Colegio de Postgraduados

Genetic effects of native maize (*Zea mays* L.) from Tamaulipas: precocity and asynchrony

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ABSTRACT

Objective: To evaluate the genetic effects governing the expression of variation in the earliness of native maize germplasm from Tamaulipas.

Design/methodology/approach: Three inbred lines (S3) and three populations of native Tamaulipas maize, along with their direct and reciprocal crosses, were evaluated during the 2020-2021 fall-winter cycle across three planting dates in Güémez, Tamaulipas. The variables analyzed included male flowering (MF), female flowering (FF), and anthesis-silking interval (ASI). Variance and diallel analyses (Griffing's Method I) were conducted to estimate general combining ability (GCA), specific combining ability (SCA), reciprocal effects (RE), maternal effects (ME), and non-maternal effects (NME).

Results: Among the crosses, those involving VHA as the female parent were notable due to the negative GCA effects for MF and FF, coupled with significant RE arising from marked and negative ME, thereby enhancing earliness in their hybrids. The L6×VHA and VHA×Morado crosses exhibited significant and negative SCA effects, indicating these combinations as heterotic patterns favoring greater earliness. Limitations/implications: The genetic effects identified in this study were contingent upon the genetic variability present in the evaluated genotypes.

Findings/conclusions: The expression of variation in MF and FF within this germplasm was influenced by additive, non-additive, and reciprocal effects, with the latter largely attributable to maternal contributions.

Keywords: *Zea mays* L., Griffing, Reciprocal effects, Maternal effects.

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INTRODUCTION

Maize is the most extensively cultivated crop in Mexico, ranking first in terms of cultivated area, with an annual production exceeding 27 million tons and an average grain yield of 4.28 t ha^{-1} across nearly 7 million hectares. In Tamaulipas alone, over 114,000 hectares were cultivated in 2023 36% under irrigated conditions, primarily

in the north, and the remaining 64% under rainfed conditions, predominantly in the central and southern regions of the state (SIAP, 2023). In these latter environments, crop development depends heavily on a highly variable and often insufficient rainfall regime, coupled with extreme temperatures frequently surpassing 35 °C. Such climatic constraints significantly affect crop performance, limiting the phenotypic and genotypic expression of many genotypes, thereby reducing final yield (Guamán *et al.*, 2020). In Tamaulipas, there is a limited availability of improved cultivars adapted to the agroecological conditions of the rainfed production systems in the central and southern regions. Moreover, several introduced commercial hybrids exhibit poor adaptability, as they were bred under markedly different environmental conditions (Godina *et al.*, 2020). However, native germplasm from this region possesses high yield potential and considerable genetic variability (González-Martínez *et al.*, 2020). Its incorporation as a base in breeding programs represents a viable alternative for developing genotypes better suited to restrictive conditions, with grain yields equal to or exceeding those of commercial hybrids (Toribio-Solís *et al.*, 2022), thereby contributing to the fulfillment of local, regional, and national grain demands. Given the thermal dynamics in the central and southern zones of the state, maize is cultivated during two annual growing cycles: the early fall-winter cycle (January to July) and the late spring-summer cycle (July to December) (Reyes & Cantú, 2004). Both cycles are characterized by average maximum temperatures reaching 38 °C (Castro-Nava *et al.*, 2011), which induces morphological and physiological alterations in the crop. In some cases, these conditions trigger early physiological maturity (Guamán *et al.*, 2020), making it essential to use short-cycle genotypes. Developing such genotypes requires access to diverse genetic sources such as native populations and a thorough understanding of their genetic variance components to optimize their use (Cervantes-Adame *et al.*, 2020). Accordingly, it is crucial to identify the genetic mechanisms governing the expression of key agronomic traits, such as earliness, stress tolerance, and grain and/or forage yield (De la Cruz Díaz-Juárez *et al.*, 2023; Quiroga-Cardona, 2020). This knowledge enables the identification of superior specific crosses which, in combination with the favorable performance of their parents, facilitates the development of agronomically superior genotypes with high yield potential (Mongesse *et al.*, 2020; Guamán *et al.*, 2020). To estimate the gene action underlying trait expression, genetic or mating designs have been widely used particularly Griffing's diallel designs (1956), which involve all possible single crosses among a group of n parents. These designs allow for the estimation of genetic variance components, facilitating the enhancement or fixation of favorable gene frequencies (Quiroga-Cardona, 2020). Diallel crossing schemes yield valuable information for selecting parental lines based on the concepts of Sprague and Tatum (1942). General combining ability (GCA) reflects the average performance of a parent across hybrid combinations and indicates additive gene action, which can be exploited through selection. Specific combining ability (SCA), on the other hand, reflects non-additive gene action, harnessed through hybridization (Mongesse *et al.*, 2020). Therefore, the aim of this study was to evaluate the genetic effects controlling the expression of variation in the earliness of native maize germplasm from Tamaulipas.

