




## Article

# Determining the Combining Ability and Gene Action for Rice Yellow Mottle Virus Disease Resistance and Agronomic Traits in Rice (*Oryza sativa* L.)

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**Abstract:** Selecting genetically diverse and complementary parental lines and superior crosses are pre-requisites in developing improved cultivars. The objectives of this study were to determine the combining ability effects and gene action conditioning rice yellow mottle virus disease (RYMVD) resistance and agronomic traits in rice (*Oryza sativa* L.). Ten parental lines and their 45 F<sub>2</sub> progenies were field evaluated in three locations using a 5 × 11 alpha lattice design with two replications. The genotype × site interaction effects were significant ( $p < 0.05$ ) for the number of tillers (NT), number of panicles per plant (NPP), number of grains per panicle (NGP), percentage of filled grains (PFG), thousand grain weight (TGW), RYMVD resistance and grain yield (GY). The analysis of general and specific combining ability (GCA and SCA) indicated involvement of both additive and non-additive gene action governing inheritance of traits. High GCA/SCA ratio estimate revealed additive genetic effect was predominant. Parental lines Mwangaza, Lunyuki, Salama M-57, Salama M-19, IRAT 256 and Salama M-55, which had negative GCA effects for RYMVD, and families such as SARO 5 × Salama M-55, IRAT 245 × Rangimbili, Rangimbili × Gigante and Rangimbili × Mwangaza, which had negative SCA effects for RYMVD, were selected for RYMV resistance breeding. The crosses Rangimbili × Gigante, Gigante × Salama M-19 and Rangimbili × Salama M-55 were selected due to their desirable SCA effects for GY. The predominance of additive gene effects for agronomic traits and RYMVD resistance in the present breeding populations suggested that rice improvement could be achieved through gene introgression using recurrent selection.

**Keywords:** cultivar development; diallel; gene action; RYMV resistance; rice breeding; yield components



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## 1. Introduction

Rice (*Oryza sativa* L.,  $2n = 2x = 24$ ) is the second most important global crop after wheat in terms of total production [1]. Globally, rice is cultivated on about 167 million hectares with an annual production of 744.4 million tons of grain [2]. More than 90% of rice is grown and consumed in Asia [3,4], while sub-Saharan Africa (SSA) region accounts for about 10% of the global rice production [5]. In East and Southern Africa region, Tanzania is the second largest producer of rice after Madagascar. Rice is ranked as the second most important staple crop after maize (*Zea mays*) in Tanzania [6,7].

Despite the contribution of rice to food and nutrition security, and enhanced livelihoods of millions of people in Tanzania, the average yield in the country is 1.5 t ha<sup>-1</sup>, which is significantly lower than the yield potential of 4.6 t ha<sup>-1</sup> reported in Asia [5]. The low productivity of rice in Tanzania is caused by a combination of biotic and abiotic stresses, and socio-economic constraints [8]. The rice yellow mottle virus (RYMV) disease

has been identified as a major biotic constraint limiting rice productivity in SSA countries including Tanzania [7,9]. The disease has since become endemic in all the rice-growing regions under both rain-fed and irrigated production farming systems [10]. The RYMV causes yield losses ranging from 20% to 100%, depending on cultivar susceptibility, and stage of growth at the onset and development of infection [6,11,12]. The RYMV disease is characterized by mottling and yellowing symptoms, resulting in reduced photosynthetic area, stunted growth, reduced tiller formation and increased grain sterility [9,11]. Locally grown, farmer-preferred rice varieties with good culinary properties have been reported to be susceptible to RYMV [13]. Hence, there is a need to develop improved rice varieties with RYMV resistance and farmer-preferred traits.

Host plant resistance is the most economical and environmentally friendly approach to control the RYMV. The development of RYMV resistant and agronomically superior genotypes requires genetically diverse and complementary parental lines and superior crosses for selection [14]. Genes conditioning RYMV resistance have been reported previously [15–17]. The *RYMV1* and *RYMV2* are the most widely reported genes [15,18,19]. Hence, RYMV resistant and agronomically suitable donor parents can be used in local pre-breeding programs to develop new populations for variety development. Gene introgression requires an understanding of the nature of gene action and trait heritability.

Assessing combining ability and gene action for RYMV resistance and agronomic traits in rice would provide a basis for the development and selection of a breeding population. Combining ability analysis can facilitate the selection of suitable parents for hybridization, and identification of promising recombinants [20–22]. Broadly, combining ability is divided into the general combining ability (GCA) effects of the parents, and the specific combining ability (SCA) effects of the crosses. The GCA is the average performance of a line in a series of hybrid combinations and relates to additive gene action. The SCA refers to the deviation of the performance of a cross-based on the average performance of its parents. The SCA effects are associated with non-additive gene actions such as dominance and epistasis [23]. In a breeding program, selection of parents showing good GCA effects and their progenies with high SCA effects for desirable traits are essential.

The diallel mating design has been extensively utilized in determining the combining ability effects in rice breeding following [24]. This mating design has been widely used in genetic analysis to investigate the inheritance of important traits of various crops including rice. The design entails crossing of a parent with other parents in all possible combinations. With diallel analysis, it is assumed that the genes in the parents are independently distributed. The mating design is useful in providing pedigreed breeding population for selection, progeny tests and to estimate genetic parameters. The diallel was used because it can facilitate analyses of progenies developed from combinations involving a wide range of parents including inbred lines or broad-based parental lines. Griffings' full diallel analysis (Method I) that includes parents, crosses and their reciprocals is used to estimate maternal effects, while Method III includes only parents that becomes the design of choice in various genetic analysis studies. Method II includes reciprocals and is used in measuring various genetic parameters. Method II reduces the number of entries from  $p^2$  cross combinations, for a full diallel, to  $p/2(p + 1)$  [24]. This lowers both labor and cost of the crossing program, particularly for crops with cleistogamous flowering system such as rice.

Several studies have been carried out on combining ability effects in rice with varied results. Refs. [25,26] reported a preponderance of additive gene action in conditioning RYMV resistance. Conversely, Ref. [27] who reported dominance gene action was responsible for conditioning resistance to RYMV. Therefore, combining ability analyses and genetic predictions are dependent on the test populations and environment. With a goal of developing rice varieties adapted to Tanzanian conditions, with strong RYMV resistance, genetically diverse rice genotypes were assembled and evaluated using agronomic traits and simple sequence repeat (SSR) markers [28]. The RYMV resistance is the trait of priority for this research. However, there is need to complement economic agronomic traits such as early flowering and maturity, panicle size or other farmer-preferred desirable traits. RYMV resis-

tant varieties must be suitable for farming conditions or meet farmer expectations in other attributes. Consequently, breeding for the RYMV resistance was considered in combination with other agronomic performance. The RMYV resistance is the most significant trait. Breeding approach based on recurrent backcrossing to at least the BC5 generation would be more appropriate, with field evaluation in Tanzania. This allowed for the selection of promising and complementary parents to be included in a rice pre-breeding program in Tanzania. Therefore, the objective of this study was to determine the combining ability effects and gene action conditioning rice yellow mottle virus resistance and agronomic traits in the selected parental lines and derived families for subsequent breeding activities.

## 2. Materials and Methods

### 2.1. Plant Materials

Ten selected rice genotypes were used to generate new populations. A description of the parental genotypes are presented in Table 1. The parents were selected from previous phenotypic and genotypic evaluations for their diversity in terms of RYMV resistance and agronomic traits. The parental varieties (accessions) were selected based on their high yield and RYMV resistance while landraces were included because of their wide adaptability to varied growing environments, agronomic and quality (aromatic) traits preferred by smallholder farmers and local markets. The selections included genotypes sourced from Sokoine University of Agriculture (SUA), landraces from local farmers, a variety from the Tanzania Agricultural Research institute (TARI) and one genotype from AfricaRice.

