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Article

Combining ability and reciprocal effects of earliness in native corn populations of Tamaulipas

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Abstract

The earliness and adaptation of native corn of Tamaulipas in restrictive environments allows considering it a source of variability for genetic improvement programs, so it is necessary to know the genetic effects that control its variation. The objective was to determine the gene action that controls the variation of the earliness of native corn populations of Tamaulipas and the relationship of earliness with grain yield. In Güémez, Tamaulipas, in the agricultural cycles of autumn-winter 2019-2020 and spring-summer 2020 with application and non-application of insecticide to combat *S. frugiperda*, the genetic effects of days to male and female flowering of six corn populations, their direct and reciprocal crosses were evaluated, through a diallel analysis with the Griffing method, the correlation between flowering and grain yield was analyzed. For male and female flowering, there were no effects of general combining ability and there were effects of specific combining ability, reciprocal and maternal: the variation between cultivars was explained in 53% for male flowering and 45% for female flowering by effects of specific combining ability, for male flowering 38% of the variation between cultivars and 43% for female flowering was due to reciprocal effects. The variation between cultivars depended on non-additive effects and there was cytoplasmic inheritance involved in their expression. Earliness was positively correlated with grain yield in the spring-summer cycle without insecticide application. With high specific combining ability, TML_3S_3×VHA and Cam×VHA stood out, to take advantage of the reciprocal effects in Cam×VHA, the order of the parents must be considered.

Keywords: *S. frugiperda*, *Zea mays*, maternal effects.

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Introduction

Corn is a grass of economic importance and wide genetic and morphological variability; it is produced in all agroecological regions of Mexico. This favors that this crop is attacked by a wide diversity of pest insects in tropical and subtropical regions, such as northeastern Mexico, where *Spodoptera frugiperda* (J. E. Smith) or fall armyworm stand out (Fernández *et al*., 2013; Yáñez *et al*., 2019). This insect, in the larval stage, mainly consumes developing leaf tissue, which decreases the photosynthetic area of the plant and consequently the grain yield (Neves *et al*., 2020; Obok *et al*., 2021).

Due to the above, synthetic insecticides are mainly used for its control (Burtet *et al*., 2017), which can lead to resistance in the insect, elimination of non-target species (Neves *et al*., 2020) and environmental pollution (Guo *et al*., 2020). An alternative to reduce these risks is the use of cultivars tolerant to leaf damage caused by *S. frugiperda* (Smith and Clement, 2011). To obtain these cultivars through genetic improvement, it is necessary to identify and have base germplasm with adaptation to specific agroecological conditions (Fuentes *et al*., 1998).

Corn-growing agricultural regions in Tamaulipas, as in much of the world, due to climate change (Yujie *et al*., 2021), present humidity restriction, extreme temperatures and a period of dog days, where the temperature exceeds 40 °C (Castro *et al*., 2013). This causes a decrease in the growth cycle in the crop (Luna *et al*., 2005), generating the need to use cultivars with high earliness (Pecina-Martínez *et al*., 2009), between 50 and 70 days to flowering, spring-summer (SS) and autumn-winter (AW), respectively.

Earliness in corn is mainly estimated by the days from sowing to male and female flowering (García *et al*., 2020). This is related to high photosynthetic efficiency, adequate distribution of assimilates, lower plant height (Dos Santos *et al*., 2019) and high harvest index (Coutiño-Estrada *et al*., 2014). Therefore, within a genetic improvement program for the tolerance of corn to *S. fruigperda* damage in the dry tropics, it is desirable to use earliness as a complementary criterion for selection and evaluation (Preciado *et al*., 2002).

However, it is considered that early cultivars have lower yields than late ones, therefore, it is necessary to characterize, in the base germplasm, the specific relationships between earliness and grain yield, and to know the genetic effects that control the expression of variation in earliness (Dzib-Aguilar *et al*., 2011). The native populations of central and southern Tamaulipas, in addition to wide variability, have potential for high yield, earliness and adaptation to restrictive environmental conditions (Pecina *et al*., 2011), since they have developed in the environments described above (González-Martínez *et al*., 2020).

