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Genetic analysis of yield traits in rice under irrigated and water stress environments

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Abstract

Experiments were conducted to study the genetics and combining ability for yield and its components under irrigated (E I) and water stress environments (E II) using F_1 hybrids derived from a full diallel mating involving four drought tolerant and four drought sensitive rice genotypes. Significant differences were observed for all the traits studied in both EI and EII environments, except harvest index in E II. Additive and non-additive gene actions for days to flowering, biomass and harvest index and non-additive gene action for grain yield in both the environments were observed. Importance of additive gene action in E I and non-additive gene action in E II was observed for grains panicle^{-1}, whereas shift in non-additive to additive from E I to E II was observed for productive tillers plant^{-1}. The significance of *gca* and *gca* x environment interaction indicated the differential contribution of parents for days to flowering, biomass and harvest index. Based on the mean values and *gca* effects, landraces Nootripathu and Norungan were adjudged as the potential parents to improve grain yield under stress, whereas CO43 and IR62266 were identified as good general combiners to improve grain yield and its component traits under irrigated environment. The hybrids *viz*., PMK2/CO43, CO43/Nootripathu, Nootripathu/Kallurundaikar, Norungan/IR64, Kallurundaikar x PMK2 and IR20 x IR62266 were identified as superior ones for improving yield under water stress.

Key words: Rice, drought, diallel analysis, gene action, combining ability

Introduction

Drought is an important limiting factor adversely affecting rice production. About 28 per cent of the world's rice is grown in rainfed lowlands. These areas frequently experience severe water deficit due to uncertain and uneven rainfall distribution and yields are seriously affected by drought [1, 2]. Another 13% of the rice is grown under upland conditions without any surface water accumulation and is always prone to water stress. Even though rice is highly susceptible to drought, the crop provides huge opportunity to breed for drought tolerance, due to its inherent capacity and availability of huge genetic variability for wider adaptations in varied ecosystems. Despite the realization about the importance of water use efficiency in crop improvement, the available genetic variability for drought tolerance has not been progressively exploited in drought improvement breeding endeavors [3, 4]. Plant breeding for drought resistance has long been part of the breeding process in most crops. During the period of the pre-scientific agriculture, the genetic improvement of plant adaptation to dry conditions was simply attained by repeatedly selecting plants that appeared to do well when drought stress occurred. As a result of many generations of selection by the farmers, we now encounter such materials which, are defined as "landraces" of the crop. Such landraces utilized by the farmers for the cultivation in drought prone environments were shown to possess distinct drought resistance but are very poor in yield. Therefore, the incorporation of drought tolerance from landraces to high yielding genotypes could be useful in improving rice production significantly [5, 6].

Breeding for drought tolerance requires knowledge on gene action and combining ability of

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yield traits under stress and non-stress environments [7, 8]. However, little information is available on the genetics of yield under water stress in crop plants. Among the various biometrical techniques available for genetic studies, the diallel analysis holds good in explaining the genetic architecture, combining ability and heterosis of traits [9]. The success of any plant breeding programme largely depends on selection of appropriate parents. Elaborate methods of analysis are presently available for the estimation of genetic parameters as well as combining ability effects for studying the genetic relationship among the parents entering diallel system. The incidence of genotype-by-environment interaction within the target genotype – environment system of a breeding program necessitates the use of multi environmental trials. Therefore, in the present investigation, eight parents with differential reactions to drought stress were crossed in a full diallel fashion to assess the nature of gene action, combining ability for yield traits under stress and non-stress conditions and to identify the best combining parents, and hybrid combinations for developing high yielding drought tolerant rice varieties.

Materials and methods

Eight genotypes of rice *viz*., PMK2, CO43, Nootripathu, Norungan, Kallurundaikar, IR20, IR64 and IR62266 were selected for present investigation. Nootripathu, Norungan and Kallurundaikar are the land races adapted to rainfed tracts of South Tamil Nadu and PMK2 is an improved variety suited for rainfed cultivation. The remaining four genotypes were high yielding varieties adapted to irrigated ecosystem. Crossing was carried out among these genotypes in all possible combinations (direct and reciprocal) to produce 56 hybrids. The field experiments of the present investigation were carried out in the experimental fields at two locations *viz*., i) Paddy Breeding Station, Tamil Nadu Agricultural University (TNAU), Coimbatore under irrigated condition (E I) (May to September) and ii) Agricultural College and Research Institute, Madurai under water stress condition (E II) (October to February).