**Table 1.** Description of rice parental genotypes used for population development.

No	Genotype	Status	Origin	RYMV Resistance	Agronomic and Grain Quality Traits
1	Salama M-57	Accession	Tanzania	Resistance	Unscented; long grain
2	IRAT 256	Accession	Tanzania	Resistance	Unscented
3	Rangimbili	Landrace	Tanzania	Susceptible	Scented; high grain quality
4	Zambia	Landrace	Tanzania	Susceptible	Scented; high grain quality,
5	Lunyuki	Accession	Tanzania	Resistance	Unscented, long grain
6	SARO 5	Variety	Tanzania	Susceptible	Scented, high yielding
7	Mwangaza	Variety	Tanzania	Resistance	Unscented; long grain
8	Salama M-55	Accession	Tanzania	Resistance	Unscented
9	Gigante	Accession	AfricaRice	Susceptible	Large panicle
10	Salama M-19	Accession	Tanzania	Resistance	Unscented; long grain

### 2.2. Population Development

Crossing blocks were initiated under a greenhouse condition at Tanzania Agricultural Research Institute (TARI), Ilonga (6°50'3.39" S and 36°59'30.17" E), with an altitude of 491 m above sea level. The temperature range and mean relative humidity during the growing period were 20–32 °C and 87.4%, respectively. The parents were planted in 10 L capacity plastic pots. Crosses were undertaken using a 10 × 10 half-diallel mating design to produce 45 F1 families, between May and August in 2018. Parents were stagger-planted at weekly intervals to synchronize flowering. A vacuum emasculation method was used [29]. Pollination was carried out between 10.00 a.m. to 12:00 noon. After emasculation, panicles were immediately covered with a pollination bag and sealed with paper clips to avoid unintended cross-pollinations. The pollinating bag was removed from the emasculated female parent and a fertile panicle from the male parent was gently dusted onto the female panicle. The flowers were bagged immediately after hand pollination. The pollinating bag covered the female parent (Figure 1) to prevent cross-pollination and to maintain high relative humidity for better fertilization. Mature seeds from each successful cross were harvested 25 to 30 days after pollination and kept separately with proper records. The seed of the F1 crosses (Figures 2 and 3) were planted for seed bulking and genetic analysis at the F2 generation.



**Figure 1.** Emasculated and pollinated rice genotypes covered with pollination bags.



**Figure 2.** Germinating F1 seed in a Petri-dish being advanced to F2.

### 2.3. Field Evaluations

#### 2.3.1. Descriptions of the Study Areas

The parental lines and their F2 crosses were field evaluated in three sites namely, Ifakara, Ilonga and Mkindo sites in Tanzania (Table 2). The experimental sites are recognized hotspots for RYMV disease [6,10]. The sites are known for the high disease pressure that develops during the growing season and can cause yield losses of 100% under epidemic conditions [10]. Evaluations were conducted during the main cropping season (December 2019 to June 2020). The climatic conditions of the study sites are summarized in Table 2. All the three sites experience a sub-humid tropical climate with a bimodal rainfall distribution. The short rainy season usually starts in October and ends in December, while the long rainy season lasts between March and May.



Figure 3. F1 plants established in plastic pots to produce F2 seeds.

Table 2. Descriptions of the three sites used for evaluation of 45 crosses and 10 parents.

Site	District	Test Condition	Latitude (S)	Longitude (E)	Altitude (masl)	Total Annual Rainfall (mm)	TMax (°C)	TMin (°C)
Ifakara	Kilombero	Rain-fed	08°03'	36°40'	271	980	27.34	17.71
Ilonga	Kilosa	Irrigated	6°74'	37°05'	607	1194	28.43	19.24
Mkindo	Mvomero	Irrigated	6°14'	38°41'	430	975	25.67	16.94

### 2.3.2. Experimental Design and Management

The 10 parents and the 45 F2 crosses were established using a 5 × 11 alpha lattice design with two replications at each site. Each genotype was planted in a plot measuring 2.4 m × 2.4 m. The seeds were planted directly at Ifakara while transplanting of 21-day old seedlings was carried out at the Ilonga and Mkindo sites. The seeds or seedlings were sown or transplanted, respectively, in each plot at a spacing of 20 cm × 20 cm, with one plant per hill. Potassium and phosphorous fertilizers were used for basal application at all sites prior to planting at a rate of 65 kg P ha<sup>-1</sup> and 54 kg K ha<sup>-1</sup>, respectively. Urea fertilizer (46% nitrogen content) was broadcasted in two equal splits (the first at tillering and the second at panicle initiation) as top dressings to deliver a total level of 60 kg N ha<sup>-1</sup>. The rest of the cultural practices, including thinning and hand weeding, were applied as recommended, to ensure uniform and healthy crop growth.

### 2.3.3. Data Collection

Data collected included the rice yellow mottle virus reaction and agronomic traits, based on the IRRI Standard Evaluation System (SES) for rice [3]. The severity of the rice yellow mottle virus (RYMV) disease reaction was scored using a scale of 1 to 9 [30] (Table 3).

Data on days to 50% flowering (DFL), number of tillers per plant (NT), plant height (PH), number of panicles per plant (NPP), panicle length (PL), number of grains per panicle (NGP), percentage-filled grains per panicle (PFG), 1000-grain weight (TGW) and grain yield (GY) were collected. The DFL were recorded by counting the number of days from sowing to when 50% of all the plants in each plot had flowered. The NT from 10 randomly selected plants in a plot were recorded at physiological maturity. PH was measured in centimeters (cm) using a ruler from the soil surface to the tip of the longest panicle at physiological maturity. The NPP was recorded by counting the number of fully exerted panicles bearing grains from a sample of selected 10 plants and their sum averaged to obtain the NPP. The PL was measured in centimeter using a ruler from the panicle base

node to the tip (end) at the base on 10 randomly selected plants per plot. NGP was counted using a seed counter and recorded as an average of samples from 10 panicles per plot. The PFG was calculated as the proportion of unfilled grains to the total number of grains from 10 sampled panicles per plot. TGW in grams was obtained by counting 1000 grains from each plot using a seed counter (Elmor C1, Biotronic Bharat, New Delhi, India) and weighing on an electronic balance (Ohaus Scout Pro Model 502 AC, Beijing, China). The GY was determined by harvesting all panicles in each plot. The panicles were threshed and winnowed to remove chaff. The weight of the grains was adjusted to 14% moisture content and was expressed in tons per hectare ( $t\ ha^{-1}$ ).