On the other hand, to comprehensively know the gene action that controls the variation of the base germplasm, a phenotypic and genotypic evaluation must be carried out, using characteristics that favor adaptation to the specific agroecological regions of interest (Ertiro *et al*., 2017). In this sense, there are tools that help to know the genetic components that control the phenotypic variation of corn populations, which allows selecting the most appropriate improvement method (González *et al*., 2016; Ferreira *et al*., 2020).

The diallel designs are defined as a set of simple crosses between a group of n parents (Sánchez-Ramírez *et al*., 2017), they allow estimating the effects of general (GCA) and specific (SCA) combining ability, reciprocal, maternal and non-maternal effects (Griffing, 1956; Ramírez-Díaz *et al*., 2019). The relative proportion of the sum of squares of reciprocal effects, GCA and SCA in relation to the sum of squares of crosses indicates the proportion of influence of each type of gene action on the variation of the germplasm evaluated, where GCA is mainly associated with additive effects, while non-additive effects are associated with SCA and reciprocal effects, the latter are the result of maternal and/or non-maternal effects (Hernández and De León, 2021).

The expression of variation in the days to flowering of corn depends mainly on the effects of GCA and SCA (De la Cruz *et al*., 2003; García *et al*., 2020), there is also influence of reciprocal effects (Cervantes-Ortiz *et al*., 2018) but there is little or no information on their proportion, due to maternal and non-maternal effects (Issa *et al*., 2018).

It is recognized that the level of genetic diversity of parents influences the expression of reciprocal effects (de la Cruz *et al*., 2003; Sánchez-Ramírez *et al*., 2017), so it is necessary to establish this type of parameters in a specific way, for each population or group of populations to be used as base germplasm for improvement. Based on the above, the objective of this study was to determine the gene action that controls the variation of the earliness of native corn populations of Tamaulipas and the relationship of earliness with grain yield.

Materials and methods

Location and management of the experiment

The experiment was carried out in the Experimental Field of 'Ingeniero Herminio García González' Zootechnical Post, belonging to the Autonomous University of Tamaulipas in Güémez, Tamaulipas, Mexico; at an altitude of 193 masl, at 23° 56' 26" north latitude and 99° 05' 59" west longitude, during the agricultural cycles AW 2019-2020 and SS 2020. The sowing dates were February 7 and August 4, respectively for each cycle.

The preparation of the land and the management of the crop were carried out in accordance with the recommendations for the production of corn in the north-central zone of Tamaulipas under irrigation conditions (Reyes, 2017a; Reyes, 2017b) and a population density of 50 000 plants ha^{-1}.

Variables evaluated and experimental treatments

In both agricultural cycles, the genetic effects of the days to male and female flowering of six corn populations, their direct and reciprocal crosses, were evaluated by means of a diallel analysis with the method I of Griffing (1956). The complete diallelic was formed during the SS 2019 agricultural cycle by manual pollination of the six populations evaluated (Table 1).

Two management strategies for *S. frugiperda* were established, with and without application of the insecticide emamectin benzoate (2.12%), the applications began from the complete exposure of the fourth leaf every 20 days until reaching flowering in a dose of 100 ml ha^{-1}, the combination of agricultural cycle and management strategy allowed the establishment of four environments.

Table 1. Corn genotypes developed from native germplasm, used to assess genetic effects during the cycles AW 2019-2020 and SS 2020, Güémez, Tamaulipas, Mexico.