Experiments both in irrigated (E I) and water stress (E II) conditions were laid out in a completely randomized block design with three replications. Parents and hybrids were planted in a single row of 3 m length with a spacing of 20 cm between rows and 15 cm between plants. Recommended agronomic and plant protection measures were carried out to maintain good crop stand. At Coimbatore (E I) the soil was deep clay with the P^H of 7.0. The rainfall in this location during the crop period was 308mm. The relative humidity was 46.7 per cent and the mean maximum and minimum temperature of 32.3^oC and 20.5^oC was recorded. The soil was sandy loam with 7.3 pH in E II and during the crop period 352 mm of rainfall, 31.3^oC of mean maximum temperature and 78.9 per cent of relative humidity was recorded. In this location irrigation was withheld 67 days after sowing to impose water stress and then onward to a total of 19 days there were no rainfall and irrigation. Therefore, 19 days of water stress was maintained. Changes in soil moisture and penetration resistance were monitored periodically in stress plots with a Theta probe and a penetrometer, respectively. Five plants at random in parents and hybrids from each replication were used to record biometrical observations *viz*., days to flowering, number of productive tillers, grains panicle^{-1}, grain yield, biomass and harvest index.

The trait mean value of each replication was used for statistical analysis. Data were analyzed separately for individual environments and also pooled analysis over environments [10] using DIALLEL-INDOSTAT software. Estimates of general combining ability (*gca*), specific combining ability (*sca*) effects, reciprocals and heterosis were obtained according to Griffing's method 1, model 1 [11].

Results and discussion

The mean performance and analysis of variance indicated that the differences among the genotypes were statistically significant for all the traits in individual environments, as well as in pooled analysis (data not shown). Pooled analysis of variance revealed that the environmental differences were statistically significant for all the traits except harvest index. The differences due to pooled analysis among the genotypes were significant for days to flowering, productive tillers plant^{-1} and biomass yield and it was non significant to for grains panile^{-1}, grain yield and harvest index. The mean squares due to genotype x environment interactions were significant for days to flowering and biomass yield and non-significant for all the other traits. The non-significant mean squares due to genotype x environment interaction for all the traits except days to flowering and biomass yield indicated the major share of genotypic component than the genotype x environment components in the expression of these traits. The significance of mean squares due to genotype, environment, genotype x environment for days to flowering and biomass yield suggested the importance of both genotype and environment components for these traits. Therefore, it is concluded form the present study and also the previous work [8, 12] that the drought tolerant, high yielding genotype of rice cannot simply be developed by crossing the drought tolerant and high yielding parents without referring to the environmental influence.

GCA and SCA variances were significant in both the environments for all the traits except for productive tillers plant^{-1}, grains panicle^{-1} and grain yield (Table 1). The GCA variance for productive tillers plant^{-1} in E I, grains panicle^{-1} in E II and grain yield in both the environments were non-significant. However, the GCA variance was greater in magnitude than SCA variance in individual environments and also in pooled analysis for all the traits except for productive tillers plant^{-1} in E I and grains panicle^{-1} in E II, wherein SCA variances were greater than GCA variance. The significance of both GCA and SCA variances observed for days to flowering, biomass and harvest index in both the environments indicated the importance of both additive and non-additive gene action for the expression of these traits [13-15]. Also the magnitude of GCA variances was higher than SCA variances indicating the predominant role of additive effects in determining the expression of these traits. Significant SCA and non significant GCA variance observed for grain yield in both the environments, productive tillers plant^{-1} in E I and grains panicle^{-1} in E II meant non-additive gene action in the expression of these traits. The non-additive control of these traits was also observed previously [16, 17].

Breeders use the criteria such as (i) comparison of GCA: SCA variance ratio and (ii) least deviation of the ratios in order to rank the characters possessing relatively more fixable additive variation, which will largely helps to exercise selection in the succeeding generations based on one or more traits. In the present investigation, days to flowering, biomass and harvest index had high GCA variance (fixable genetic portion) than SCA variance (non-fixable genetic portion) and thus simple selection would confer rapid improvement of these traits. Selection for grain yield in both environments, productive tillers plant^{-1} in the irrigated environment and grains panicle^{-1} in the water stress environment could be delayed to later generations until the non-additive portion had mitigated to additive portion as these traits showed higher magnitude of SCA variance than GCA variance in the respective environments [18, 19]. The genotype x environment interaction is a major source of bias that affects general and specific combining ability testing. In this study, the genotype x environment interaction was significant for days to flowering, productive tillers and biomass and it was partitioned into GCA x E and SCA x E (Table 2). The GCA x E and SCA x E were found to be significant for days to flowering and biomass suggesting the need for selecting different parental lines to develop populations specific to irrigated and water stress environments [8].