MATERIALS AND METHODS

The experiment was conducted during the 2020-2021 fall-winter and 2021 spring-summer growing cycles at the "Posta Zootécnica Ing. Herminio García González" Experimental Station of the Universidad Autónoma de Tamaulipas, located in the municipality of Güémez, Tamaulipas (23° 56' 26" N, 99° 05' 59" W; 193 masl). The region has a subtropical, semi-arid, and extremely warm climate, with an average annual temperature of 23.8 °C and precipitation of 721.1 mm. Three S3 inbred lines derived from Tula (L1 and L6) and Padilla (L3) were evaluated, along with three maize populations derived from native germplasm: Padilla and San Carlos (VHA), Tula, Llera, and Ocampo (VCII), and Antiguo Morelos (Morado), all from Tamaulipas. These parents, along with their direct and reciprocal crosses, comprised a total of 36 genotypes.

The variables evaluated were male flowering (MF), female flowering (FF), and floral asynchrony (ASI). MF and FF were measured as the number of days from planting until 50% of the plants shed pollen or exhibited exposed silks, respectively. ASI was calculated as the difference between MF and FF.

To control fall armyworm (*Spodoptera frugiperda*), three applications of Denim® 19 (emamectin benzoate) were performed at a rate of 200 mL ha^{-1} per application. The first was applied at full expansion of the fifth leaf, the second at the ninth leaf, and the third at the flag leaf stage. Sowing was performed manually on three planting dates (March 1, March 30, and October 14, 2021), at a population density of 50,000 plants ha^{-1} under irrigated conditions (gravity-fed irrigation: one 20 cm pre-planting irrigation and three 15 cm supplementary irrigations). Fertilization was applied at a rate of 120N-60P-00K, with 50% of the nitrogen and all of the phosphorus applied at planting, and the remaining nitrogen applied during the first hoeing, 32 days after planting.

Weed control was performed manually at the full expansion of the eighth and fourteenth leaves. The experimental unit consisted of a single 5-meter row, with 0.80 meters between rows. The experiment followed a randomized complete block design with a split-plot arrangement: planting dates as the main plots and genotypes as subplots, with three replications. Based on genotype earliness, an analysis of variance and a 6×6 diallel analysis were performed using Griffing's Method I under Model I (fixed effects) to estimate general combining ability (GCA), specific combining ability (SCA), reciprocal effects (RE), maternal effects (ME), and non-maternal effects (NME). The analysis was conducted using the DIALLEL-SAS05 program developed by Zhang and Kang (1997) and Zhang *et al.* (2005).

RESULTS AND DISCUSSION

Significant differences ($P \leq 0.05$) were observed among environments and among crosses for male flowering, female flowering, and floral asynchrony (Table 1). Similarly, the interaction between crosses and environment showed significant effects ($P \leq 0.05$) for these traits, indicating that both the crosses and parental lines exhibited differential responses across the evaluated planting dates (Table 1).