Genotype	Type	Collection	Year of Collection	Municipalities of Origin	Geographical coordinates	
					N	W
PWL_1S_3	Line S3	3001	2003	Padilla	23°59’00”	98°52’00”
TGL_2S_3	Line S3	3007	2003	Tula	22°59’00”	99°43’00”
TML_3S_3	Line S3	3012	2003	Tula	22°59’00”	99°43’00”
PWL_6S_3	Line S3	3001	2003	Padilla	23°59’00”	98°52’00”
VHA	Variety	-	2004	Center-South	-	-
Cam	Native	2011	2011	Hidalgo	24°10’00”	99°21’00”

Experimental design

The experiment was established in a randomized complete block design with three repetitions, in an arrangement of split plots for each cycle. The two management strategies of *S. frugiperda* with application and without application of insecticide were located in the large plot and the corn cultivars in the small plot. The total usable area of each experiment was 864 m^2. The experimental unit was delimited in an area of 4 m^2.

The days to male and female flowering were determined. The first was obtained by counting the days elapsed from the date of sowing until the moment in which 50% of the plants of each experimental unit presented panicles with pollen release in its middle part. The second was determined by counting the days from the sowing date until the time when 50% of the plants in each experimental unit exposed stigmas in the female inflorescence (CIMMYT, 1995).

Statistical analysis

An analysis of variance was performed for each of the variables, with the value of the mean minus the standard deviation (μ-σ), the crosses with the lowest number of days to flowering (of greater earliness) compared to the mean were determined and a mean comparison test was performed with the Tukey method with a significance level of α= 0.05 to determine differences between the test environments.

For the estimation of the genetic effects of GCA, SCA and reciprocal effects, the diallel analysis of Griffing (1956) was used by means of method I and model I, in which the parental lines, direct and reciprocal F_1 crosses were examined, for which the Diallel-SAS05 algorithm proposed by Zhang *et al*. (2005) was used, which allows the division of reciprocal effects into maternal and non-maternal. A correlation analysis was performed between the days to male and female flowering and the grain yield per plant, jointly and individually in each environment. All statistical analyses were performed using the Statistical Analysis System (SAS, 2002).

The contribution of GCA, SCA and reciprocal effects to the variation of this germplasm was calculated based on the proportion (%) of the sum of squares of the source, with respect to the total sum of squares, while the reciprocal effects were partitioned into maternal and non-maternal effects.

Results and discussion

The statistical analysis showed significance ($p< 0.05$) between environments and between cultivars for male and female flowering; on the contrary, there was no significant interaction ($p\geq 0.05$) for environment × cultivar (Table 2). The above demonstrates that the differential environmental conditions determined by the combination of agricultural cycle and management strategy of *S. frugiperda* had a similar effect for the expression of days to flowering of each of the cultivars evaluated; that is, the cultivars presented a similar response to the environmental changes determined by the combination of agricultural cycle and management strategy of *S. frugiperda*.

Table 2. Diallel analysis for male and female flowering of crosses between native corn populations, during the cycles AW 2019-2020 and SS 2020, Güémez, Tamaulipas, Mexico.

Source of variation	Male flowering		Female flowering	
	Sum of squares	Significance	Sum of squares	Significance
Environment	16 381.5	<0.0001	14 032.3	<0.0001
Cultivar	629.2	<0.0001	463.2	0.0002
E×C	611.5	0.8397	587	0.6473
GCA	55.8	0.154	57.9	0.0877
SCA	332.9	<0.0001	207.3	0.004
RE	240.5	0.0038	198	0.0063
RE×E	44.5	0.9692	51.7	0.891
GCA×E	42.7	0.2903	38.2	0.2721
SCA×E	35.5	0.99	58.5	0.8289
ME	137.8	0.0016	94.8	0.0073
nME	102.7	0.1416	101.2	0.0813
ME×E	7.9	0.95	10.8	0.8749
nME×E	36.6	0.8667	41	0.737

E= environment; C= cultivar; GCA= general combining ability; SCA= specific combining ability; RE= reciprocal effects; ME= maternal effects; nME= non-maternal effects.

No significant effects of GCA were observed for the variables evaluated and there was no statistical significance for the interaction of GCA × environment (Table 2). On the contrary, there were significant effects of SCA, reciprocal and maternal for both variables evaluated, the significant effect of SCA indicates that within the evaluated germplasm there is variability for the gene expression of male and female flowering due to non-additive effects (García *et al*., 2020).

