

General and specific combining abilities of popcorn for the High Valleys of Mexico

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Abstract

The demand for popcorn (*Zea mays* L.) in Mexico is increasing every day, but its annual national production is insufficient, and the demand of 80 thousand tonnes is fulfilled with imports. The supply of improved national varieties of this type of corn is very scarce. In order to identify outstanding popcorn materials, this work estimated the effects of general and specific combining abilities, and maternal and reciprocal effects for the yield of six elite populations of popcorn and their diallel crosses. The materials were evaluated in an experimental design of randomized complete blocks with three replications in 2018, 2019 and 2020. According to the results, population 6 (PB6), due to its high yield, would have a high contribution to the expression of the yield of its progeny and could be included in a genetic breeding program for popcorn. The crosses with the highest specific combining ability for yield were PB3 x PB6 and PB6 x PB3, respectively. The popcorn populations in this work that presented high effects of general combining ability for yield can be used to develop synthetic varieties or continue to advance them with more selection cycles, while crosses with high specific combining ability can be used to obtain popcorn hybrids in Mexico.

Keywords:

Zea mays L., general combining ability, popcorn, specific combining ability, populations, yield.

Introduction

The annual consumption of popcorn (*Zea mays* L.) in Mexico is estimated at 80 000 t, of which only 596 t are produced in the country (SIAP, 2019) and the rest is imported. This situation makes Mexico dependent on imports of popcorn, so the generation of improved national materials of this type of corn is urgently required. The lack of 'popping' varieties and technological lag have made it difficult to structure a national popcorn production program that would satisfy domestic consumption (Valadez-Gutiérrez *et al.*, 2014).

Almost all the popcorn consumed in the country is imported, mostly from the United States of America. Nonetheless, in Mexico, there are breeds of corn that produce 'popping' grains, which, in theory, are suitable for producing 'popped corn', but with a low capacity for expansion, so the market and consumers do not accept them. Such corn could be used in breeding programs to obtain popcorn varieties and hybrids in Mexico.

However, in this regard, there are precedents that the first hybrid of popcorn (H 367 P) was released in Mexico in 1977 (Miranda, 1977; Ángeles, 2000) and the popcorn variety V 460 P was released in 2012 (Valadez *et al.*, 2014), which is an incentive. The center of origin of popcorn is Mesoamerica and this type of corn is considered the most primitive (Mangelsdorf and Smith, 1949); numerous evidences show that its degree of rusticity and ability to pop are related to teocintle (Piperno and Pearsall, 1993), but its relationship with other groups of corn is still under discussion (Ziegler, 2001).

This origin gives popcorn a high adaptation to the ecological conditions of Mexico and a great diversity that can be used for genetic improvement. Among the methods to study the qualities of a set of popcorn parents are the diallel designs proposed by Griffing (1956), which allow estimating their genetic parameters, such as their general combining ability (GCA) and specific combining ability (SCA); in addition, it is possible to define the most appropriate method of genetic breeding to predict superior crosses and combine the best characteristics of agricultural importance (Melani and Carena, 2005; Cai *et al.*, 2012).

SCA is more important than GCA in a breeding program aimed at obtaining hybrids (Hoegemeyer and Hallauer, 1976) as better use of dominance and epistasis can be made with SCA. Given that Mexico needs to generate outstanding popcorn materials to reduce its dependence on foreign grain and in view of the strategic interest in offering improved varieties using the available national native germplasm, for more than 20 years, the Cuautitlán Faculty of Higher Studies (FESC, for its acronym in Spanish) of the National Autonomous University of Mexico (UNAM, for its acronym in Spanish) and the Valle de México Experimental Field (CEVAMEX, for its acronym in Spanish) of the National Institute of Forestry, Agriculture, and Livestock Research (INIFAP, for its acronym in Spanish) have work on this matter.

This work consisted of the development of popcorn varieties to offer competitive alternatives to producers; in the genetic improvement process applied during all this time, emphasis was placed on the yield criterion and the popping trait was somewhat left aside. As a result of these works, there are experimental varieties and elite populations, in which the technology for their production is generated (Espinosa *et al.*, 2018).