Breeding value of parents

The estimates on *gca* effects and the mean performance of the parents would help the breeder to understand the genetic architecture and potentiality of the selected parents in F_1 and later generations [8]. Ramalingam *et al*. [20] established a close relationship between *per se* performance and *gca* effects. This information will be helpful in choosing the appropriate

Table 1. Analysis of variance for combining ability for yield and component traits under irrigated (E I) and water stress (E II) environments

Sources of variation	Mean sum of squares							
	GCA		SCA		RCA		GCA/SCA	
	EI	EII	EI	EII	EI	EII	EI	EII
Days to flowering	741.73**	232.98**	34.31**	29.96**	10.77**	47.87**	21.58:1	7.77:1
Productive tillers plant^{-1}	6.61	7.76**	9.54**	3.36**	7.22**	4.06**	0.69:1	2.31:1
Grains panicle^{-1}	2451.52**	73.37	416.04**	199.34*	346.74**	281.73**	5.90:1	0.36:1
Biomass (g)	1560.28**	221.01**	523.97**	110.71**	233.43**	166.25**	2.97:1	1.99:1
Grain yield (g)	41.20	17.19	63.29*	10.19**	37.03**	12.29**	0.65:1	1.68:1
Harvest index	0.01**	0.008*	0.005	0.006**	0.002	0.007**	1.83:1	1.33:1

*Significant at 5% level, **Significant at 1% level

Table 2. Pooled analysis of variance for combining ability for yield and component traits over environments in rice

Sources of variation	*gca*	*sca*	*rca*	Environment	*gca* x environment	*sca* x environment	*rca* x environment	*gca*:*sca*
Days to flowering	435.76**	36.38**	32.36**	3884.83**	538.94**	27.89**	26.28**	11.97:1
Productive tillers	9.69*	7.07*	6.26*	273.19*	4.68	5.83*	5.01	1.37:1
Grains panicle^{-1}	1129.40*	359.23	373.15	48850.48*	1395.4	256.15	255.29	3.14:1
Biomass (g)	1014.71**	402.22*	178.25	27738.36*	766.57**	232.24	221.43	2.25:1
Grain yield (g)	49.92*	51.49**	36.39*	2435.58*	8.44	21.99	12.93	0.96:1
Harvest index	0.003	0.006	0.006	0.16	0.015*	0.005	0.003	0.5:1

*Significant at 5% level, **Significant at 1% level

parents for the exploitation of variation and extracting superior genotypes through recombination breeding. The objective appears to be realizable only when these parents were evaluated for their combining ability attributes over environments. Breeding for drought tolerance in rice is always centered on the choice of parents of early to medium duration coupled with high yield. The parents exhibiting positive *gca* effects towards long duration may not be a good choice under such circumstances. Therefore, in the present study the parents exerting significant *gca* effects towards the desirable directions were identified. The *gca* effects of the parents for all the yield traits under stress and non-stress environments are given in Table 3. The mean performance of the parents evaluated in irrigated and water stress environments differed from one another for all the traits except for grain weight. The *per se* performance for days to flowering in Norungan and Kallurundaikar showed significant variation among the environments. These two parents took more than 120 days for flowering in E I, while in E II they flowered on 78 and 83 days, respectively. This variation in flowering was primarily due to photosensitive nature of these two parents. The evaluation of genotypes under E I was carried out during *kharif* season (May to September), which was not favorable to induce flowering among the photosensitive genotypes. In E II, stress was imposed by withholding irrigation for a period of 19 days during reproductive stage. The water stress affected the genetic expression of biomass, grain yield and harvest index. Lafitte *et al*. [21] also reported similar influence of water stress on these traits. The performance of genotypes for productive tillers plant^{-1} remained stable over environments and tiller formation was not affected by the water stress in the E II, since stress was imposed only during the flowering stage. However, considerable differences were noticed for grain yield among the parents and hybrids, due to the adverse effect of water stress on grain filling. The landraces, Nootripathu and Norungan were found to be tolerant to water stress based on their high *per se* performance under water stress. These results support the previous findings indicating higher drought tolerance of these two landraces [22]. CO43, IR20, IR64 and IR62266 were found to be susceptible to water stress. Estimation of *gca* effects and *per se* performance revealed that the parents Nootripathu, Norungan and Kallurundaikar showed significant negative *gca* effects for days to flowering. CO43 showed significant *gca* effects and higher mean values for grain yield and its component traits, IR62266 showed significant *gca* effects for productive tillers per plant in E I. Based on the mean values and *gca* effects Nootripathu, Norungan and Kallurundaikar are suitable for incorporation of earliness and drought tolerance traits. CO43 and IR62266 would serve as good general combiners for grain yield and yield related traits. The diallel analysis across environments identified good trait-specific combiners *viz.*, Nootripathu for earliness, CO43 and IR20 for grains panicle^{-1}, CO43, Norungan and Kallurundaikar for grain yield under water stress based on *gca* effects. Previous workers also judged the breeding potential of the parents based on *gca* effects and mean performance [22, 23].

