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Maternal genetic effect of resistance to rice yellow mottle virus disease in rice

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Abstract

Reciprocal selection is a breeding procedure for population improvement and hybrid development. Both female and male parents contribute genes to their offspring, but the influence of female parent often extends beyond simple genetic transmission. Nine parents were crossed in a full diallel and evaluated for maternal genetic effects for resistance to rice yellow mottle virus disease. This study was conducted in a green house at National Crops Resources Research Institute, Uganda. In the F_2 generation evaluated, eight out of the 14 reciprocal crosses showed significant reciprocal effects. The results revealed that cytoplasmic gene effects played a role in modifying resistance to RYMV with enhanced resistance when the resistant parent was used as female. Parental lines Gigante, Nerica 4 and Nerica 6 as the female produced progenies with better resistance than when they were used as the male parent. Segregation patterns generally suggested the presence of one or two genes with modifications beyond Mendelian ratios. This also revealed that the resistance to RYMV was affected by a very complex interaction of cytoplasm and nuclear genes. In the light of these results, care should be taken in consideration while selecting the female parents in hybridization programs.

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Introduction

Among the several factors limiting rice production in Uganda, rice yellow mottle virus (RYMV) is the most important biological constraint (Musiime *et al.*, 2005).The Uganda rice breeding programme has introduced new rice cultivars to broaden their existing germplasm and increasing rice yield through different strategies including improvement of resistance to RYMV (ochola and Tusiime, 2011). To improve resistance through the introgression of resistance into susceptible cultivars requires an understanding of the nature of inheritance and also the gene action controlling resistance (Kornegay *et al.*, 1980) including reciprocal effects. The reciprocal effect for a trait is based on the assumption that the F_2 plants from direct crosses and reciprocal crosses have same mean value for the trait under study. If the difference exists between F_2 and its reciprocal F_2 population, they would be expected to be due to maternal effects and this contributes consequently for the design and interpretation of genetic studies (Mosjidis and Yermanos, 1984).

Maternal effects were recognized as long ago and three classes are known to contribute to the phenotype of its offspring beyond the equal chromosomal expected from each parent. The first is cytoplasmic genetic contributions such as mitochondria and chloroplast genes; the second implies the mother's own nuclear genes and third the mother's environment (Kearsey and Pooni, 1996). Studies have been carried out widely to explore the importance of maternal effects. Duckworth (2009) studied the maternal effects in environments experienced by parental and offspring generations and how those effects enable the continuity of life cycles. His findings contributed to rapid range expansion and the evolution of colonization strategies. Crean and Marshall (2009) reported that under fluctuating environments maternal effects generate variance in offspring phenotypes and suggested that maternal effects on variation in offspring size within individual clutches is a bet-hedging strategy when the environment of offspring development is not predictable from the environment experienced by the maternal generation. Using reciprocal crossing, maternal effects have been reported for several traits in rice, including grain weight and filled-grain ratio (Dayun *et al.*, 2011), grain quality trait (Asfaliza *et al.*, 2012), protein content (Shi CH *et al.*, 1996), milling quality traits (Shi CH and Zhu J, 1995), plant regeneration rates (Hu QR and Croughan T.P, 1989), hybrid vigor (Virmani, S.S, 1990) and crossability (IRRI, 1993). In disease resistance studies, the maternal effects were reported to direct the inheritance of resistance to rice bacterial blight (BLB) in some combinations (Habarurema *et al.*, 2012).

In Uganda, the introduction of new rice varieties by the breeding program has yet yielded minimal results to control rice yellow mottle virus disease because the nature of inheritance and gene action controlling resistance to this disease in the most introduced and local varieties is not known. Past studies on inheritance of resistance to RYMV reported the importance of additive and non-additive gene effects in some selected genotypes to determine resistance to RYMV disease (Mogga *et al.*, 2010; Paul *et al.*, 2003). However, the information on the maternal genetic effect for resistance to RYMV is scanty while should contribute to improve resistance of rice genotypes to RYMV. The present study necessitates to determining the frequency of crosses showing substantial reciprocal effects and evaluates the effect of reciprocal crosses in improving resistance to RYMV in rice cultivars.

Material and methods

Research site and genetic material

The research was conducted at National Crops Resources Research Institute, Namulonge, Uganda. Four interspecific (N-1, N-4, N-6 and Naric 1) and five intraspecific (two locals K5 and K85, and three introduced WAC 116, WAC117 and Gigante) rice genotypes were used in this study.