Since 1997, quality protein sources (QPM) have been combined with native popcorn varieties and lines brought from Tamaulipas and abroad with the intention of adding expansion quality to the popcorn, then several backcrossing cycles were carried out towards popcorn quality (Espinosa *et al.*, 2018). This research aimed to determine the genetic components of GCA, SCA, and reciprocal and maternal effects involved in the yield expression of six varieties of popcorn adapted to the High Valleys of Mexico and their respective crosses.

Materials and methods

The study was carried out in six environments located in the State of Mexico. During the spring-summer cycles of 2018, 2019 and 2020, it was sown on FESC-UNAM lands located in Cuautitlán Izcalli (19° 41' north latitude, 99° 11' west longitude, 2 274 m altitude), which have a clayey loam

soil; in 2018, it was also evaluated on lands of the Huexotla ejido, municipality of Texcoco (19° 27' north latitude, 98° 51' west longitude, 2 326 m altitude), which have a silty loam soil; in 2019 and 2020, it is found in Santa Lucía de Prías, Coatlinchán Texcoco (19° 29' north latitude, 98° 52' west longitude, 2 300 m altitude) with sandy loam soil.

The genotypes evaluated included six populations of popcorn: PB1, PB2, PB3, PB4, PB5, and PB6, which were integrated since 1997, for which native popcorn varieties, lines from Tamaulipas, and lines brought from the United States of America were combined with the intention of adding quality to the popped corn, then several backcrossing cycles were carried out towards popcorn quality. Four controls and 15 direct and 15 reciprocal crosses corresponding to a complete diallel were also included [Griffing (1956) Method I] (Table 1).

Table 1. Scheme of direct (upper right diagonal) and reciprocal (lower left diagonal) crosses of the six populations (PB).

	PB1	PB2	PB3	PB4	PB5	PB6
PB1		PB1xPB2	PB1xPB3	PB1xPB4	PB1xPB5	PB1xPB6
PB2	PB2xPB1		PB2xPB3	PB2xPB4	PB2xPB5	PB2xPB6
PB3	PB3xPB1	PB3xPB2		PB3xPB4	PB3xPB5	PB3xPB6
PB4	PB4xPB1	PB4xPB2	PB4xPB3		PB4xPB5	PB4xPB6
PB5	PB5xPB1	PB5xPB2	PB5xPB3	PB5xPB4		PB5xPB6
PB6	PB6xPB1	PB6xPB2	PB6xPB3	PB6xPB4	PB6xPB5	

In each locality, an experiment was established where the genotypes were distributed in a randomized complete block design with three replications at a density of 65 000 plants ha⁻¹, and the experimental plot consisted of a furrow 5 m long by 0.8 m wide. The sowing was carried out in June of the three years in the three localities. In 2018, in Huexotla, there was moisture in the soil at the time of sowing and three supplemental irrigations were applied, in 2019 and 2020, in Santa Lucía, sowing irrigation was applied and then two supplemental irrigations; in the FESC-UNAM, in the three years, only one irrigation was applied to the sowing and the subsequent moisture was met with rainfall.

In the growing period to the harvest date, information was obtained on 18 quantitative traits related to morphological characteristics and yield composition. The harvest was manual between November and December. In each plot, all the ears of corn were harvested, and their field weight (FW) was recorded.

The statistical genetic analysis was performed with the SAS[®] v 9.0 program (SAS, 1996) for the yield variable with Griffing's (1956) Model I (fixed-effect), Method I (complete diallel), which examines parental lines and direct and reciprocal crosses, through the Diallel-Sas program proposed by Zhang and Kang (2003), which allowed the split of reciprocal effects (RecE) into maternal (MatE) and non-maternal effects (NMatE). The relative importance of GCA and SCA was assessed with the formula proposed by Baker (1978): $[2xMS_{GCA}] / [2xMS_{GCA} + MS_{SCA}]$ where MS_{GCA} is the mean square of the GCA and MS_{SCA} is the mean square of the SCA.

Results and discussion

Analysis of variance

Significant differences ($p \leq 0.01$) were detected between environments, crosses, GCA, SCA, as well as in the interaction of environment by crosses, GCA and SCA for the yield variable. In the case of male (MF) and female (FF) flowering, as well as plant height (PH) and ear length (EL), they behaved in a similar way as no highly significant differences were found in SCA or interactions; regarding, volumetric weight (VW), only highly significant differences were detected between environment and GCA (Table 2).