The significance for reciprocal effects showed that the average number of days to male and female flowering of the direct cross (i, j) is different from that of the reverse cross (j, i) for at least one pair of parents (i, j), so populations that serve as female or male parents should be specifically considered (Núñez-Terrones *et al*., 2019). This was the result of significant maternal effects, which indicates that female and male flowering expression in these crosses was controlled by cytoplasmic genes (Mahgoub, 2011).

The expression of variation among the evaluated cultivars is explained in 52.91% for male flowering and 44.75% for female flowering by SCA effects (Table 2), while 38.22% of the variation in male flowering between cultivars and 42.74% for female flowering was due to reciprocal effects (Table 2). This indicates that non-additive effects were more important in the expression of genetic variation, both for male and female flowering; that is, the observed number of days elapsed from sowing to flowering in crosses is mostly due to dominance or non-additive effects and this may be due to genetic divergence between populations for these variables (De la Cruz *et al*., 2003).

Therefore, the improvement of earliness in these populations should be done through processes of recurrent reciprocal selection or hybridization (Rodríguez *et al*., 2020) and the formation of a particular cross should specifically consider the lines that will serve as a female or male parent (Núñez-Terrones *et al*., 2019). For male flowering, crosses TML_3S_3×VHA and Cam×VHA presented significant SCA with a negative estimator (Table 3), which indicates that they had fewer days to male flowering than expected according to the GCA of the populations that participated as parents (Mahgoub, 2011), with an average of 63.4 and 63.7 days respectively (Table 4).

Table 3. Estimators and significance of specific combining ability in corn populations for male and female flowering, during the cycles AW 2019-2020 and SS 2020, Güémez, Tamaulipas, Mexico.

	PWL_1S_3	TGL_2S_3	TML_3S_3	PWL_6S_3	Cam	VHA
PWL_1S_3		0.0115	0.7129	-0.1828	-0.5231	-0.0926
TGL_2S_3	-0.0556		-0.4745	-0.8287	-0.5023	-0.1551
TML_3S_3	0.3264	0.0486		0.2893	-0.5926	-1.037^{*}
PWL_6S_3	0.0139	-1.3055^{**}	0.0764		0.0949	-0.3495
Cam	-0.1528	-0.3889	-0.3819	0.0972		-0.9398^{*}
VHA	0.0208	-0.0069	-0.7916	-0.1458	-0.7708	

Male flowering above the diagonal; female flowering under the diagonal. *= significant ($p < 0.05$); **= highly significant ($p < 0.01$).

Similarly, for the days to female flowering the cross TGL_2S_3×PWL_6S_3 presented significant SCA with a negative estimator (Table 3) with an average of 65 days (Table 4). Taking into account the above and considering the absence of effects of GCA in this germplasm (Table 2), it can be considered that this behavior is due to a low accumulation of additive genes for male and female flowering in these crosses, with predominance of the parents with expression of over dominance for these variables, where the existence of allelic interaction (SCA) in the evaluated progeny is demonstrated (Gutiérrez *et al*., 2002).

Table 4. Days to male and female flowering of corn populations and their crosses, during the cycles AW 2019-2020 and SS 2020, Güémez, Tamaulipas, Mexico.

♂ ♀	PWL$_1$S$_3$	TGL$_2$S$_3$	TML$_3$S$_3$	PWL$_6$S$_3$	Cam	VHA
Male flowering (days)						
PWL$_1$S$_3$	64.7	65.2	65	63.4	63.2	66.3
TGL$_2$S$_3$	64	66.4	63.2	62.3^*	63.6	65.4
TML$_3$S$_3$	65.1	64.3	65.1	62.5^*	63.5	64.2
PWL$_6$S$_3$	64.2	63.8	65.4	64.3	64.5	63.7
Cam	64.7	64.2	63.6	63.3	66.7	64.9
VHA	63.1	63.7	62.7^*	63.9	62.4^*	67.5
Female flowering (days)						
PWL$_1$S$_3$	66.2	67.7	66.8	65.4^*	65.9	67.5
TGL$_2$S$_3$	65.5^*	68.7	67.2	64^*	65.8	68.2
TML$_3$S$_3$	67.1	66.7	67.7	65.2^*	66.3	66.9
PWL$_6$S$_3$	66.6	66	67.5	66.9	67.1	66
Cam	66.7	67	66.5	65.4^*	68.2	67.1
VHA	66.1	65.9	65.7	66.6	65.2^*	68.9