Breeding value of hybrids

Scope for exploitation of hybrids for further breeding cycles in any crop largely depends on (i) high mean performance of the hybrids over a range of environments (ii) the specific combining ability effects of the parents and (iii) the magnitude of heterosis towards the desirable direction. In plant breeding, it is commonly assumed that when good performing parents are crossed with each other, they are expected to produce better hybrids. However. this assumption may not be true all the time [24]. The hybrids identified based on mean performance, *sca* effects and heterosis could be exploited in heterosis breeding or to advance them to further breeding cycles to identify useful transgressive segregants. The heterosis and *sca* effects are estimated values. Whereas *per se* performance is the realized value, therefore weight age should be given to *per se* performance while making selection among cross combinations [25]. Based on *per se* performance, Nootripathu/CO43, Nootripathu/Kallurundaikar, IR64/Norungan and IR62266/IR20 were superior for grain yield in both the environments. These hybrids are top ranked for one or more yield components. It is observed from this study that the general combining ability of the parents was directly related to the *per se* performance of the hybrids (CO43/Norungan and CO43/Kallurundaikar) than to *sca* effects and heterosis. To improve self pollinated crops, the *sca* effects do not contribute tangibly, however it would be very much useful wherever commercial exploitation of heterosis is possible [18]. In the present study the estimates of *sca* effects revealed that 14 hybrids from E I and 10 from E II, out of 56, were found to be good specific

Table 3. General and specific combining ability effects for yield and component traits under irrigated (E I) and water stress (E II) conditions in rice