The diallel analysis for male flowering (MF), female flowering (FF), and anthesis-silking interval (ASI) revealed statistically significant effects ($P \leq 0.05$) for general combining

Table 1. Statistical significance of genetic effects in six maize parents and their hybrids.

Source	**MF (days)**		**FF (days)**		**ASI (days)**	
	SS	**Pr>F**	**SC**	**Pr>F**	**SS**	**Pr>F**
Crosses	1252.8	*	904.2	*	282.8	*
Environment	11257.9	*	18972.8	*	1175.3	*
C×E	559.2	*	493.0	*	317.8	*
GCA	566.6	*	238.4	*	81.6	*
GCA×E	12.6		23.2		1.8	
SCA	221.2	*	229.1	*	115.1	*
SCA×E	40.3		56.2		3.8	
RE	465.1	*	436.7	*	86.1	*
RE×E	63.9		64.3		3.3	
ME	418.3	*	302.2	*	26.7	
ME×E	22.5		23.0	*	0.8	
NME	46.7		134.5	*	59.4	*
NME×E	41.4		41.3		2.4	

MF: Male flowering; FF: Female flowering; ASI: Anthesis-silking interval; SS: Sum of squares; Pr>F: Statistical significance ($P \leq 0.05$); C×E: Genotype×environment interaction; GCA: General combining ability; GCA×E: General combining ability×environment interaction; SCA: Specific combining ability; SCA×E: Specific combining ability×environment interaction; RE: Reciprocal effects; RE×E: Reciprocal effects×environment interaction; ME: Maternal effects; ME×E: Maternal effects×environment interaction; NME: Non-maternal effects; NME×E: Non-maternal effects×environment interaction.

ability (GCA), specific combining ability (SCA), and reciprocal effects (RE) (Table 1). This indicates that the genetic variability expressed in these traits is associated with additive, non-additive, and reciprocal gene action (De la Cruz Díaz *et al.*, 2023; Hernández & De León, 2021). Therefore, this germplasm shows potential for use as a genetic base in breeding programs aimed at improving earliness. The partitioning of the sum of squares for the crosses indicated that variation in MF was primarily explained by GCA (45.2%), followed by RE (37.1%) and SCA (17.7%) (Table 1). This suggests that MF variation is mainly governed by additive genetic effects. In contrast, FF variation was more strongly influenced by RE (48.3%), with lower contributions from GCA (26.4%) and SCA (25.3%). These findings support informed decisions regarding the use of these populations as male or female parents (Hernández & De León, 2021).

Regarding ASI, its expression was predominantly controlled by non-additive (dominance) effects, with SCA accounting for 40.7% of the variance, followed by RE (30.4%) and GCA (28.9%). This highlights the importance of parental specificity within crosses, due to the complementary interaction between alleles from each parent (dominance effect) and interactions among alleles at different loci involved in the transmission of the trait (epistatic effect) (Maioli *et al.*, 2021). Each trait's variability was influenced by different types of genetic effects, which can largely be attributed to the high genetic diversity both within and among the evaluated populations (Kamara *et al.*, 2021). The RE observed for MF were attributed to significant maternal effects (ME) (Table 1), whereas for FF, both maternal (ME) and non-maternal (NME) effects contributed. Conversely, RE for ASI were primarily due to significant NME ($P \leq 0.05$). As noted by De la Cruz Díaz-Juárez *et al.* (2023), maternal effects are associated with extra-nuclear DNA inherited from the female parent, beyond the expected chromosomal contribution from both parents (Roach & Wulff, 1987), underscoring the critical role of the female parent in hybrid performance. Non-maternal effects, on the other hand, result from the interaction between nuclear and cytoplasmic DNA (Wu & Matherson, 2001).