**Table 3.** RYMV disease severity rating scale and description [29].

Rating Scale	Description
1	Highly resistant (no symptoms observed)
3	Resistant (leaves green, but with sparse dots or streaks, less than 5% reduction of height)
5	Moderate resistant (Leaves green or pale green with mottling, 6–25% height reduction)
7	Susceptible (Leaves pale yellow or yellow, 26–75% height reduction, flowering slightly delayed)
9	Highly susceptible (Leaves yellow or orange, more than 75% height reduction, no flowering)

#### 2.3.4. Data Analysis

The performance of each cross and parent was determined through the analysis of variance using the REML procedure of GenStat 24th edition [31] and data normality was tested using the Shapiro–Wilkes test before the analysis of variance (ANOVA). Means separation was performed using the Fishers' Unprotected Least Significant Difference (LSD) procedure at a 5% probability level. Separate ANOVAs were conducted using REML approach for each location and later combined data analysis were calculated across locations after a test for homogeneity of variance was conducted. Parents and crosses were considered as fixed effects, while replication was considered as a random effect in computing the ANOVA for combining ability effects. Griffing's [24] diallel method 2, model 1, was used to estimate the GCA and SCA effects as:

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + \frac{1}{bc} \sum_k e_{ijkl}$$

where  $Y_{ij}$  = observed value of the cross between parent  $i$  and  $j$ ;  $\mu$  = The population (general) mean;  $g_i$  and  $g_j$  = GCA effects of  $i$ th and  $j$ th parents, respectively;  $s_{ij}$  = SCA of the cross between parents  $i$  and  $j$ ;  $e_{ijkl}$  = environmental effect associated with  $ijkl$ th individual observation in  $k$ th replication. The GCA for each parent was calculated as described by [22]:

$$GCA_P = X_P - \mu.$$

The SCA effects of the crosses were computed from the formula:

$$SCA_X = X_X - E(X_X) = X_X - [GCA_P + \mu];$$

where  $GCA_P$  = general combining ability effect of the parent;  $X_P$  = Mean of the parent;  $\mu$  = Overall mean of all crosses;  $SCA_X$  = specific combining ability of the parent in the cross;  $X_X$  = observed mean value of the cross;  $E(X_X)$  = expected values of the cross basing on the GCA of the parent.

Baker's ratios were also computed to estimate the relative importance of additive and non-additive gene action in the expression of traits using Baker's general predicted ratio (GPR) as follows:

$$GCA/SCA = 2MSGCA / (2MSGCA + MSSCA)$$

where MSGCA = mean square for GCA and MSSCA = mean square for SCA.

A ratio of >0.5 implies that GCA is more important than SCA in the inheritance of the character and a ratio of <0.5 implies that SCA is more important than GCA in the inheritance of the character [32].

### 3. Results

#### 3.1. Analysis of Variance and Mean Performance

The mean squares and significant tests among genotypes revealed that NT, NPP, NGP, PFG, TGW and GY were significantly ( $p \leq 0.05$ ) affected by genotype  $\times$  site interaction effects (Table 4). The genotypes exhibited significant differences for all assessed traits. Genotype performance also varied across the sites for all the traits except for the RYMV reaction.

**Table 4.** Mean squares and significant tests for 10 traits among 10 parents and 45 F2 crosses of rice evaluated in three locations in Tanzania.

Sources of Variation	df	DFL	NT	PH	NPP	PL	NGP	PFG	TGW	RYMVD	GY
Site	2	1694.03 ***	208.37 ***	863.30 ***	90.87 ***	64.95 ***	3493.17 ***	416.9 ***	3.65 *	0.18 ns	6.61 ***
Rep (Site)	2	85.92 ***	33.27 ***	1760.60 ***	3.68 ns	7.71 *	17.55 ns	19.82 ns	2.37 *	0.1 ns	0.1 ns
Block (Rep)	20	8.00 ns	4.81 **	129.9 ns	4.23 **	4.14 ***	257.45 ***	25.91 ns	1.99 ***	0.24 ns	0.2 *
Genotype	54	441.33 ***	6.43 ***	342.2 ***	4.99 ***	5.98 ***	1649.19 ***	477.17 ***	6.87 ***	26.81 ***	0.97 ***
Genotype $\times$ Site	108	6.949 ns	3.29 *	76.9 ns	3.47 **	2.19 ns	236.45 ***	45.23 ***	1.47 ***	0.45 ns	0.32 ***
Error	102	9.33	1.98	104	1.95	1.67	81.4	25.93	0.82	0.83	0.11

Note: df = degree of freedom; DFL = Days to 50% flowering; NT = number of tillers/plant; NPP = number of panicle/panicle; PH = plant height; PL = panicle length; NGP = number of grains/panicle; PFG = percentage filled grains/panicle; TGW = thousand grain weight; RYMVD = rice yellow mottle virus disease reaction; GY = grain yield; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ; ns, non-significant.

Mean values, coefficients of variation (CVs), and least significant differences (LSDs) of the genotypes evaluated across three locations are presented on Table 5. The mean DTF was 81.5 days (Table 5). Cross Lunyuki  $\times$  Mwangaza was the earliest to attain 50% flowering at 66 days, which was followed by crosses Mwangaza  $\times$  Salama M-19 and IRAT 256  $\times$  Rangimbili both at 67 days. Zambia  $\times$  Salama M-55 was the latest cross to flower and mature at 116 days. The parent Mwangaza was the earliest to reach 50% flowering, after 66 days (Table 5). The NT ranged from 9 to 14 with a mean of 10.6. In terms of tillering capacity, the crosses IRAT 256  $\times$  Zambia and IRAT 256  $\times$  Lunyuki produced the maximum NT of 14 and 13, respectively. The PH ranged between 97.4 and 132 cm, with a mean of 115.2 cm. Crosses SARO  $\times$  Gigante, SARO  $\times$  Salama M-55 and Rangimbili  $\times$  Mwangaza were the shortest with PHs of 97.4 cm, 101.4 cm and 101.6 cm, respectively. Cross IRAT 256  $\times$  SARO was the tallest at 157.7 cm. The parent Rangimbili recorded with the highest PH of 132.7 cm. The mean number of NPP varied from 9 to 13, with a grand mean of 9.5 NPP (Table 5). The highest number of NPP was 13, and 12 observed on the crosses IRAT 256  $\times$  Lunyuki and IRAT 256  $\times$  Zambia, in that order. The mean PL of the test genotypes was 23.7 cm. The longest PL crosses across the testing environments were Zambia  $\times$  SARO and Rangimbili  $\times$  Salama M-55 with PL of 25.3 cm and 25.2 cm, respectively. The mean NGP of the test genotypes was 124.5. The crosses with the maximum NGP were Salama M-57  $\times$  IRAT 256, Rangimbili  $\times$  Gigante, Gigante  $\times$  Salama M-19 and Salama M-55  $\times$  Gigante, with 147, 146, 145 and, 144 NGP, in that order. The parents Salama M-55 and Salama M-19 had the highest NGP of 171 and 157, respectively. The PFG values varied from 64.2 to 97.1% with a mean of 84.1%. The best performing crosses were Gigante  $\times$  Salama M-19,

Rangimbili × Mwangaza, Salama M-57 × Lunyuki, and IRAT 256 × Mwangaza with PFG of 96.6%, 95.4%, 95.3% and 95.1%, respectively. The parental lines Mwangaza, Salama M-55 and Salama M-19 recorded with the highest means for PFG. The mean TGW was 32.3 g. Families Rangimbili × Mwangaza, Lunyuki × Mwangaza, Mwangaza × Salama M-19 and Mwangaza × Gigante had the highest TGW value of 34.3 g, 34 g, 33.8 g and 33.7 g, respectively. The RYMVD symptoms ranged from 1 to 7 with the overall mean score of 3.5. Crosses Salama M-57 × IRAT 256, Salama M-57 × Lunyuki, Salama M-57 × Mwangaza, Salama M-57 × Salama M-19, IRAT 256 × Rangimbili, IRAT 256 × Mwangaza, Rangimbili × Mwangaza, Lunyuki × Mwangaza, Lunyuki × Salama M-19, SARO × Salama M-55, Mwangaza × Salama M-19, Salama M-55 × Gigante, and Salama M-55 × Salama M-19 had the sources of RYMVD resistance with lowest RYMVD score of 1. The parental lines Salama M-57, IRAT 256, Lunyuki, Mwangaza, Salama M-55, and Salama M-19 showed resistance to RYMVD with a score of 1. The GY differed from 2.7 to 4.7 t ha<sup>-1</sup> with a mean of 3.7 t ha<sup>-1</sup>. The crosses with the highest GY values (Table 5) were Salama M-57 × IRAT 256, Rangimbili × Salama M-55, Rangimbili × Gigante, Gigante × Salama M-19, Salama M-55 × Gigante, IRAT 256 × Rangimbili, and Salama M-57 × SARO had mean grain yield of > 4.0 t ha<sup>-1</sup>. The parental lines Salama M-19, Salama M-57, Salama M-55, and IRAT 256 had the highest means for grain yield, producing 4.0 t ha<sup>-1</sup> each.