Development and evaluation of reciprocal crosses

A full diallel mating design was used to generate F1 families. Due to a high level of sterility in rice, causing

failure to obtain some crosses, forty one F_1 direct and reciprocal crosses were generated. Fourteen crosses were reciprocals and were selfed to generate F_2 populations. The diallel-generated F_2 populations and their nine parents were planted in 4 wooden boxes (measuring 7 × 1.5 × 0.6m) filled with pre-sterilised soil in the screen house, using a 25 × 2 alpha lattice design with two replications. The plants were supplied with 60 gm of urea per box 6 days after transplanting, and 40 gm of NPK (17-17-17) 10 days after transplanting. The fertilizers were applied to avoid yellowing due to malnutrition, which can be confused with symptoms of the disease. The plants were inoculated with isolate collected from Iganga (Eastern Uganda), confirmed in this study to be more virulent. The inoculation was achieved two weeks after transplanting using the finger-rub technique. To obtain inoculum, one gram of infected leaf tissue was first crushed in a drop of doubly- distilled water using sterile mortar and pestle until 80% of the leaf tissue material was macerated. The resultant leaf extract was diluted by addition of 10 ml of doubly- distilled water and used to infect plants by soaking the cotton wool in a viral suspension and rub on two upper leaves from leaf base to the tip. The inoculation was repeated one week later to ensure that adequate levels of inoculum pressure were attained. Severity of RYMV disease symptoms was scored using the IRRI standard scale of 1-9 (IRRI, 2002). In this scale 1= no symptoms observed; 3= leaves green but with sparse dots or streaks and less than 5% reduction of height; 5= leaves green or pale green with mottling and 6%-25% reduction of height, flowering slightly delayed; 7 = leaves pale yellow or yellow and 26-75% reduction of height, flowering delayed; and 9 = leaves yellow or orange with more than 75% reduction of height, no flowering or some plants dead. The plants were scored at one, two, three and four weeks after inoculation.

Diallel analysis of reciprocals effects

Reciprocal effects were estimated using Method 1 Model 1 as described by Griffing (1956). This method is expected to provide unbiased estimates of population parameters. The statistical model for this analysis was:

$\mathbf{Y_{ijk} = \mu + g_i + g_j + s_{ij} + r_{ij} + e_{ijk}}$, where μ is the overall mean, g_i is the GCA effect of the i^{th} parent, g_j is the GCA effect of the j^{th} parent, s_{ij} is the SCA effect of the ij^{th} genotype, r_{ij} is the reciprocal effect of the ij^{th} genotype, and e_{ijk} is the environmental effect of the ijk^{th} observation.

The analysis of variance (ANOVA) used for the study of reciprocal effects was adopted from Singh and Chaudary (2004), following Griffing's (1956) method one, model one, as described in Table 1. The reciprocal effects were calculated using the formulas provided by Dabholkar, (1992) as modified by Gibson for missing crosses (2011, unpublished paper):

SEgi =sqrt $((p/ni)*(p-1)/ (r*2p^2))\ \sigma^2_e$;

SE Sji= sqrt $((p^2-2p+2) /(r*2p^2))\ \sigma^2_e$;

SE rij = sqrt $_{1/2}\ \sigma^2_e$

where; SEgi is standard error for GCA effects, SE Sji is standard error for SCA effects and SE rij is standard error for reciprocal effects, g_i is the GCA effect of the i^{th} parent, s_{ij} is the SCA effect of the ij^{th} genotype, r_{ij} is the reciprocal effect of the ij^{th} genotype, ni is number of parental combinations, r is the proportion of reciprocals that are present and σ^2_e is the error mean square.

Estimating the number of genes influencing resistance to RYMV

Segregation ratios of the F_2 populations were computed to estimate the number of genes influencing RYMV resistance and dissect pattern of inheritance. Chi-square goodness-of-fit was used to test the deviation of observed frequencies of a particular class from the expected frequencies:

$$x^2 = \sum_{classes} \left(\frac{N_o - N_e}{N_e}\right)^2$$

Where N_e is the expected count for a class or group, and N_o is the count obtained.

Several phenotypic classes were tested: 3:1 (single dominant gene); 15:1 (duplicate dominant epistasis); 9:7 (duplicate recessive epistasis) (Fehr, 1987; Allard, 1999; Singh and Chaudhary, 2004).