♀= maternal parent; ♂= paternal parent. Direct crosses above the diagonal, parents on the diagonal; reciprocal crosses under the diagonal; *= less than μ-σ; μ= mean; σ= standard deviation.

Thus, it was observed that crosses with significant SCA had fewer days to male and female flowering compared to their parents (Table 4). This is consistent with what was established by de la Cruz *et al*. (2003), who point out that, in general, the development of crosses is faster than that of their parents; mainly due to the hybrid vigor or heterosis, which favors high rates of development and growth compared to their parents. The differences shown for male and female flowering between the crosses evaluated may be indicative of genetic diversity among the parent populations, as noted by Guillén-De la Cruz *et al*. (2009).

For male flowering the crosses PWL$_1$S$_3$×VHA, TML$_3$S$_3$×PWL$_6$S$_3$ and Cam×VHA showed significant reciprocal effects and for female flowering PWL$_1$S$_3$×TGL$_2$S$_3$, TGL$_2$S$_3$×PWL$_6$S$_3$, TGL$_2$S$_3$×VHA and TML$_3$S$_3$×PWL$_6$S$_3$ (Table 5). The above means that direct cross is different from reciprocal cross (Picón-Rico *et al*., 2018) and it is verified in Table 4, where it can be seen that, between direct and reciprocal crosses, there are differences of 3.2, 3 and 2.8 days respectively, for male flowering and for female flowering of 2, 2, 2.5 and 2.3 days (Table 4).

Considering all the above, for male and female flowering, VHA×Cam stands out with 62.4 and 65.2 days respectively, values lower than the general mean minus the standard deviation (Table 4). Demonstrating a greater earliness, a favorable characteristic for its adaptation to short growth cycles (Luna *et al*., 2005), such as those that occur in most agroecological regions of Tamaulipas (Pecina-Martínez *et al*., 2009).

Table 5. Estimators of reciprocal effects for male and female flowering in native corn populations, during the cycles AW 2019-2020 and SS 2020, Güémez, Tamaulipas, Mexico.

	PWL_1S_3	TGL_2S_3	TML_3S_3	PWL_6S_3	Cam	VHA
PWL_1S_3		0.5833	-0.0416	-0.4166	-0.7083	1.625^{**}
TGL_2S_3	1.0833^{*}		-0.5833	-0.75	-0.2916	0.875
TML_3S_3	-0.125	0.25		-1.4583^{**}	-0.0416	0.75
PWL_6S_3	-0.5833	-1^{*}	-1.125^{*}		0.5833	-0.125
Cam	-0.4167	-0.5833	-0.0833	0.8333		1.25^{*}
VHA	0.7083	1.1667^{*}	0.625	-0.2917	0.9167	

Male flowering above the diagonal; female flowering under the diagonal; *= significant ($p< 0.05$); **= highly significant ($p< 0.01$).

Significant maternal effects were determined in the parents PWL_6S_3 and VHA, the first with a positive estimator and the second with a negative estimator; both for male and female flowering (Table 6). The above indicates that some of the crosses that had VHA as their maternal parent presented a lower number of days to flowering compared to their reciprocal crosses; as observed in PWL_1S_3×VHA and Cam×VHA with 66.3 and 64.9 days to male flowering respectively, while VHA×PWL_1S_3 and VHA×Cam recorded 63.1 and 62.4 days respectively (Table 4 and 5).

Table 6. Estimators of maternal effects for male and female flowering in corn populations, during the cycles AW 2019-2020 and SS 2020, Güémez, Tamaulipas, Mexico.