**Table 5.** Means for agronomic traits and RYMVD reaction of 10 parental genotypes and 45 F2 crosses of rice evaluated across locations in Tanzania.

Genotypes	DFL	NT	PH	NPP	PL	NGP	PFG	TGW	RYMVD	GY
Crosses										
Salama M-57 × IRAT 256	77	11	113.9	9	22.9	147	93.7	31.8	1	4.7
Salama M-57 × Rangimbili	76	11	121.7	9	24.8	131	93.4	30.5	3	3.8
Salama M-57 × Zambia	76	11	117.7	9	24.6	121	70.9	31.8	5	2.9
Salama M-57 × Lunyuki	76	9	113.8	9	22.4	87	95.3	32.0	1	4.0
Salama M-57 × SARO	74	12	117.2	11	23.2	108	91.7	31.7	3	4.1
Salama M-57 × Mwangaza	69	10	119.1	10	24.2	120	91.4	32.8	1	3.9
Salama M-57 × Salama M-55	75	11	119.2	10	23.8	98	76.9	32.3	5	3.4
Salama M-57 × Gigante	79	12	114.3	10	23.7	114	78.5	31.8	5	3.8
Salama M-57 × Salama M-19	78	10	118.8	9	22.8	94	89.7	32.5	1	3.8
IRAT 256 × Rangimbili	67	11	108.1	10	21.3	142	94.9	32.3	1	4.2
IRAT 256 × Zambia	75	14	128.5	12	23.7	122	81.1	31.8	5	3.0
IRAT 256 × Lunyuki	77	13	112.7	13	22.0	116	78.8	31.3	5	3.6
IRAT 256 × SARO	78	12	132.0	10	22.6	108	79.4	30.7	5	3.5
IRAT 256 × Mwangaza	68	10	109.2	9	21.8	121	95.1	33.8	1	4.0
IRAT 256 × Salama M-55	69	11	118.4	10	23.3	89	67.6	32.0	5	3.0
IRAT 256 × Gigante	69	12	111.3	11	22.4	127	78.8	32.3	5	3.8
IRAT 256 × Salama M-19	78	11	116.8	11	21.3	99	71.2	31.5	7	2.8
Rangimbili × Zambia	86	11	124.9	11	24.7	126	69.5	30.8	5	3.5
Rangimbili × Lunyuki	76	10	117.6	9	23.8	129	86.6	30.7	3	3.1
Rangimbili × SARO	71	12	107.4	11	22.2	101	79.7	30.8	5	3.7
Rangimbili × Mwangaza	68	9	101.6	8	21.3	113	95.4	34.3	1	3.5
Rangimbili × Salama M-55	87	10	123.4	9	25.2	148	84.6	31.3	3	4.6
Rangimbili × Gigante	85	11	110.9	10	23.6	146	93.4	32.7	3	4.6
Rangimbili × Salama M-19	82	10	120.5	9	23.7	85	72.2	31.7	5	3.1
Zambia × Lunyuki	75	11	126.4	10	24.0	92	70.1	30.0	5	3.1
Zambia × SARO	82	11	128.3	10	25.3	105	71.9	31.3	7	3.2
Zambia × Mwangaza	69	10	118.2	9	23.7	97	87.7	32.7	3	3.5
Zambia × Salama M-55	116	9	115.4	8	24.8	136	78.5	32.3	5	3.9
Zambia × Gigante	80	12	118.4	10	24.6	109	70.2	33.0	5	3.3
Zambia × Salama M-19	70	12	120.5	9	23.6	90	73.3	31.0	5	2.7
Lunyuki × SARO	82	12	115.4	11	23.3	124	77.0	31.8	5	3.6
Lunyuki × Mwangaza	66	10	111.6	9	22.8	124	93.1	34.0	1	3.9



Table 5. Cont.

Genotypes	DFL	NT	PH	NPP	PL	NGP	PFG	TGW	RYMVD	GY
Lunyuki × Salama M-55	77	11	123.3	10	23.1	121	87.7	32.2	3	3.7
Lunyuki × Gigante	77	10	117.2	10	23.5	123	92.4	32.5	3	3.8
Lunyuki × Salama M-19	77	11	112.6	9	21.8	107	91.8	31.8	1	3.9
SARO × Mwangaza	79	12	112.9	10	23.5	93	85.0	30.8	3	3.6
SARO × Salama M-55	68	11	101.4	10	23.3	133	91.6	30.5	1	4.0
SARO × Gigante	89	12	97.4	11	22.5	130	81.5	31.5	5	3.7
SARO × Salama M-19	79	11	111.3	10	23.3	105	84.3	30.2	3	3.4
Mwangaza × Salama M-55	71	10	119.3	9	23.7	100	67.8	33.2	5	3.0
Mwangaza × Gigante	72	11	115.6	10	24.5	103	69.5	33.7	5	3.0
Mwangaza × Salama M-19	67	9	113.7	8	23.7	110	90.6	33.8	1	3.3
Salama M-55 × Gigante	83	11	117.9	9	23.9	144	87.1	33.5	1	4.3
Salama M-55 × Salama M-19	72	11	120.8	10	24.1	133	84.5	32.2	1	3.1
Gigante × Salama M-19	85	10	109.1	9	23.7	145	96.6	33.0	3	4.5
Parents										
Salama M-57	80	9	120.4	9	22.9	111	96.1	31.7	1	4.5
IRAT 256	75	11	108.6	10	22.1	115	95.0	31.3	1	4.2
Rangimbili	95	10	132.7	9	25.2	124	68.5	29.7	7	3.2
Zambia	96	9	122.7	8	25.4	136	75.2	33.3	7	3.5
Lunyuki	74	11	129.2	11	23.6	122	94.1	29.5	1	3.6
SARO	93	11	100.2	10	21.5	115	66.8	30.7	7	3.3
Mwangaza	66	12	102.3	9	22.7	134	97.1	34.8	1	3.6
Salama M-55	87	11	126.3	9	25.3	171	96.9	33.2	1	4.6
Gigante	89	12	97.1	11	23.3	94	64.2	34.5	7	2.9
Salama M-19	105	11	111.6	10	23.2	157	96.1	31.6	1	4.6
Mean	81.5	10.6	115.2	9.5	23.7	124.5	84.1	32.3	3.5	3.7
LSD	5.53	2.81	19.85	2.77	2.58	18.30	10.33	1.83	1.38	0.68
CV (%)	3.41	13.13	8.41	14.30	5.43	7.63	6.08	2.81	19.34	9.24

Note: DFL = days to 50% flowering; NT = number of tillers/plant; PH = plant height; NPP = number of panicle/panicle; PL = panicle length; NGP = number of grains/panicle; PFG = percentage filled grains/panicle; TGW = thousand grain weight; RYMVD = rice yellow mottle virus disease reaction; GY = grain yield; LSD = least significance difference; CV = coefficient of variation. 3.2. Combining Ability Effects of Parents and Their Crosses.