Table 2. Mean squares for yield, male flowering, female flowering, plant height, and volumetric weight of diallel crosses with popcorn populations in the High Valleys of Mexico.

Variation factors	DF	Yield	MF	FF	PH	VW
Environment	5	356950476**	743.8**	1075.4**	6.9**	1038.1**
Crosses	35	23437657**	15.9**	22.2**	0.16**	39.3*
GCA	5	75872456.6**	35.6**	21.5**	0.43**	87.75**
SCA	15	8940684.7**	8.9	11.4	0.07	20.21
MatE	5	43093328.6**	24.7**	69.5**	0.24**	20.68
RecE	15	20456363.5**	16.3**	33.2**	0.16**	42.18*
Env x crosses	175	2576993**	6.7	7.15	0.09	31.26*
Env x GCA	4	8162806.4**	1.9	4.8	0.03	51.4
Env x SCA	15	2172078.9**	2.3	3.2	0.02	23.11
Error	420	1244922	5.7	6.8	0.08	24.17
CV (%)		22.7	3.1	3.3	13.3	6.38
Mean		4923	77	80	210	77.04
GCA: SCA		0.94	0.89	0.79	0.92	0.91

** , * = $p \leq 0.01$, 0.05 , respectively; MF= male flowering; FF= female flowering; PH= plant height; VW= volumetric weight; DF= degrees of freedom; MS= mean squares; GCA= general combining ability; SCA= specific combining ability; MatE= maternal effects; RecE= reciprocal effects; Env= environment; CV (%)= coefficient of variation in percentage.

The statistical differences between crosses are attributed to the expression of genetic variation among them and it is related to the type of gene action expressed in each cross, such as additivity and dominance generated by the interaction of the parental populations. The differences expressed between environments indicate that environmental conditions in different years and their effects on genotypes have changed, which results from differences between climate, soil, and growing conditions. These contrasts were shown in the significant interaction of the environment by cross, which Hallauer *et al.* (2010) attribute to the wide variation of crosses involved in the population lineage used.

The significant differences shown between crosses led to the sum of squares being divided into GCA and maternal effects of parent populations, and SCA and reciprocal effects of crosses. In the case of yield, both GCA and SCA showed significant differences ($p \leq 0.01$), indicating genetic contrasts due to additive and non-additive effects, whose contribution of GCA was 94%. For the other variables evaluated, only GCA exhibited significant differences ($p \leq 0.01$), suggesting that the highest proportion of the genetic variability observed in populations was associated with additive effects (Guillen de la Cruz *et al.*, 2009), whose contribution was 89% for male flowering, 79% for female flowering, 92% for plant height, 91% for ear length, and 91% for volumetric weight.

Authors such as López-López *et al.* (2021) mention that Baker (1978) proposed the relationship between GCA and SCA to infer its importance in the behavior of offspring. A value close to 1 indicates a higher probability of behavior based on GCA alone. In addition, the relative proportion of the effects of GCA and SCA defined by the mean square indicates the type of gene action (Antuna *et al.*, 2003), where GCA is mainly related to additive effects and SCA to non-additive effects.

Therefore, based on the results of this study, it indicates that the additive genetic variance in the populations is greater than the non-additive variance. The contribution of the mean squares of the GCA to the variation was higher than that presented by the SCA for the aforementioned variables (male flowering, female flowering, ear length and volumetric weight). Maternal effects (MatE) were significant ($p \leq 0.01$); that is, the evaluated trait (yield) was determined by both nuclear and cytoplasmic genes, which means that these particular crosses can be performed and used in both directions (direct and reciprocal).

Reciprocal effects (RecE) also showed significant differences ($p \leq 0.01$), which is attributed to the effects of the interaction between nuclear and cytoplasmic DNA (Sánchez-Hernández *et al.*, 2011) in the crosses. The significant interaction of Env x crosses conditioned the division of the effects of the interaction of Env x GCA and Env x SCA, which were also significant ($p \leq 0.01$).

Effect of the GCA of populations

Differences were found between populations ($p \leq 0.01$) for yield (Table 3); PB6 (5 179 kg ha⁻¹) presented the highest value and PB5 (1 663 kg ha⁻¹) the lowest. The PB6 population will have a high contribution to the expression of the yield its progeny due to the accumulation of additive effects, results that are similar to those reported by Palemón *et al.* (2012); in addition, the PB6 parent could be included in a genetic improvement program of corn by selection to contribute with favorable alleles for yield (Guillén de la Cruz *et al.*, 2009) and later also be used to derive lines for the formation of yielding popcorn hybrids.