Results

Response of F_2 rice populations to rice yellow mottle virus disease

The results presented in Table 2 showed that some reciprocal crosses were numerically different in resistance to RYMV; Gigante × K5 (mean=5.6) and K5 × Gigante (mean=7.0); Gigante × Nerica 4 (mean=4.8); Nerica 4 × Gigante (mean=6.0); Nerica 4 × Nerica 1(mean=3.9) and Nerica 1 × Nerica 4 (mean=5.4). In general, the average parental mean was better than the average mean of the crosses.

Table 1. Skeletal analysis of variance for reciprocal effects for resistance to RYMV disease in 9 rice genotypes using Griffing's Method 1Model I.

Source	Df	MS	F	Expected MS	Variance components
Genotypes	80				
GCA	8	Mg	Mg/Me	$\sigma^2_e + 2p/(p-1)[\Sigma gi^2]$	$\sigma^2 g = (Mg - Me)/2p$
SCA	36	Ms	Ms/Me	$\sigma^2_e + 2/p(p-1)[\Sigma\Sigma sij^2]$	$\sigma^2 s = (Ms - Me)/2$
Recip	36	Mr	Mr/Me	$\sigma^2_e + 2/p(p-1)[\Sigma\Sigma rij^2]$	$\sigma^2 r = (Mr - Me)/2$
Error	160	Me		σ^2_e	$\sigma^2 e = Me$
Baker's ratio; $X = 2\sigma^2 g/(2\sigma^2 g + \sigma^2 s)$					
NS-CGD = $2\sigma^2 g/(2\sigma^2 g + \sigma^2 s + \sigma^2 e) \approx h^2$					
BS-CGD = $(2\sigma^2 g + \sigma^2 s)/(2\sigma^2 g + \sigma^2 s + \sigma^2 e) \approx H$					

P = Parents, Mg, Ms, Mr and Me = mean squares for GCA, SCA and reciprocals, respectively.

gi, sij, and rij = effects of GCA, SCA and reciprocals, respectively. NS-CGD = narrow-sense coefficient of genetic determination. BS-CGD = broad-sense coefficient of genetic determination.

Reciprocal effect

The results in Table 3 showed that reciprocal effects that are associated with cytoplasmic or maternal inheritance from the female parent were also highly significant ($P \leq 0.001$). A diallel analysis was made in the F_2 generation, eight out of the 14 reciprocal crosses showed significant reciprocal effects. These included K5 × Gigante, Nerica 4 × Gigante, Naric 1 × K5 with significant positive reciprocal effects.The reciprocal effects for the crosses Nerica 4 × K5, Nerica 4 × Nerica 1 and Nerica 6 × Nerica 4 were also highly significant ($P \leq 0.001$) but negative. The crosses Naric 1 × Nerica 1and WAC 117 × Nerica 6 displayed positive and significant ($P \leq 0.01$ an d $P \leq 0.05$, respectively) reciprocal effect (Table 4).

Table 2. Mean severity scores of RYMV for F_2 progenies (above diagonals) and their reciprocals (below diagonals) arising from nine parents (bold diagonals) in a 9x9 diallel.

	Male								
	Gig	K5	K85	N1	N4	N6	Naric 1	WAC 116	WAC117
Female									
Gig	3.3	5.6	6.2	6.3	4.8			4.0	
K5	7.0	6.8	7.1	5.4	6.4		5.0		
K85			7.0	6.5	6.7			6.7	
N1	6.6	5.0	6.8	4.4	5.4	3.5	3.6	4.6	6.3
N4	6.0	5.0	6.6	3.9	4.9	4.3	4.6	4.5	
N6		3.8			3.4	3.8	3.3		4.4
Naric 1	3.3	6.0	5.6	4.4	4.3	3.2	3.2		
WAC 116						4.3		3.0	
WAC 117					5.5	5.2			3.0
SEM=0.22; LSD=0.61; CV%=6.1									
Avg Mean (Parents)=4.38									
Avg Mean (Crosses)=5.15									

Gig= Gigante, N=Nerica. The scores are based on a 1-9 scale: 1-1.5= highly resistant; 1.6-3.5= resistant; 3.6-5.5= moderately resistant; 5.6-7.5= susceptible; 7.6-9= highly susceptible.