### 3.2. Combining Ability Effects of Parents and Their Crosses

The GCA and SCA variances for RYMVD reaction and assessed agronomic traits were significant ( $p < 0.001$ ) (Table 6). The GCA and SCA effects for most agronomic traits exhibited marked variability across the test sites exhibited by their significant interaction with the site variance. In contrast, the GCA and SCA effects for RYMVD were not affected by site variance.

**Table 6.** Mean squares and significant tests of general and specific combining ability effects for agronomic traits and RYMVD reaction across three sites in Tanzania.

Sources of Variation	df	DFL	NT	PH	NPP	PL	NGP	PFG	TGW	RYMVD	GY
Site	2	1694.03 ***	208.37 ***	863.32 ***	90.87 ***	64.95 ***	3493.17 ***	416.90 ***	3.65 **	0.05 ns	6.61 ***
Rep(site)	3	192.59 ***	66.94 ***	1180.31 ***	29.39 ***	6.25 ***	14.13 ***	13.38 ***	1.99 ns	0.10 ns	0.15ns
GCA	9	1258.56 ***	17.28 ***	1013.74 ***	14.79 ***	24.49 ***	2072.20 ***	1172.52 ***	36.37 ***	57.31 ***	1.80 ***
SCA	45	438.71 ***	4.77 ***	283.51 ***	4.14 **	3.47 **	2253.02 ***	514.30 ***	3.60 ***	14.19 ***	1.62 ***
GCA × site	18	11.24 ns	6.22 ***	65.34 ns	7.14 ***	5.19 ***	399.08 ***	61.65 ***	3.54 ***	0.50 ns	0.54 ***
SCA × site	90	7.37 ns	3.7 *	92.76 ns	3.55 **	2.12 ns	260.04 ***	46.48 ***	1.52 ***	0.30 ns	0.32 ***
Error	162	9.43	2.63	103.57	2.31	1.96	75.2	25.05	0.90	0.44	0.11
Baker's Ratio		0.7	0.8	0.8	0.8	0.9	0.5	0.7	0.9	0.8	0.5

Note: DF = degree of freedom; DFL = Days to 50% flowering; NT = number of tillers/plant; PH = plant height; NPP = number of panicle/panicle; PL = panicle length; NGP = number of grains/panicle; PFG = percentage filled grains/panicle; TGW = thousand grain weight; RYMVD = rice yellow mottle virus disease; GY = grain yield; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ; ns, non-significant.

### 3.3. General Combining Ability Effects of the Parents

The GCA effects for agronomic traits and RYMVD reaction varied widely among the parental lines (Table 7). Lines with negative GCA effects for RYMVD reaction scores and DFL are ideal for developing RYMVD resistant and early flowering cultivars, in that order. Parents Mwangaza, IRAT 256, Lunyuki and Salama M-57 had low negative GCA effects for DFL. SARO 5, IRAT 256, Gigante and Salama M-57 had high positive GCA for NT and NPP. Gigante and SARO 5 recorded with low negative GCA effects for PH. Parents Zambia and Salama M-55 had high positive GCA effects for PL. Further, Salama M-55, Rangimbili and Salama M-57 had large positive GCAs for NGP. Positive GCAs were also observed for the PFG on Salama M-57, Mwangaza, and Lunyuki. The parents IRAT 256, Mwangaza and Gigante had the highest GCA effects for TGW. Negative GCAs for RYMVD reaction were observed for parents Mwangaza, Lunyuki, Salama M-57, Salama M-19, IRAT 256 and Salama M-55. Parental lines Salama M-57, IRAT 256, and Salama M-19 exhibited the highest GCA effects for GY, making them suitable candidates for GY improvement.

**Table 7.** General combining ability effects for yield and yield components and RYMVD reaction of 10 parental genotypes across three sites.

Genotype	DFL	NT	PH	NPP	PL	NGP	PFG	TGW	RYMVD	GY
Salama M-57	−1.92 ***	0.34 **	1.76 *	0.26 *	0.08 ns	4.88 ***	4.60 ***	−0.12 ns	−0.73 ***	0.33 ***
IRAT 256	−4.46 ***	0.60 ***	−0.61 ns	0.74 ***	−1.00 ***	0.14 ns	1.01 **	2.15 **	−0.34 ***	0.25 ***
Rangimbili	2.21 ***	−0.42 ***	2.18 **	−0.39 ***	0.30 ns	5.74 ***	−1.01 **	−0.64 ***	0.27 ***	0.01 ns
Zambia	4.93 ***	−0.12 ns	5.69 ***	−0.24 *	1.03 ***	−2.63 ***	−7.88 ***	−0.05 ***	1.66 ***	−0.34 ***
Lunyuki	−2.71 ***	0.16 ns	2.80 ***	0.26 *	0.29 **	2.17 ***	3.55 ***	−0.57 ***	−0.76 ***	−0.01 ns
SARO 5	2.00 ***	0.81 ***	−4.31 ***	0.60 ***	−0.43 ***	−5.38 ***	−3.56 ***	−0.96 ***	0.86 ***	−0.06 *
Mwangaza	−8.37 ***	−0.75 ***	4.13 ***	−0.58 ***	−0.23 ***	−3.70 ***	4.29 ***	1.39 ***	−1.09 ***	−0.10 ***
Salama M-55	2.55 ***	−0.27 *	3.03 ***	−0.35 **	0.70 ***	11.82 ***	0.16 ns	0.31 ***	−0.23 ***	0.17 ns
Gigante	2.88 ***	0.42 ***	−5.75 ***	0.36 **	0.12 ns	2.49 ***	−3.49 ***	0.91 ***	0.91 ***	0.04 ns
Salama M-19	2.89 ***	−0.10 ns	−0.67 ns	−0.15 ***	−0.26 **	−1.43 ***	2.33 ***	−0.12 ns	−0.56 ***	0.22 **

Note: DF = degree of freedom; DFL = Days to 50% flowering; NT = number of tillers/plant; PH = plant height; NPP = number of panicle/panicle; PL = panicle length; NGP = number of grains/panicle; PFG = percentage filled grains/panicle; TGW = thousand grain weight; RYMVD = rice yellow mottle virus disease; GY = grain yield; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ; ns, non-significant.

### 3.4. Specific Combining Ability Effects of Crosses

The crosses exhibited marked variation based on the SCA effects for the assessed traits (Table 8). The families, including Zambia × Salama M-19, SARO 5 × Salama M-55, Salama M-55 × Salama M-19 and Rangimbili × SARO 5, had low negative SCA effects for DFL in a desirable direction. Salama M-57 × SARO 5, IRAT 256 × Zambia, IRAT 256 × Lunyuki and Zambia × Salama M-19 had large positive SCA effects values for NT. Crosses SARO 5 × Salama M-55, Rangimbili × Mwangaza, IRAT 256 × Rangimbili and SARO 5 × Gigante recorded low SCA effects for PH. The highest positive SCA effects for NPP were obtained from the crosses IRAT 256 × Zambia, IRAT 256 × Lunyuki, Salama M-57 × SARO 5 and Rangimbili × Zambia. Crosses Zambia × SARO 5, Mwangaza × Gigante and Salama M-57 × Rangimbili had high positive SCA effects for PL. The crosses Salama M-57 × IRAT 256, Gigante × Salama M-19, Rangimbili × Gigante, IRAT 256 × Rangimbili and Lunyuki × Mwangaza had large positive SCA effects for NGP. Likewise, SARO 5 × Gigante, Lunyuki × SARO 5, Rangimbili × Salama M-55, Salama M-57 × Rangimbili and Salama M-55 × Gigante had high positive SCA estimates for NGP. Rangimbili × Gigante, Gigante × Salama M-19, SARO 5 × Salama M-55, IRAT 256 × Rangimbili recorded with high positive SCA effects for PFG. Crosses Rangimbili × Mwangaza, Lunyuki × Mwangaza, Lunyuki × SARO 5 and IRAT 256 × Rangimbili had positive SCA effects for TGW. Crosses SARO 5 × Salama M-55, IRAT 256 × Rangimbili, Rangimbili × Gigante, Rangimbili × Mwangaza and Salama M-57 × IRAT 256 had low negative SCA effects for RYMVD. Rangimbili × Gigante, Gigante × Salama M-19, Rangimbili × Salama M-55, Salama M-57 × IRAT 256, IRAT 256 × Rangimbili and Mwangaza × Salama M-19 had high positive SCA effects value for GY. Crosses IRAT 256 × Mwangaza, Lunyuki × Mwangaza, Zambia × Gigante and Zambia × Salama M-55 also had high SCA effects for GY.

