

Maize sperm cells are also able to fuse with female gametes of related species, which will permit investigation of a number of additional fertilization related questions. In vivo studies using maize pollen and female flowers of maize relatives such as *Tripsacum dactyloides*, for example, showed a very high rate of fertilization events. In the apomict *T. dactyloides*, the unreduced egg cell develops autonomously into an embryo without fertilization, but the unreduced central cell requires fertilization by one of the two male gametes. What is the fate of the second sperm cell? Does it often fertilize a synergid, as a high number of twin embryos are observed in *T. dactyloides* (Bantin et al., Sex. Plant Reprod. 14:219-226, 2001), or does it degenerate? Moreover, this line will allow studies of the fate of sperm-deposited protein/RNA after fertilization, as the α -tubulin promoter used to generate this line is switched off after fertilization (Kliwer and Dresselhaus, unpublished). Seeds and promoter sequences of this transgenic line are available from the Jackson lab.

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Selection strategies for tolerance to Mal de Río Cuarto disease in different evaluation environments

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Mal de Río Cuarto (MRC) is the most important viral disease of maize in Argentina. The production of maize for grain is greatly affected by MRC disease, which is caused by a virus of the family *Reoviridae*, genus *Fijivirus*, and transmitted by the planthopper, *Delphacodes kuscheli* Fennah (Homoptera: *Delphacidae*) (Nome et al., 1981; Ormaghi et al., 1993).

Characterizing genotype testing sites and identifying environments with negligible genotype x environment crossover interaction is important for plant breeders wishing to identify superior germplasm and (or) genotypes for a wide range of environments. Genotype x environment (G x E) interactions can be an impediment to genetic progress in maize (*Zea mays* L) breeding for Argentina. Therefore, identifying appropriate environments where the selection should be carried out is an important aspect of a plant breeding program in order to maximize the efficiency of selection. Indirect selection efficiency is related to the heritability of the trait and to the genetic correlation between environments.

The objective of this work was to study the effect of different environments on the relative efficiency (*E*) of direct selection in relation to indirect selection for MRC. The trials were conducted with 111 recombinant inbred lines (RILs) derived from a cross between a susceptible inbred line, Mo17, and a tolerant inbred line, BLS14. The trials were conducted during 2004, 2005 and 2006 at Río Cuarto (64° 20'W, 33° 8'S, 334 masl), and during 2004 and 2005 at Sampacho (64° 42'W; 33° 19'S, 510 masl). The year-location combinations were regarded as different environments (Río Cuarto 2004, Río Cuarto 2005, Río Cuarto 2006, Sampacho 2004 and Sampacho 2005). The experimental design at each environment was a randomized complete block design with two replications.

At the beginning of male flowering, 60–70 days after planting, the RILs were evaluated for several traits related to symptoms of MRC disease, which allowed us to estimate the grade of severity of the disease. A four-grade disease severity scale proposed by Ormaghi et al. (1999) (0: no symptoms; 1: enations; 2: enations and "hokey pole" ears; 3: enations, shortened superior internodes and small ears with few or no kernels) was used for each plant and data averaged for a plot.

Indirect selection efficiency is derived from the selection response model using the formula for the ratio of correlation to direct response:

$$E = r_g h_Y / h_X$$

where r_g is the genetic correlation for the trait measured in the environment of selection Y and in the environment of interest X, and h_Y and h_X are square roots of the broad sense heritability of the grade of severity of the disease in Y and X environments, respectively. The efficiency model *E* is based on the assumption that selection intensities *i* of direct and indirect selection are the same. The equation of efficiency of indirect selection states that if $E > 1$, indirect selection is more efficient than direct selection, and if $E < 1$, direct selection is more efficient.

The genetic correlation between the environment of selection Y and in the environment of interest X to the grade of severity of the MRC, can be estimated from the equation:

$$r_g = \sigma_g^{(XY)} / \sqrt{(\sigma_g^2(X) \sigma_g^2(Y))}$$

where $\sigma_g^{(XY)}$ is the genetic covariance between X and Y, and $\sigma_g^2(X)$ and $\sigma_g^2(Y)$ is the genotypic variance component of the X and Y, respectively.