Additionally, for FF, a significant interaction between ME and environment (ME×E) was detected ($P \leq 0.05$), indicating that at least one parent expressed variable maternal effects across different environments (El-Shahed *et al.*, 2021). Consequently, this genetic effect was analyzed separately by planting date to determine the specific environments where maternal effects were present for FF. On average, parental lines exhibited 69.0 days to MF, 73.2 days to FF, and an ASI of 4.1 days, compared to 68.0, 71.7, and 3.6 days, respectively, for the hybrids. This similarity in means is largely due to the broad variation observed among the hybrids, which ranged from 65.2 to 71.3 days for MF, 68.3 to 76.3 days for FF, and 2.2 to 5.6 days for ASI (Table 2).

Five hybrids VHA×L6, VHA×L3, VHA×L1, VHA×VCII, and VHA×MOR stood out for male flowering (MF), and six VHA×L6, VHA×L3, VHA×L1, VHA×MOR, L3×VCII, and VCII×L6 for female flowering (FF), with mean values lower than the overall mean minus one standard deviation (Table 2), indicating enhanced earliness (Chukwuma *et al.*, 2020), a desirable trait under restrictive subtropical conditions such as those in Mexico. Among these hybrids, those with VHA as the female parent were especially notable, exhibiting mean values below 66 and 71 days for MF and FF, respectively (Table 2). This performance is attributed to significant ($P \leq 0.05$) and negative general combining ability (GCA) effects for MF and FF in the VHA population (Table 3).

Likewise, significant reciprocal effects ($P \leq 0.05$) were observed in the crosses involving VHA, attributable to significant ($P \leq 0.05$) and negative maternal effects (Table 4). These effects contributed to the enhanced earliness observed in the hybrids where VHA was used exclusively as the female parent (Table 4).

The hybrids VHA×L6 and VHA×Morado stood out individually, showing significant ($P \leq 0.05$) and negative specific combining ability (SCA) effects (Table 3), along with mean values of 65.2 and 65.9 days to male flowering (MF), respectively both below the mean minus one standard deviation (Table 2). These findings suggest that these crosses represent heterotic patterns for enhanced earliness (Coelho *et al.*, 2020; Maioli *et al.*, 2021). Overall, the expression of variation in MF and female flowering (FF) within this germplasm was governed by additive, non-additive, and reciprocal effects the latter resulting from significant ($P \leq 0.05$) maternal influences. This suggests that these populations have strong potential as base germplasm for breeding programs targeting earliness (De la Cruz Díaz-Juárez *et al.*, 2023). Such variability can first be exploited through selection processes (López-López *et al.*, 2021), followed by reciprocal recurrent selection (Comstock *et al.*, 1949) and hybridization (Kamara *et al.*, 2021). Additionally, consideration should be given to the parental role (female *vs.* male) when capitalizing on non-additive effects (Hernández & De León, 2021; Mongesse *et al.*, 2020).

Table 2. Comparison of flowering means in the 6×6 diallelic crosses of native maize from Tamaulipas evaluated in Güémez, Tamaulipas.