**Table 8.** Specific combining ability effects for agronomic traits and RYMVD reaction among 45 crosses assessed in three sites in Tanzania.

Crosses	DFL	NT	PH	NPP	PL	NGP	PFG	TGW	RYMVD	GY
Salama M-57 × IRAT 256	5.17 ***	−0.57 ns	−3.19 ns	−1.04 *	0.39 ns	33.23 ***	4.56 **	0.09 ns	−1.45 ***	0.56 ***
Salama M-57 × Rangimbili	−2.85 **	0.56 ns	1.80 ns	0.35 ns	1.04 *	11.79 ***	6.31 ***	−0.75 *	−0.07 ns	−0.15 ns
Salama M-57 × Zambia	−5.89 ***	0.36 ns	−5.68 ns	0.25 ns	0.11 ns	10.17 **	−9.24 ***	−0.00 ns	0.55 ns	−0.60 ***
Salama M-57 × Lunyuki	2.58 *	−1.38 *	−6.69 ns	−1.08 *	−0.77 ns	−24.08 ***	3.65 *	0.68 ns	−1.04 ***	0.12 ns
Salama M-57 × SARO 5	−4.80 ***	1.94 ***	3.78 ns	1.45 **	0.15 ns	0.08 ns	7.16 ***	0.73 *	−0.65 ***	0.21 ns
Salama M-57 × Mwangaza	1.07 ns	0.38 ns	5.52 ns	0.67 ns	1.00 ns	10.35 **	−1.00 ns	−0.45 ns	0.30 ns	0.07 ns
Salama M-57 × Salama M-55	−3.68 ***	0.91 ns	−1.50 ns	0.83 ns	−0.40 ns	−27.40 ***	−11.37 ***	0.14 ns	2.43 ***	−0.70 ***
Salama M-57 × Gigante	−1.01 ns	−0.14 ns	2.36 ns	−0.10 ns	0.07 ns	−1.95 ns	−6.09 ***	−0.96 **	0.63 *	−0.17 ***
Salama M-57 × Salama M-19	−1.51 ns	−0.75 ns	1.75 ns	−0.21 ns	−0.39 ns	−18.02 ***	−0.74 **	0.73 *	−0.57 *	−0.36 ***
IRAT 256 × Rangimbili	−8.97 ***	−0.27 ns	−9.43 **	0.23 ns	−1.40 **	18.11 ***	11.35 ***	1.11 ***	−2.45 ***	0.47 ***
IRAT 256 × Zambia	−4.01 ***	1.93 ***	7.48 *	1.75 ***	0.24 ns	6.32 *	4.50 **	0.02 ns	−0.84 ***	−0.33 ***
IRAT 256 × Lunyuki	5.96 ***	1.72 **	−5.42 ns	1.56 **	−0.11 ns	−0.32 ns	−9.19 ***	0.03 ns	2.57 ***	−0.12 ns
IRAT 256 × SARO 5	2.40 *	−0.15 ns	20.97 ***	−0.43 ns	0.68 ns	−4.94 ns	−1.58 ns	−0.23 ns	0.96 ***	−0.16 ns
IRAT 256 × Mwangaza	2.28 *	−0.94 ns	−2.04 ns	−0.78 ns	−0.34 ns	7.02 *	6.32 ***	0.58 ns	−1.09 ***	0.42 ***
IRAT 256 × Salama M-55	−7.30 ***	−0.47 ns	0.02 ns	−0.39 ns	0.16 ns	−41.50 ***	−17.04 ***	−0.17 ns	2.05 ***	−0.82 ***
IRAT 256 × Gigante	−7.97 ***	0.42 ns	1.73 ns	0.40 ns	−0.10 ns	6.53 *	−2.21 ns	−0.43 ns	0.24 ns	0.06 ns
IRAT 256 × Salama M-19	1.36 ns	0.08 ns	2.12 ns	0.53 ns	−0.82 ns	−17.54 ***	−15.62 ***	−0.24 ns	3.71 ***	−0.85 ***
Rangimbili × Zambia	0.81 ns	0.64 ns	1.05 ns	1.31 *	−0.03 ns	4.88 ns	−5.12 ***	−0.49 ns	−0.45 ns	0.14 ns
Rangimbili × Lunyuki	−2.22 *	−0.47 ns	−3.36 ns	−0.68 ns	0.35 ns	7.24 *	0.49 ns	−0.14 ns	−0.04 ns	−0.55 ***
Rangimbili × SARO 5	−11.44 ***	0.92 ns	−6.40 ns	0.58 ns	−1.06 *	−17.38 ***	0.81 ns	0.41 ns	0.35 ns	0.05 ns
Rangimbili × Mwangaza	−4.07 ***	−1.23 *	−12.37 ***	−1.00 ns	−2.13 ***	−7.39 *	8.59 ***	1.57 ***	−1.70 ***	−0.06 ns
Rangimbili × Salama M-55	4.18 ***	−0.04 ns	2.24 ns	0.05 ns	0.84 ns	12.09 ***	1.94 ns	−0.35 ns	0.43 ns	0.76 ***
Rangimbili × Gigante	1.02 ns	−0.14 ns	−1.45 ns	0.01 ns	−0.22 ns	19.09 ***	14.45 ***	0.39 ns	−2.37 ***	0.91 ***
Rangimbili × Salama M-19	−1.48 ns	−0.56 ns	3.08 ns	−0.66 ns	0.28 ns	−37.42 ***	−12.69 ***	0.41 ns	1.77 ***	−0.58 ***
Zambia × Lunyuki	−6.26 ***	0.06 ns	1.95 ns	0.31 ns	−0.10 ns	−21.31 ***	−8.99 ***	−1.39 ***	0.57 *	−0.19 ns
Zambia × SARO 5	−3.48 ***	−0.20 ns	10.99 **	0.41 ns	1.34 **	−5.65 ns	−0.07 ns	0.33 ns	0.96 ***	−0.08 ns
Zambia × Mwangaza	−5.78 ***	−0.21 ns	0.67 ns	0.01 ns	−0.51 ns	−15.11 ***	7.88 ***	−0.68 *	−1.09 ***	0.26 *
Zambia × Salama M-55	3.31 ***	−1.49 **	−9.25 *	−1.50 **	−0.34 ns	8.30 **	2.74 ns	0.07 ns	0.05 ns	0.34 ***
Zambia × Gigante	−6.36 ***	0.65 ns	2.51 ns	0.49 ns	0.08 ns	−8.97 ***	−1.90 ns	0.14 ns	−0.43 ns	−0.00 ns
Zambia × Salama M-19	−15.86 ***	1.27 **	−0.48 ns	0.09 ns	−0.60 ns	−24.12 ***	−4.65 **	−0.84 *	0.38 ns	−0.56 ***
Lunyuki × SARO 5	4.15 ***	0.32 ns	1.01 ns	0.37 ns	0.60 ns	13.53 ***	−6.44 ***	1.16 ***	1.38 ***	0.05 ns
Lunyuki × Mwangaza	−0.80 ns	−0.10 ns	−2.97 ns	−0.58 ns	−0.09 ns	17.69 ***	1.74 ns	1.34 ***	−0.68 ***	0.41 ***
Lunyuki × Salama M-55	−1.55 ns	0.58 ns	1.49 ns	0.61 ns	−0.68 ns	−6.45 *	0.49 ns	0.41 ns	0.46 ns	−0.13 ns
Lunyuki × Gigante	−1.39 ns	−0.79 ns	4.24 ns	−0.68 ns	0.25 ns	4.50 ns	8.81 ***	0.15 ns	−0.68 **	0.13 ns
Lunyuki × Salama M-19	−2.22 *	−0.35 ns	−5.42 ns	−0.77 ns	−1.08 *	−7.42 **	2.42 ns	0.51 ns	−0.54 *	0.22 **
SARO 5 × Mwangaza	6.81 ***	0.78 ns	5.39 ns	0.65 ns	0.72 ns	−16.27 ***	0.79 ns	−1.61 ***	−0.29 ns	0.15 ns
SARO 5 × Salama M-55	−15.28 ***	−0.65 ns	−13.22 ***	−0.38 ns	−0.34 ns	7.88 *	11.45 ***	−0.86 **	−3.15 ***	0.28 *
SARO 5 × Gigante	6.06 ***	0.36 ns	−8.54 **	0.01 ns	−0.60 ns	14.87 ***	5.07 **	−0.46 ns	−0.29 ns	0.06 ns
SARO 5 × Salama M-19	−4.94 ***	−0.25 ns	0.33 ns	0.20 ns	0.59 ns	−6.38 *	2.03 ns	−0.77 *	−0.15 ns	−0.14 ns
Mwangaza × Salama M-55	−1.57 ns	0.47 ns	4.43 ns	0.28 ns	−0.15 ns	−25.81 ***	−20.16 ***	−0.55 ns	3.13 ***	−0.69 ***
Mwangaza × Gigante	−0.57 ns	0.52 ns	9.53 *	0.08 ns	1.21 *	−13.47 ***	−14.83 ***	−0.64 ns	2.32 ***	−0.24 ***
Mwangaza × Salama M-19	−5.73 ***	−0.91 ns	2.54 ns	−0.66 ns	0.83 ns	−2.78 ns	0.49 ns	0.55 ns	−0.20	0.46 ***
Salama M-55 × Gigante	−0.82 ns	−0.36 ns	4.70 ns	−0.56 ns	−0.34 ns	11.27 ***	7.01 ***	0.07 ns	−0.54 *	−0.69 ***
Salama M-55 × Salama M-19	−11.98 ***	0.81 ns	2.51 ns	0.55 ns	0.23 ns	4.26 ns	−1.41 ***	−0.23 ns	−0.73 **	−0.69 ***
Gigante × Salama M-19	0.35 ns	−0.79 ns	−0.39 ns	−0.80 ns	0.42 ns	25.75 ***	14.20 ***	0.20 ns	−0.87 ***	0.85 ***