Heritability estimates of the grade of severity of the disease evaluated in each environment were estimated as:

$$h^2 = (\sigma_g^2) / [(\sigma_g^2) + (\sigma_e^2/r)]$$

where *r* denotes the number of replicates and the subscript g indicates variance components associated with genotypes and e, experimental error.

Table 1. Genetic correlation (r_g) for the grade of severity of MRC between environment of selection and environment of interest, and predicted efficiency (*E*) of indirect selection relative to direct selection.

Environment of selection ^a	Environment of interest	r_g	S.E. ^b	<i>E</i>
R4	S4	0.30	0.25	0.24
	R5	0.17	0.21	0.15
	S5	0.03	0.19	0.03
S4	R6	-0.03	0.23	-0.03
	R4	0.30	0.25	0.37
	R5	-0.21	0.16	-0.24
R5	S5	0.24	0.20	0.28
	R6	0.44	0.27	0.53
	R4	0.17	0.21	0.19
S5	S4	-0.21	0.16	-0.19
	S5	-0.02	0.15	-0.02
	R6	0.01	0.19	0.01
R6	R4	0.03	0.19	0.03
	S4	0.24	0.20	0.21
	R5	-0.02	0.15	-0.02
S5	R6	0.09	0.18	0.10
	R4	-0.03	0.23	-0.03
	S4	0.44	0.27	0.36
R6	R5	0.01	0.19	0.01
	S5	0.09	0.18	0.09

^aR4 = Río Cuarto 2004, S4 = Sampacho 2004, R5 = Río Cuarto 2005, S5 = Sampacho 2005 and R6 = Río Cuarto 2006

^bStandard errors of the genetic correlations between environments

Due to the low genetic correlations estimated, genetic mechanisms involved in determining the grade of severity of the disease MRC may not be the same for different environments (Table 1). This complicates selection of genotypes from these RILs.

However, estimated h^2 showed high values (Table 2), which indicates that the grade of the disease is controlled by a high proportion of genes with additive effect and some independence with the medium. Since the E had values <1 (Table 1), the direct selection strategy in each environment represents the best alternative and the indirect selection strategy may not have good prospects.

Table 2. Heritability (h^2) in five environments of evaluation for the grade of severity of MRC in 111 RILs of maize.

Parameter	Environment ^a				
	R4	S4	R5	S5	R6
Heritability ^b	0.70	0.45	0.56	0.60	0.66

^aR4 = Río Cuarto 2004, S4 = Sampacho 2004, R5 = Río Cuarto 2005, S5 = Sampacho 2005 and R6 = Río Cuarto 2006

^b $h^2 = (\sigma^2_g) / [(\sigma^2_g) + (\sigma^2_e/r)]$

Diallel analysis of Mal de Río Cuarto tolerance and yield components in maize

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Mal de Río Cuarto (MRC) is a devastating disease of maize in Argentina. The disease reduces grain yield (GY) and causes several symptoms, such as enations, reduced root systems, shortened superior internodes, flattened stems, leaves with small leaf areas, atrophic tassels, "hokey pole" ears and small ears with few or no kernels. The identification of heterotic patterns plays an important role in the selection of germplasm to develop hybrids. Analysis of diallel crosses provides preliminary data about heterotic relationships (Hallauer and Miranda Filho, Quantitative Genetics in Maize Breeding. Iowa State Univ. Press, Ames, IA, 1981; Hallauer and Miranda, Quantitative Genetics in Maize Breeding, 2nd Edition. Iowa State Univ. Press, Ames, IA, 1988). Our objective for this study was to estimate general (GCA) and specific combining ability (SCA) (Sprague and Tatum, J. Am. Soc. Agron. 34:923-932, 1942) in twelve lines of maize evaluated through diallel crosses, without reciprocals, for tolerance to MRC, grain yield and its components. The maize lines were BLS14, BLS1, BLS16, BLS61, BLS76, BLS91, BLS96, BLS101, BLS104, LP109, LP521 and LP125R.

