	0.01	1.94**	Complementary
8	Chlorophyll content	Irrigated	NDR 359 x N22	29.97*	1.4	9.74**	1.76**	4**	-0.7	Duplicate
			NDR 359 x Vandana	21.21*	1	21.3**	10.92**	4.7**	-0.55	Duplicate
		Rainfed	NDR 359 x N22	29.41*	1.42	-3.33	-0.84	3.08	-3.12	Complementary

Sl. No.	Trait	Environment	Cross	Estimation of Genetic factors						Epistais
				[5]	[5]	[5]	[5]	[5]	[1]	
9	Proline content	Irrigated	NDR 359 x Vandana	32.35*	1.09	-17.4	-3.46	1.26	17.34*	Duplicate
			NDR 359 x N22	37.65*	-0.97*	-23.68	-9.32	4.47**	36.71*	Duplicate
			NDR 359 x Vandana	19.07*	-3.75*	26.79**	12.04**	8.45**	-0.1	Duplicate
10	Stomatal conductance	Rainfed	NDR 359 x N22	46.82*	-0.39**	-17.11	-7.72	-2.11**	18.06*	Duplicate
			NDR 359 x Vandana	34.9*	2.84	3.58**	0.98**	3.14	9.13**	Complementary
			NDR 359 x N22	999.98*	23.31*	-105.99	-58.32	10.7**	158.41*	Duplicate
11	Number of panicles per plant	Irrigated	NDR 359 x Vandana	965.55*	21.73*	-18.57	-22.32	6.28**	90.45**	Duplicate
			NDR 359 x N22	962.09*	-12.48	45.28**	39.24**	-13.02	60.84**	Complementary
			NDR 359 x Vandana	1087.64*	5.3**	-275.37	-104.08	29.71**	325.87*	Duplicate
12	Number of filled grains in main panicle	Rainfed	NDR 359 x N22	4.99**	1.79	10.1**	3.48**	4.31	0.96**	Complementary
			NDR 359 x Vandana	7.38*	1.32	-2.9	1.56**	0.38	2.12**	Duplicate
			NDR 359 x N22	3.81	0.75	-1.57	-	-	-	-
13	Number of chaff grains in main panicle	Irrigated	NDR 359 x Vandana	0.64	1	3.29**	2.36	0.1	-0.5	Duplicate
			NDR 359 x N22	62.13*	14.85*	64.95**	26.36**	-4.35	-20.98	Duplicate
			NDR 359 x Vandana	49.3*	23.24*	76.6**	30.8**	-1.64	-32.8	Duplicate
14	100 grain weight (g)	Rainfed	NDR 359 x N22	44.79*	14.15	-26.73	-6.04	3.95**	31.34*	Duplicate
			NDR 359 x Vandana	-0.04	17.94	57.51**	35*	-0.04	5.94**	Complementary
			NDR 359 x N22	77.72*	15.62	-115.78	-52.88	-11.62	45.96*	Duplicate
15	Total grain yield per plant (g)	Irrigated	NDR 359 x Vandana	24.13**	15.81	19.29**	0.52**	-5.51	-22.22	Duplicate
			NDR 359 x N22	33.14*	-1**	-27.28	-12.04	-0.1	6.24**	Duplicate
			NDR 359 x Vandana	32.62*	1.12	-20.17	-13.64	-3.42	1.3**	Duplicate
16	100 grain weight (g)	Rainfed	NDR 359 x N22	1.97	0.25	-0.56**	-0.04**	-0.06**	0.94	Duplicate
			NDR 359 x Vandana	2.54	-0.06*	-0.96*	-0.3*	0.1	0.62	Duplicate
			NDR 359 x N22	1.92	0.18	-0.25**	0.01	-0.05**	0.48	Duplicate
17	Total grain yield per plant (g)	Irrigated	NDR 359 x Vandana	1.89	0.16	0.11	-	-	-	-
			NDR 359 x N22	8.92**	4.87	31.85**	18.04*	2.63**	-13.22	Duplicate
			NDR 359 x Vandana	3.65**	5.55	36.45*	22.62*	-1.48	-15.43	Duplicate
18	Total grain yield per plant (g)	Rainfed	NDR 359 x N22	7.71*	0.5	-6.33	-0.8	0.7	7.05*	Duplicate
			NDR 359 x Vandana	3.85*	0.12	6.44**	3.44*	0.07	-1.43	Duplicate

** - Significant at P = 0.01, * - Significant at P = 0.05

epistasis. These findings agree with Kumar et al. [33], except for grain yield per plant, where they reported the existence of complementary epistasis. Similar findings were also reported by Nayak et al. [34], Singh et al. [17], Roy and Senapati [35]. It may be because of the presence of dispersed alleles at interacting loci for these traits. In general, duplicate epistasis hampers the trait improvement through selection. Hence, a higher magnitude of dominance [h] and dominance × dominance [i] type of gene interaction effects would not be preferred. In such situation, selection should be postponed for several generations until a high level of gene fixation is realized. In addition, intermating between promising selections may be vital in accumulating favorable alleles [36]. Complementary epistasis was noticed for the trait, number of early bearing tillers per plant except for NDR 359 × N22 (rainfed). In such condition, additive components were often underestimated as compared to dominance components [37].

4. CONCLUSION

The present study indicates that, epistasis has a key role in the expression of almost all the traits in both the environment. Thus, formulating the breeding program only based on additive and dominance gene effects will be misleading. Dominance gene effect along with non-allelic interactions have profound effect on the genetic control of majority of the yield traits. Therefore, early generation selection will be misleading for these traits. Based on the observation, it is suggested that, bi-parental mating followed by recurrent selection or diallel-selective mating is preferable. This allows intermating among the selected superior segregates in different cycles, which will be useful to recover superior homozygote in later generations. However, the drought tolerance related traits like proline content and stomatal conductance were governed by additive component as well. Since, selection based on progeny performance exploits additive component of genetic variance, this can be followed for improving the above drought tolerance related traits.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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