Genotype	MF (days)	FF (days)	ASI (days)
VHA×L6	65.2 *	68.3 *	3.1
VHA×L3	65.2 *	69.9 *	4.7 *[1]
VHA×L1	65.6 *	70.0 *	4.4
VHA×VCII	65.7 *	71.0	5.3 *[1]
VHA×MOR	65.9 *	69.7 *	3.8
L3×VCII	66.6	69.7 *	3.1
L1×L3	66.7	70.8	4.1
L6	66.8	69.8 *	3.0
L6×L3	66.8	71.1	4.3
VCII×L6	67.2	69.6 *	2.3 *
L1×L6	67.3	70.8	3.5
L6×L1	67.3	70.3	3.0
L3×L1	67.4	71.4	4.0
VCII×L3	67.4	72.7	5.2 *[1]
L6×VHA	67.8	72.1	4.3
VCII×L1	67.9	71.6	3.7
L3×VHA	68.0	71.7	3.7
MOR×L3	68.2	71.0	2.8 *
L1×VCII	68.3	71.6	3.3
L3×MOR	68.4	70.6	2.2 *
MOR×L6	68.4	71.8	3.3
VHA	68.4	71.9	3.4
L1×MOR	68.5	71.3	2.8 *
VCII×VHA	68.6	72.6	4.0
L1	68.7	72.6	3.9
L3×L6	68.8	73.3	4.5
MOR×L1	69.3	72.1	2.8 *
L6×VCII	69.7	72.9	3.3
L1×VHA	69.8	73.6	3.8
VCII×MOR	69.8	72.3	2.6 *
VCII	70.3 *[1]	75.9	5.6 *[1]
MOR	70.6 *[1]	72.7 *[1]	2.1 *
MOR×VHA	70.8 *[1]	74.8 *[1]	4.0
L3	70.9 *[1]	75.7	4.8
MOR×VCII	71.1 *[1]	74.5 *[1]	3.4
L6×MOR	71.2 *[1]	76.3	5.2 *[1]
μ	68.2	71.9	3.7
σ	1.7	1.9	0.9

MF: Male flowering; FF: Female flowering; ASI: Anthesis-silking interval; μ: Overall mean; σ: Standard deviation; $\leq\mu-\sigma$; $\leq\mu-2\sigma$; $\geq\mu+\sigma$; $\geq\mu+2\sigma$.

Table 3. Estimates and significance of general combining ability (GCA; diagonal), specific combining ability (SCA; above the diagonal), and reciprocal effects (RE; below the diagonal) for MF, FF, and ASI.

Parents	L1	L3	L6	VHA	VCII	Morado
FM (days)						
L1	−0.0062	−1.1512	−0.1327	0.1728	0.0895	0.6451
L3	0.5556	−0.7006 *	−0.9383 *	0.5895	−0.6049	−0.2160
L6	−0.1667	0.6667	−0.5525 *	−0.7253 *	0.0802	−0.1975
VHA	2.2222 *	2.2778 *	1.1111 *	−0.8025 *	−0.6142	−1.0586 *
VCII	0.7222	−0.2222	0.8333	−1.4444 *	0.1142	0.9136 *
Morado	−0.3333	−0.8889	−0.1667	−2.6111 *	−1.6111 *	1.9475 *
FM (days)						
L1	0.0926	−0.7778 *	−0.4815	−0.0556	−0.4630	0.4074
L3	0.6667	−0.3148 *	−0.4074	0.6296	−0.4444	−1.0741 *
L6	0.1667	0.9444 *	−0.5556 *	−0.7963 *	−0.9259 *	1.1667 *
VHA	1.5000 *	1.8889 *	1.7778 *	−0.5370 *	0.2222	−0.9630 *
VCII	0.1667	−1.3333 *	1.0556 *	−0.7778	0.0926	0.9074 *
Morado	−0.3889	−1.3889 *	0.7222	−2.0556 *	−1.8889 *	1.2222 *
ASI (days)						
L1	0.0988	0.3735	−0.3488	−0.2284	−0.5525 *	−0.2377
L3	0.1111	0.3858 *	0.5309	0.0401	0.1605	−0.8580 *
L6	0.3333	0.2778	−0.0031	−0.0710	−1.0062 *	1.3642 *
VHA	−0.7222 *	−0.3889	0.6667	0.2654	0.8364 *	0.0957
VCII	−0.5556	−1.1111 *	0.2222	0.6667	−0.0216	−0.0062
Morado	−0.0556	−0.5000	0.8889 *	0.5556	−0.2778	−0.7253 *

*GCA: General combining ability; SCA: Specific combining ability; RE: Reciprocal effects; MF: Male flowering; FF: Female flowering; ASI: Anthesis-silking interval; Statistically significant (P≤0.05).

Table 4. Estimates and significance of maternal effects for male and female flowering of parental lines across evaluated environments during the 2021 fall-winter and spring-summer cycles.