Parent	Male flowering		Female flowering	
	Estimator	Significance	Estimator	Significance
PWL_1S_3	0.1736	0.3851	0.1111	0.5505
TGL_2S_3	-0.2222	0.2665	-0.2083	0.2633
TML_3S_3	-0.0208	0.9169	-0.118	0.5258
PWL_6S_3	0.5139	0.0105	0.5416	0.0039
Cam	0.2847	0.1548	0.1944	0.2964
VHA	-0.7291	0.0003	-0.5208	0.0054

Conversely, when PWL_6S_3 was the maternal parent, at least one cross had a higher number of days to male and female flowering compared to the cross where this population participated as the paternal parent. An example of this is PWL_6S_3×TML_3S_3 with 65.4 and 67.5 days to male and female flowering respectively, compared to TML_3S_3×PWL_6S_3 with 62.5 and 65.2 days (Table 4). The above shows that the variation of the expression of male and female flowering is controlled by cytoplasmic or extranuclear inheritance (Sánchez-Ramírez *et al*., 2017), which must be taken into consideration when defining the order of the parents in the crosses to be carried out (Andrio-Enríquez *et al*., 2015).

When the four environments evaluated were considered, no significant correlation ($p > 0.05$) was observed between grain yield per plant and days to male and female flowering (Table 7). This same result was observed in the AW agricultural cycle, in both management strategies of *S. frugiperda* and in the SS cycle only with application of emamectin benzoate.

Table 7. Coefficient of correlation between male and female flowering with grain yield, during the cycles AW 2019-2020 and SS 2020, Güémez, Tamaulipas, Mexico.

	Male flowering		Female flowering		Grain yield per plant (g)
	Coefficient of correlation	(days)	Coefficient of correlation	(days)	
Combined¤	0.04276	64.3	0.03942	66.6	92.1
No insecticide AW	-0.10366	70.5 a	-0.09085	72.2 a	93
With insecticide AW	0.04212	70.4 a	-0.03563	72.4 a	95.1
No insecticide SS	-0.22928*	58.2 b	-0.30501**	60.9 b	82.6
With insecticide SS	-0.13055	58 b	-0.1034	60.9 b	97.7

¤= the four test environments together; AW= autumn winter; SS= spring summer; *= significant ($p < 0.05$); **= highly significant ($p < 0.01$); a, b= averages with different literal by column are statistically different (Tukey $\alpha = 0.05$).

Conversely, in the SS agricultural cycle when no insecticide was applied to *S. frugiperda*, a significant and positive correlation of grain yield per plant with male and female flowering was observed (Table 7), this indicates that the earliest cultivars had a higher grain yield per plant. This is due to the fact that the SS cycle presents environmental conditions of higher temperature at the beginning of the growth cycle compared to the AW agricultural cycle (González *et al*., 2016; Reyes, 2017a), which reduces the length of the growth period (Ruiz-Corral *et al*., 2002; Kalimuthu *et al*., 2015), favoring the development and growth of early cultivars (Luna *et al*., 2005).

In this agricultural cycle, a higher incidence of *S. frugiperda* has been reported, compared to the AW cycle (Cantú *et al*., 2010; Peterson *et al*., 2017) and in this study when no insecticide was applied, there was a greater average leaf damage caused by *S. frugiperda*, 2.96 on a scale of 0 to 5, compared to the AW agricultural cycle without insecticide application of 1.81 and with insecticide application in both cycles without apparent leaf damage (data not shown), which allows inferring that cultivars of greater earliness have better adaptation to environmental conditions with the presence of pests and high temperature.

Conclusions

The variability for male and female flowering between cultivars is mainly explained by specific combining ability and reciprocal effects; the latter are the result of maternal effects. The earliness observed in the crosses TML$_3$S$_3$×VHA, Cam×VHA and TGL$_2$S$_3$×PWL$_6$S$_3$ shows cytoplasmic inheritance. In restrictive environments of high temperature and presence of *S. frugiperda*, early cultivars have higher grain yields.

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