Frequency distribution for RYMV severity scores in F_2 populations

The F2 distribution histograms of RYMV resistance for seven crosses are presented in Figure 1- 4. Reciprocal differences were significant in diallel analysis; hence, reciprocal crosses were included to check if they affect the interpretation of the F2 distribution. The crosses and their reciprocals segregated differently. For example, in Gig × K5 (Gigante as female), the majority of plants were more resistant than the mid-parent, while in K5 × Gig (K5 as female), the majority of plants were as susceptible as K5, and distinctly more susceptible than the mid-parent. A similar difference was observed for the cross Nerica 4 × K5 and its reciprocal K5 × Nerica 4. In the latter cross, where Nerica 4 was the female parent, moderately resistant plants dominated, whereas when K5 was the female parent, the majority of plants were highly susceptible. Generally, the mean scores for severity of RYMV in the F_2 populations from according to whether the resistant parent is female shifted away from the mid-parent values. They showed less resistance than the mid-parent value, and tended towards susceptibility. The only exception was the cross Nerica 4 × K5, which displayed better resistance than the mid-parent (Figure 2).

Table 3. Mean squares and variance components from the analysis of variance for RYMV disease scores in rice parental and F2 populations from a 9 x 9 diallel cross.

Source of variation	d.f	m.s	v.c
Genotypes	49	1.64***	
GCA	8	6.51***	0.65
SCA	27	0.83***	0.39
Recip	14	0.41***	0.18
Error	49	0.05	
[a]BR (2δ2g)/(2δ2g + δ2s)			0.77
[b]BSCGD (2δ2g + δ2s)/(2δ2g + δ2s + δ'2e) ≈ H			0.97
[c]NSCGD (2δ2g)/(2δ2g + δ2s + δ'2e) ≈ h2			0.75

*** significant at 0.001 probability level ; [a] BK= Baker's Ratio (Relative importance of GCA and SCA according to Baker (1978); [b] Broad sense coefficient of genetic determination (analogous to H); [C] Narrow sense coefficient of genetic determination (analogous to h^2); δ^2g and δ^2s, are GCA and SCA components respectively; δ^2e is the error component averaged over two replications. The calculation of all MS and Coefficient of Genetic Determination values are based on entry means.

Gigante as the female parent crossed with K85 scored significantly worse than with K5 (6.2 vs 5.6, P< 0.05), a difference clearly shown in the segregation pattern (Figure 3). K85 × WAC 116 was significantly worse than Naric 1 × K85 (6.7 vs 5.6, P<0.001), even though K85 as the male parent typically had a score near 7.0. Again, the segregation was clearly shifted toward susceptibility in Naric 1 × K85 (Figure 4).

Table 4. Reciprocal effects for resistance to Rice yellow mottle virus disease in the F_2 rice populations

	Male								
	Gig	K5	K85	N1	N4	N6	Naric 1	WAC 116	WAC 117
Gig									
K5	0.73***								
K85									
N1	0.13 [ns]	-0.21 [ns]	0.15 [ns]						
N4	0.63***	-0.71***	-0.04 [ns]	-0.75***					
N6					-0.46***				
Naric 1		0.50***		0.41**	0.13 [ns]	-0.08 [ns]			
WAC 116									
WAC 117						0.38*			
S.E recip						0.16			

*, **, *** significant at 0.05, 0.01, 0.001 probability levels respectively; [ns] not significant at 0.05 probability; S.E recip is the standard error for reciprocal effect (S.E-recip=sqrt(Err.MS/2).

Chi-square goodness of fit for RYMV resistance

As shown by Table 5, all crosses presented produced phenotypically recognizable groups (i.e. "Resistant" or "Susceptible"). Therefore a chi-square (χ^2) goodness of fit test was used to compare the observed segregation with hypothesized ratios. The Nerica 4 × K5 cross fit a 3R:1S ratio; whereas with K5 as the female (K5 × Nerica 4) fit a 1R:3S ratio. In Gig × K5 cross, with Gigante as female parent, conformed a 3R:1S ratio. While with K5 as a female parent, conformed 1R:15S ratio. Gigante × K85 fit a 7R:9S ratio while Naric 1 × K85 fit a 9R:7S ratio. K85 × WAC 116 agreeing to 1R:3S ratio.

Table 5.1 Analysis of phenotypic segregation ratios for resistance to susceptible and susceptible to resistance in F_2 progenies of crosses when tested against different genetic models (reciprocals analyzed separately).