Note: DF = degree of freedom; DFL = Days to 50% flowering; NT = number of tillers/plant; PH = plant height; NPP=number of panicle/panicle; PL = panicle length; NGP = number of grains/panicle; PFG = percentage filled grains/panicle; TGW = 1000 grain weight; RYMVD = rice yellow mottle virus disease reaction; GY = grain yield; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ; ns, non-significant.

## 4. Discussion

### 4.1. Analysis of Variance and Mean Performance of Genotypes

The significant differences for agronomic traits and RYMVD reaction among the parental lines and their progenies (Table 4) indicated the existence of adequate genetic variability for establishing a successful rice-breeding program. The observed variation is underpinned by differences in genetic constitution among the parental lines, which may have evolved from different gene pools, and provided useful segregants among the F2 progenies. The parental lines included landraces, accessions and varieties. The genetic groups have different characteristics, which gave rise to the observed variation in the F2. For instance, landraces are known to be segregating at numerous loci, while varieties are the products of careful and deliberate selection that makes them very different from landraces [33].

Genetic variability for agronomic traits such as DFL, NT, PH, NPP, NGP, TGW and GY has been also reported in previous studies. For instance, Ref. [4] who found significant genotypic variation among rice accessions evaluated in Bangladesh. Ref. [26] who found significant genotypic variation for RYMV disease reaction and agronomic traits in rice in Uganda. Ref. [34] who reported significant variation in yield and its contributing traits in newly developed rice genotypes in China. In the present study, across sites variability

was not detected for the RYMVD reaction among the test genotypes (Table 4). This was attributed to the high disease pressure found at each of the test sites, ensuring even levels of RYMVD infection and disease development. This is contrast to [11,35], who reported that RYMV disease infection and disease development were affected by the test environments. Nine crosses were highly resistant to RYMV disease, with scores of 1.0, indicating that they possessed strong RYMV resistance, possessing the *RYMV1* or *RYMV2* genes, or new resistance gene(s). Refs. [15,18] who reported the *RYMV1* and *RYMV2* genes were responsible for resistance to RYMV disease in most African rice varieties. Families such as Salama M-57 × IRAT 256, Salama M-57 × Lunyuki, Salama M-57 × Salama M-19, IRAT 256 × Rangimbili, IRAT 256 × Mwangaza, Rangimbili × Mwangaza, Lunyuki × Mwangaza and SARO 5 × Salama M-55 were identified as new sources of RYMV resistance genes for breeding.

There were significant genotype × location interaction effects for agronomic traits across three test sites. For instance, crosses Rangimbili × Salama M-55 and Salama M-57 had the higher mean values for GY and NGP, respectively, at the Ilonga site than the Ifakara and Mkindo sites. This was probably because different rainfall and temperature conditions existed between the three locations, the highest rainfall being at the Ilonga site. Rainfall and air temperature affected rice yield responses in the Guinea Savannah Zone [36]. Yield components are quantitative traits and their expressions is affected by the genotype × environment interactions. Rice genotypes were evaluated in Nigeria yielding significant environmental influence on agronomic performance [37]. The significant genotype × environment interaction effects provides opportunities to identify genotypes with specific or broad adaptation. Some of the crosses, such as Salama M-57 × IRAT 256, Rangimbili × Salama M-55, Rangimbili × Gigante, Salama M-55 × Gigante, and Gigante × Salama M-19, performed well at all three sites with a high level of stability. Such genotypes would be ideal for developing cultivars with broader yield stability across sites. There is an opportunity to select transgressive segregants amongst the new families. The cross Salama M-57 × IRAT 256 yielded better than the parents across test environments, indicating superior genetic combinations.

Selection of superior rice genotypes across sites should target multiple traits including NT, PL, NGP, PFG and TGW, aiming to increase adaptability to biotic and abiotic stresses. Crosses such as Salama M-57 × IRAT 256, Salama M-19 × Gigante, Rangimbili × Gigante, Rangimbili × Salama M-55, Salama M-55 × Gigante, IRAT 256 × Rangimbili and IRAT 256 × Mwangaza exhibited desirable grain yield and RMVD resistance, which make them suitable candidates for breeding.