Genotypes	DF		PTN		GPP		BM		GY		HI	
	E I	E II	E I	E II	E I	E II	E I	E II	E I	E II	E I	E II
						gca effects						
PMK2	-5.73**	-0.43	-1.13**	-0.27	3.33	1.69	-7.27**	-6.03**	-2.19**	-1.75**	0.006	0.014
CO43	1.15**	5.09**	0.02	0.52*	19.32**	-1.58	4.59*	1.19	1.71*	0.49	-0.003	0.018
Nootripathu	-5.02**	-7.05**	-0.17	-0.06	2.61	-2.12	-0.45	3.42**	0.95	1.23**	0.014	0.001
Norungan	9.79**	-2.76**	-0.28	-0.7 *	7.19*	-2.77	13.85**	0.91	2.06**	1.04*	-0.026**	0.012
Kalluraundaikar	10.97**	-1.55**	0.43	-0.66 *	-7.45*	-0.31	13.94**	0.59	0.98	0.29	-0.046**	-0.004
IR20	-3.87**	2.47**	0.09	-0.63 *	7.15*	3.23	-4.66*	-1.63	-1.24	-1.15**	0.002	-0.019
IR64	-5.54**	1.41**	-0.11	0.93**	-14.34**	-0.161	-10.70**	5.36**	-1.02	-1.26**	0.035**	-0.06**
IR62222	-1.74**	2.82**	1.14**	0.89 **	-17.81**	2.05	-9.29**	3.82*	-1.25	0.55	0.020**	0.038
					sca effects for selected cross combinations							
PMK2 x CO43	-6.96**	-8.03**	0.68	0.85	12.89	-1.96	-4.62	4.59	2.59	3.04**	0.076**	0.012
PMK2 x Nootripathu	7.37**	0.48	1.58*	2.44**	6.75	-11.26	12.70**	-5.28	6.17**	-1.52	0.022	-0.006
CO43 x Nootripathu	4.01**	-3.91**	-1.34*	-1.69*	25.85**	0.85	5.23	6.84	5.67**	2.29*	0.045*	-0.032
CO43 x Norungan	-2.48*	0.30	1.38*	1.65*	13.86	3.16	21.17**	4.15	9.60**	1.02	0.018	-0.015
CO43 x Kallurundaikar	-2.90**	8.10**	3.26**	-1.25	-25.92**	-4.8	-30.80**	0.97	3.76*	-2.22*	-0.040*	-0.06**
Nootripathu x Kallurundaikar	8.85**	-0.43	0.83	1.50*	7.38	14.75*	6.69	10.93**	3.81*	3.58**	0.013	0.014
Norungan x CO43	-0.67	-10.8**	2.00*	3.50**	9.87	-16.50*	38.10**	-0.46	13.75**	0.10	0.045*	0.013
Norungan x IR64	-0.46	3.15*	2.20**	0.90	5.13	-17.59*	19.28**	3.48	6.70**	2.97**	0.005	0.038
Norungan x IR62266	-0.78	-2.09*	1.01	0.27	1.47	-0.59	10.45	-0.21	4.06**	1.37	0.010	0.054
Kallurundaikar x PMK2	0.50	-1.17	0.40	-0.83	-1.15	24.67**	-4.33	5.55	4.88**	2.17*	0.065**	0.028
Kallurundaikar x CO43	-0.92	-1.17	1.67*	-0.67	19.25**	-18.00*	16.57**	-7.87	8.78**	2.02	0.045*	0.09**
Kallurundaikar x IR62266	2.11*	-3.30**	4.39**	0.38	26.50**	4.79	14.28*	-3.04	8.91**	1.27	0.055*	0.072*
IR20 x Kallurundaikar	0.18	5.16**	-2.42**	0.33	-9.37	-6.33	7.20	11.28**	-1.20	2.77**	0.037	-0.017
IR20 x IR64	0.04	1.09	-0.09	0.79	-18.86**	-8.26	19.74**	7.71*	6.51**	-2.31*	-0.004	-0.10
IR20 x IR62266	0.58	0.67	1.92*	-0.83	14.54	14.75	17.91**	9.91*	6.87**	2.92**	0.014	-0.02

*Significant at 5% level; **Significant at 1% level; E I: Irrigated environment; E II: Water stress environment DF- Days to flowering; PTN-Productive tiller number; GPP- Grains per panicle; BM- Biomass (g), GY- Grain yield (g); HI- Harvest index.

combiners based on *per se* performance and *sca* effects. It is important to note that six crosses (PMK2/O43, CO43/Nootripathu, Nootripathu/Kallurundaikar, Norungan/IR64, Kallurundaikar/PMK2 and IR20/IR62266) showed positive and significant *sca* effects for grain yield over environments. These crosses also showed higher mean performance for grain yield and showed significant *sca* effects for one or more yield traits. It is noteworthy that at least one of the parents involved in these crosses was good general combiner for grain yield under stress, indicating that these crosses will eventually yield desirable transgressive segregants. For improving grain yield under water stress, due importance should be given to these crosses to identify new genotypes with high grain yield under stress. It is observed that the crosses showing consistently positive *sca* effects over environments also exhibited high *per se* performance. Therefore, *per se* performance and *sca* effects were considered as a criterion to identify the best crosses for further advancement. All the high performing crosses involving parents with high x high, high x low and low x high general combiners, indicated that non-additive gene actions, which are unfixable in nature were involved in the selected cross combinations. These crosses of high x low or low x high *gca* with the expression of high positive *sca* effects might be due to the dominant x additive, dominant x dominant and recessive x dominant epistasis [22, 23, 26] and these hybrids are expected to produce desirable transgressive segregation in later generations.

It is evident from the results that yield improvement in rice for water limited environments is possible by selecting appropriate parents based on *per se* performance and combining ability and to choose suitable breeding programmes based on nature of gene action and combining ability. CO43 and IR62266 were found to be good general combiners for grain yield and yield components under EI, while Nootripathu, Norungan and Kallurundaikar were identified as good general combiners to improve yield under water stress (E II). The present study identified the importance of both additive and non-additive components of genetic variances in governing the inheritance of yield and other traits.

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