		No of	Observed		Expected			P-value
Cross	Type	plants	R	S	R	S	$\chi 2=\Sigma (o-e)2/e)$	(=0.05)
Ratio 3:1								
Gig x K5	R x S	14	10	4	10	3	0.42ns	0.517
K5 x Gig	S X R	35	2	33	9	26	86.15***	1.7E-20
N4 x K5	R x S	36	28	8	27	9	0.15ns	0.699
K5 x N4	S X R	31	9	22	8	23	33.02***	9.1E-09
Naric1 x K85	R x S	36	24	12	27	9	1.33ns	0.249
Ratio 1:3								
K5 x N4	S X R	31	9	22	8	23	0.17ns	0.680
N4 x K5	R x S	36	28	8	9	27	53.48***	2.6E-13
K85 x WAC 116	S X R	33	8	25	8	25	0.01ns	0.920
Gig x K85	R x S	35	12	23	9	26	1.34ns	0.247
Gig x K5	R x S	14	10	4	4	10	20.79***	5.1E-06
Ratio 7:9								
Gig x K85	R x S	35	12	23	15	20	1.05ns	0.306
Naric1 x K85	R x S	36	24	12	16	20	7.2**	0.007
Ratio 9:7								
Naric1 x K85	R x S	36	24	12	20	16	1.08ns	0.299
Gig x K85	R x S	35	12	23	20	15	7.2**	0.007
Ratio 1:15								
K5 x Gig	S X R	35	2	33	2	33	0.02ns	0.888

χ^2= Chi-square test; o= number of plants observed; e= number of plants expected; Gig= Gigante; N4=Nerica 4

R, S; Resistant and susceptible parents respectively; ns Non- significant at P =0.05;

, * Significant at 0.01, 0.001 probability levels respectively.

Discussion

One of the main goals of this experiment was to attempt to find a way the contribution of maternal genetic effect in the selected rice genotypes. While not all of the results were significant, the overall direction of results showed that using the one of the following parents: Gigante, Nerica 4 and Nerica 6 as the female produced progenies with better resistance. The majority reflected the resistance level of the female parent, suggesting that resistance to RYMV is influenced by maternal inheritance. The mean scores for RYMV severity in the F_2 populations from both reciprocal crosses and different crosses involving one parent in common shifted away from the mid-parent values. With additive effects alone, the mean phenotypes of the F_2 generations are expected to be the average of the means of the two parental phenotypes (Adamczyk and Meredith, 2004). Dominance effects cause generations of hybrids to resemble one parental phenotype more than the other. When additional epistatic effects are present, hybrid phenotypes differ unpredictably from the parental phenotypes, deviating from the expectation for additive plus dominance effects (Adamczyk and Meredith, 2004; Schluter *et al.*, 2004). Therefore, the unpredictable distribution in the crosses in this study generally suggested some form of epistasis and/or interactions between nuclear and cytoplasmic genes.

The analysis of segregation ratios revealed that two crosses Gig × K5 and Nerica 4 × K5 conformed to the

3:1 ratio, suggesting the presence of at least one gene that showed dominance (Allard, 1999). Crosses K5 × Nerica 4 and K85 × WAC 116 agreed to a 1:3 ratio, indicating the presence of at least one gene that showed susceptibility. The cross Naric 1 × K85 fit a 9:7phenotypic ratio, suggesting the involvement of two complementary dominant genes (duplicate recessive epistasis). Meanwhile, Gig × K85 conformed to a 7:9 phenotypic ratio indicating the involvement of two complementary recessive genes (duplicate dominant epistasis) (Fehr, 1987; Allard, 1999). The cross, K5 x Gig conformed a 1:15 ratio, indicating the presence of two independent genes with susceptible duplicate epistatic gene action.

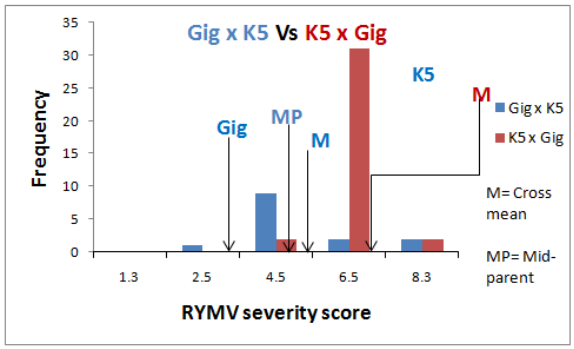

Fig. 1. Distribution frequency of RYMV ratings for Gigante × K5 and its reciprocal cross K5 ×Gigante evaluated at NaCRRI-Namulonge in 2012.