The lines and their 66 crosses were planted on 21 November 2007 through a complete randomized block experimental design with two replications at Río Cuarto, Argentina (33°8'S 64°20'W). All plants were artificially infested with viruliferous insect vectors of MRC (*Delphacodes kuscheli* Fennah). Data were collected for the grade of severity of MRC disease (GS), number of kernel/m² (KN), unit weight of kernels (WK), and grain yield, standardized to 14.5% moisture (GY). Data were subjected to an ANOVA analysis using Griffing's method 2 model II (Griffing, Aust. J. Biol. Sci. 9:463-493, 1956), by means of a diallel computer program (Magari and Kang, J. Hered. 85:336, 1994). Significance was estimated with t tests. The relative importance of general and specific combining ability on progeny performance was estimated as the ratio: $2\sigma^2_{ACG} / (2\sigma^2_{ACG} + \sigma^2_{ACE})$ (Baker, Crop Sci. 18:533-536, 1978) where σ^2_{ACG} and σ^2_{ACE} are the variance components for GCA and SCA. A value of 1 indicates that all genetic variance is additive. Analysis

of variance revealed that mean square values for GCA were highly significant ($p \leq 0.01$) for the traits studied, with the exception of grain yield. The variations due to SCA were highly significant ($p \leq 0.01$) for all traits studied. The ratios $2\sigma^2_{ACG} / (2\sigma^2_{ACG} + \sigma^2_{ACE})$ were 0.15, 0.08, 0.19 and 0 for GS, NK, WK and GY, respectively, indicating that non-additive effects predominated in the expression of these traits. Marino and Teyssandier (Congreso Anual de la Sociedad Argentina de Genética, Buenos Aires, 1982) reported the same results for tolerance to MRC, and Bhatnagar et al. (Crop Sci. 44:1997-2005, 2004) and Srdic et al. (Maydica 52:261-264, 2007), indicated that SCA effects were highly significant for GY. In our scoring, negative effects on combining ability are associated with tolerance to disease and positive effects with susceptibility. For GS, the highest GCA values were observed for line BLS1 (-0.39), followed by BLS16 (-0.2), and for WK the highest values were observed for line LP109 (0.03), followed by BLS104 (0.02) (Table 1). These parental lines presented highly significant GCA effects

Table 1. General combining ability (GCA) effects of each parental line for different characters.

Line	GS		NK		WK (g)	
BLS61	0.02	ns	57.85	ns	-0.01	ns
BLS91	0.07	ns	-69.54	ns	0.01	ns
BLS101	0.00	ns	-181.68	ns	0.01	ns
BLS76	-0.09	ns	32.95	ns	-0.01	ns
BLS96	-0.08	ns	-36.04	ns	-0.00	ns
BLS104	0.37	**	-74.64	ns	0.02	**
BLS16	-0.2	**	103.85	ns	-0.03	**
BLS14	0.04	ns	195.38	ns	-0.01	ns
BLS1	-0.39	**	119.1	ns	-0.01	ns
LP109	0.08	ns	-29.68	ns	0.03	**
LP521	0.09	ns	-16.93	ns	0.00	ns
LP125R	0.07	ns	-100.61	ns	0.00	ns

* Significant at 5% and ** significant at 1% probability level. GS=grade of severity of MRC disease, NK=number of kernel/m² and WK=unit weight of kernel.

for GS and WK, while the effects for NK were not significant. The highest SCA effects were observed for hybrids BLS101 x BLS104, LP109 x LP125R, BLS91 x BLS16 and LP109 x LP125R for GS, NK, WK and GY, respectively. The hybrid that manifested the best behavior for GS also presented good performance for the other traits, in contrast to the hybrid that manifested the greatest SCA for GY, which displayed negative effects for GS. We conclude that the lines with high general combining ability would be a valuable source of germplasm to develop hybrids that combine tolerance to MRC and good yield.

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Discriminant analysis to identify molecular markers associated with Mal de Río Cuarto (MRC) resistance

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In Argentina, the production of maize for grain is highly affected by MRC-disease, which is caused by a virus of the family *Reoviridae*, genus *Fijivirus* and transmitted by the planthopper