Parents	MF (days)	FF (days)		
		FF (days) - March 1	FF - March 30	FF - October 14
L1	0.6000 *	0.2778	0.6667 *	0.1111
L3	0.2556	0.1944	−0.3889	−0.0833
L6	0.2556	−0.0278	0.6111 *	0.6389
VHA	−1.9333 *	−1.5833 *	−2.0000 *	−0.4167
VCII	−0.3000	−0.5833 *	−0.2778	0.3611
Morado	1.1222 *	1.7222 *	1.3889 *	−0.6111

*MF: Male flowering; FF: Female flowering; Statistically significant (P≤0.05).

Conversely, the VCII, L3, and Morado parental lines exhibited higher MF values. Three parents and three hybrids had MF and FF means exceeding the overall mean plus one standard deviation (Table 2), indicating lower earliness relative to the germplasm average. For FF, the first two parents consistently showed delayed flowering ($\geq\mu+\sigma$).

Similarly, the crosses Morado×VHA, Morado×VCII, and L6×Morado had MF and FF values above $\mu+\sigma$ (Table 2), attributable to positive and significant GCA effects from the Morado population, positive and significant SCA effects in Morado×VCII, and significant reciprocal effects in Morado×VHA (Table 3), which were the result of positive and significant maternal effects from Morado (Table 4). Moreover, Morado×VCII and L6×Morado also exhibited significant non-maternal effects for days to FF (Table 5), indicating that variation in this trait is partially influenced by interactions between nuclear and cytoplasmic genes. These findings underscore the extensive variability in flowering traits present within this germplasm.

Only five hybrids Morado×L3, L1×Morado, Morado×L1, VCII×Morado, and the Morado parent had ASI values below the overall mean minus one standard deviation (Table 2). These results were associated with significant and negative general combining ability (GCA) effects, as well as significant and negative specific combining ability (SCA) effects in Morado×L3 (Table 3), demonstrating the influence of both additive and non-additive effects on ASI variation within this germplasm (Sultan *et al.*, 2016). Consequently, improvement of this trait is feasible through the exploitation of additive variance via selection and non-additive variance via hybridization or reciprocal recurrent selection (Comstock *et al.*, 1949; López-López *et al.*, 2021). Therefore, ASI may be considered a suitable criterion for selection and evaluation in maize breeding programs (De la Cruz Díaz-Juárez *et al.*, 2023; Mongesse *et al.*, 2020). It is also worth noting that although L3×VCII exhibited significant and negative non-maternal effects (Table 5), it showed a high ASI mean (5.2 days), exceeding $\mu+\sigma$ (Table 2), due to positive SCA effects for both MF and FF (Table 3).

Table 5. Estimates and significance of non-maternal effects for female flowering (above the diagonal) and anthesis-silking interval (ASI) (below the diagonal) in 30 evaluated hybrids.

Patents	L1	L3	L6	VHA	VCII	Morado
L1		0.2222	0.2222	−0.1852	−0.3519	0.0926
L3	−0.0463		1.4444 *	0.6481	−1.4074 *	−0.4630
L6	0.6759 *	0.7778 *		0.0370	0.4815	1.1481 *
VHA	−0.2963	0.1944	0.7500 *		0.3889	0.1111
VCII	−0.3241	−0.7222 *	0.1111	0.4722		−0.8889 *
Morado	−0.0093	−0.2963	0.5926 *	0.1759	−0.4630	

* *: Statistically significant (P≤0.05).

CONCLUSIONS

The expression of earliness variation in the evaluated germplasm was influenced by both additive and non-additive genetic variance, as well as reciprocal effects resulting from maternal contributions. The VHA population stood out as a key source of earliness variability in its progeny, due to favorable general combining ability and reciprocal effects derived from maternal influences. The hybrids VHA×L6 and VHA×Morado are considered heterotic patterns for enhancing earliness.

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