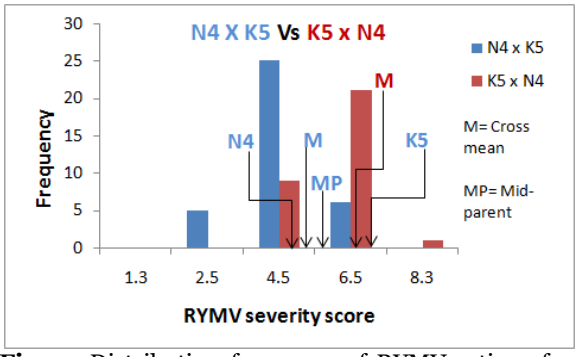

Fig. 2. Distribution frequency of RYMV ratings for Nerica 4 × K5 cross and its reciprocal cross K5 × Nerica 4 evaluated at NaCRRI-Namulonge in 2012.

In past studies, a high resistance gene was reported with at least five alleles; two in Oryza sativa and three in oryza glaberrima (Traoré *et al.*, 2010). Later, Thiemélé *et al.* (2010) reported a second major resistance gene RYMV 2 through an allelism test. A single recessive resistance gene was reported in Gigante (Ndjiondjop *et al.*, 1999). In a recent study by Mogga *et al.* (2010) reported 3R:1S ratio in the Gigante × IR 64 cross and suggested a single dominant gene for resistance in Gigante. Similar results were found in the current study.

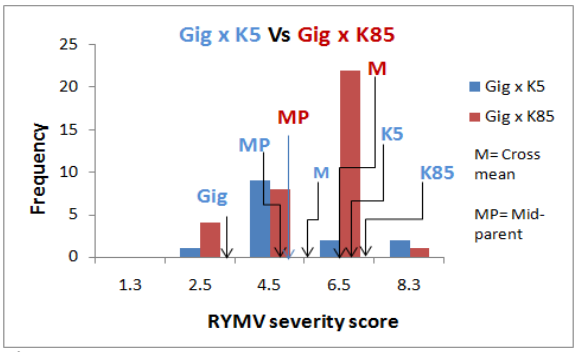

Fig. 3. Distribution frequency of RYMV ratings for two R × S crosses involving Gigante as a parent in common evaluated at NaCRRI-Namulonge in 2012.

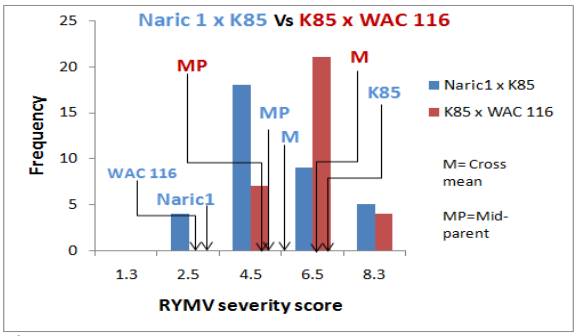

Fig. 4. Distribution frequency of RYMV ratings for R × S crosses involving K85 as a parent in common evaluated at NaCRRI- Namulonge in 2012.

Past studies by Kumwenda (1988) who reported that tolerance to RYMV was primarily an expression of two dominant genes in up-land rice. Mansaray (1994) confirmed the presence of both duplicate and complementary epistasis for RYMV resistance. In another inheritance study by Paul *et al.* (2003), 403R: 1217 S and 313R:826S ratios in crosses Tog 7258 × 7291 and Tog 7258 × 5674 respectively were reported and they believed that the resistance in O. glaberrima was controlled by a minimum of 2-4 recessive gene pairs. These ratios deviated from his expected ratios 67 R: 189S suggesting epistatic effects. In the current study, both the analysis of F2 distribution and the chi-square test suggest that the pattern of segregation was controlled by a very complex interaction of cytoplasmic and nuclear genes,

with the presence of one or two genes with modifications beyond Mendelian ratios. In general, resistance was enhanced when the resistant parent was used as female, suggesting that resistance to RYMV is influenced by maternal inheritance. Therefore, we recommend that care should be taken in selecting the female parents in hybridization programs when breeding for resistance to RYMV.

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