#### 4.2. Combining Ability Effects and Gene Action

Establishment of a successful breeding program depends on the magnitude of the combining ability effects of parents and trait heritability to the offspring. The study found significant GCA and SCA effects for all the traits, indicating that both additive and non-additive gene actions condition the inheritance of RYMV resistance and the tested agronomic traits. This implies that crosses and recurrent selection programs can be used to exploit both additive and non-additive gene action to enhance grain yield in rice. The GCA effects indicate that selection of high performing parents would contribute to the generation of superior crosses for cultivar development. Previous studies reported the significance of both additive and non-additive gene action in the expression of agronomic and yield traits [38–40]. The GCA and SCA effects exhibited variability across sites showing that environmental variance influenced the ability of parents to pass favorable traits to their offspring. The high GCA: SCA ratios calculated for all the traits in this study indicated that additive gene effects were preponderant over non-additive gene effects, and therefore a recurrent selection approach would be effective for trait improvement. Similarly, [41] who found that additive gene action was preponderant for several agronomic traits including DFL, NT, NGP, PFG and GY. Other studies have reported that additive

gene action has a predominant role in the inheritance of agronomic traits and RYMVD resistance in rice [4,26,42,43].

#### 4.3. General Combining Ability Effects of Parents for RYMV Resistance and Agronomic Traits

The selection of parents based on *per se* performance does not always result in producing superior crosses [44]. The combining ability effects of parents are useful in selecting parents that can potentially improve target traits in the offspring. Selection is often based on mean performance in one or several environments but *per se* performance may not always result in the generation of superior crosses. Genotypes such as Mwangaza, IRAT 256 and Lunyuki exhibited negative GCA effects for DFL, indicating that they had the genetic potential to reduce the average number of days to flowering. Early flowering has significant benefits by escaping terminal drought stress if seasonal rains end early. Similarly, Ref. [45] who found negative GCAs for DFL and PH. Gigante, SARO 5 and Mwangaza were selected as good combiners for PH displaying negative GCA effects for shortness. Therefore, significant negative GCA effects for DFL and PH are useful for the development of early dwarf varieties that are preferred in rainfall-constrained environments to escape potential drought stress. Parents SARO 5 and IRAT 256 were identified as good combiners for NT and NPP, expressing higher and positive GCA effects. Also, Ref. [45] who reported significant positive GCA effects for NT and NPP. The parental lines exhibited high and positive GCA effects for PL, NGP, PFG and TGW, suggesting their desirability for improvement of yield-related components because of their greater contribution of these traits to high grain yield. Previous studies reported the significance of using parents with high and positive GCA effects for the improvement of agronomic traits [40,46]. Parental lines with negative scores for RYMVD were considered the best combiners for increasing RYMV resistance. Ref. [47] who reported that negative GCA and SCA effects are desirable for disease resistance. The parents Mwangaza, Lunyuki, Salama M-57, Salama M-19, IRAT 256 and Salama M-55 were selected as good combiners for RYMVD resistance due to their negative GCA effects. These genotypes may possess the *RYMV1* and *RYMV2* genes or novel gene(s) responsible for RYMV resistance. These could be useful as sources of RYMV resistance in developing new cultivars suitable under Tanzanian growing conditions. Ref. [26] who reported significant GCA effects for resistance to RYMV. Salama M-57, IRAT 256 and Salama M-19 had high and positive GCA effects for grain yield, suggesting that the selected parental genotypes were good general combiners for grain yield by contributing favorable alleles. Previous studies also reported good general combiners for yield and yield traits in rice genotypes [41]. These genotypes could be regarded as good sources of additive genes for grain yield improvement [43].

#### 4.4. Specific Combining Ability Effects

A high value of the SCA effect of a cross for a particular trait reflects the contribution of non-additive gene action. This genetic parameter is particularly important for hybrid breeding [22]. Crosses with significant SCA effects in the desired direction would warrant further field evaluation to identify the best segregants. Crosses with high SCA effects are important targets for selection of transgressive segregants [48]. The crosses Zambia × Salama M-19, SARO 5 × Salama M-55, Salama M-55 × Salama M-19 and Rangimbili × SARO 5 were selected for their negative SCA effect for DFL. These are early flowering genotypes that reduce exposure to terminal drought. Salama M-57 × SARO 5, IRAT256 × Zambia, IRAT 256 × Lunyuki and Zambia × Salama M-19 were selected with better NT. Negative SCA effects are required for PH to develop short stature cultivars. Thus, the crosses SARO 5 × Salama M-55, Rangimbili × Mwangaza, IRAT 256 × Rangimbili and SARO 5 × Gigante were selected to develop ideotypes with medium height plants. Crosses IRAT 256 × Zambia, IRAT 256 × Lunyuki and Salama M-57 × SARO 5 were selected for their desirable SCA effects for NPP. Further, crosses Zambia × SARO 5, Mwangaza × Gigante and Salama M-57 × Rangimbili were best specific combiners for PL. Salama M-57 × IRAT 256, Gigante × Salama M-19, Rangimbili × Gigante and IRAT 256 × Rangimbili

had superior NGP values, supported by their high and positive SCA effects. Rangimbili × Gigante, Gigante × Salama M-19, SARO 5 × Salama M-55 and IRAT 256 × Rangimbili were selected with better PFG scores. Crosses Rangimbili × Mwangaza, Lunyuki × SARO 5, and IRAT 256 × Rangimbili were the best specific combiners for TGW. The best crosses expression of RYMV resistance were SARO 5 × Salama M-55, IRAT 245 × Rangimbili, Rangimbili × Gigante, Rangimbili × Mwangaza and Salama M-57 × IRAT 256. These crosses had significantly lower and negative SCA effect for RYMVD possessing *RYMV* resistance genes (Table 7). The hybrids Rangimbili × Gigante, Gigante × Salama M-19, Rangimbili × Salama M-55 and Salama M-57 × IRAT 256 were good specific combiners for grain yield because they expressed high SCA effects for grain yield. In a previous study [40] superior SCA effects were reported for grain yield in rice varieties. Crosses selected with desirable SCA effects for RYMVD, GY, PFG and NGP can be used to generate new rice varieties. The families Rangimbili × Gigante and Salama M-57 × IRAT 256 are recommended for further breeding or production in RYMV endemic agro-ecologies in Tanzania or similar agro-ecologies.

## 5. Conclusions

The present study found marked differences in the performance of the test parents and their families. Significant GCA and SCA effects were detected for the assessed traits among tested crosses and parents, which implies that both additive and non-additive effects influence these traits in the selected parents and crosses, in that order. The predominance of additive gene effects for RYMVD resistance and agronomic traits in the studies breeding populations suggested that rice improvement could best be achieved through gene introgression via the recurrent selection method. Parents Mwangaza, Lunyuki, Salama M-57, Salama M-19, IRAT 256 and Salama M-55 had negative GCA effects are good general combiners for RYMVD resistance and are recommended for future breeding programs and agro-ecologies of Tanzania infested with RYMV disease. Parental lines Salama M-57, IRAT 256, and Salama M-19 are suggested for future breeding program for GY. Based on the SCA effects, among the families, good specific combiners included SARO 5 × Salama M-55, IRAT 245 × Rangimbili, Rangimbili × Gigante and Rangimbili × Mwangaza had negative SCA effects for RYMVD, which could be useful for selection of RYMVD resistant progenies. The crosses Rangimbili × Gigante, Gigante × Salama M-19 and Rangimbili × Salama M-55 are good specific combiners for GY. Overall, the selected promising rice parents and families with significant GCA and SCA effects in the desired direction will be useful genetic resources of RYMV resistance for further breeding or production in RYMV endemic agro-ecologies. Further stability tests and farmers participatory evaluation of the selected genotypes across representative growing environments are required in developing lines with farmer-preferred traits, resistance to RYMV and high yields. This will allow recommendation of new lines adapted to specific or broad rice environments in Tanzania. Further evaluations in multiple test environments ensures selection of RYMV resistant lines with limited disease escape.

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