All parent populations presented desirable values for the various variables evaluated, with special emphasis on male flowering (-0.708) for PB2 (75 days to MF) and volumetric weight for PB6 (78.2 kg hl⁻¹).

Table 3. Effects of GCA for yield and agronomic variables evaluated in six popcorn populations in six environments. Spring-summer 2018 to 2020.

Population	Yield	MF	FF	PH	VW
PB1	-276.02**	-0.181	-0.27	-0.08**	-0.54
PB2	-268.9**	-0.708**	-0.44**	0.02	-0.02
PB3	134.9*	0.25	0.4*	0.02	-0.27
PB4	140.3*	0.028	-0.04	0.05**	-0.62*
PB5	-740.6**	0.17	0.16	-0.02	1.06**
PB6	1 010.8**	0.44**	0.2	0.01	0.38

** , * : $p \leq 0.01$ and $p \leq 0.05$; MF= male flowering; FF= female flowering; PH= plant height; VW= volumetric weight.

Parents showed higher (positive) maternal effect values for yield (Table 4), indicating that parents can express their potential in the assessed variable in the case of their direct crosses; that is, when used exclusively as female parents. PB2 and PB5 presented negative values for the yield variable, so it is expected that their direct and reciprocal crosses will behave unfavorably; that is, if the parents are used as females, their progeny will show detriment in grain yield (Núñez-Terrones *et al.*, 2019; López-López, 2021).



Table 4. Maternal effects for yield and agronomic variables evaluated in six popcorn populations in six environments. Spring-summer 2018 to 2020.

Population	Yield	MF	FF	PH	VW
PB1	671.6 ^{**}	0.15	-0.32	0.015	0.32
PB2	-678 ^{**}	0.294	0.65 ^{**}	0.002	-0.23
PB3	431.2 ^{**}	0.156	0.37	0.02	-0.19
PB4	113.4	0.344	0.56 ^{**}	0.03	0.55
PB5	-570.9 ^{**}	-0.222	0.11	-0.08 ^{**}	-0.44
PB6	32.7	-0.722 ^{**}	-1.16 ^{**}	0.01	-0.015

^{**}, ^{*} = $p \leq 0.01$ and $p \leq 0.05$; MF= male flowering; FF= female flowering; PH= plant height; EL= ear length; VW= volumetric weight.

Effect of SCA of the crosses of populations

The effect of SCA on yield was variable for most crosses (Table 5). Twelve direct crosses were superior ($p \leq 0.01$) to the others with a yield between 3 416 and 6 945 kg ha⁻¹. The direct crosses with the highest SCA for yield were PB1 x PB3 (5 604 kg ha⁻¹) and PB5 x PB6 (5 279 kg ha⁻¹).

Table 5. Effect of the SCA of 15 direct crosses and 15 reciprocal crosses of the crossing of six popcorn populations, for grain yield and agronomic variables evaluated in six environments. Spring-summer 2018 to 2020.

Type of cross	CPP	Yield		MF		FF		PH		VW	
		SCA	(kg ha ⁻¹)	SCA	days	SCA	days	SCA	cm	SCA	(kg hl ⁻¹)
DC	PB1	-768.94 ^{**}	3858	-0.167	77	0.14	79	0.01	200	0.09	77
	x PB2										
	PB1	547.9 ^{**}	5604	0.403	77	0.12	79	0.02	200	0.76	78.1
	x PB3										
	PB1	257.4	5690	0.736 [*]	77	0.48 [*]	80	-0.001	204	-1.27	75.5
	x PB4										
	PB1	-367.9 [*]	5414	0.292	78	0.4	79	-0.03	205	-0.3	78.4
	x PB5										
	PB1	-165.1	5807	-0.431	78	-0.45	81	-0.01	200	-0.71	74.1
	x PB6										
	PB2	476.9 [*]	4097	-0.125	75	-0.34	80	-0.03	204	0.05	76.4
	x PB3										
	PB2	393.6 [*]	4207	0.014	77	0.04	80	-0.02	212	0.48	76.7
	x PB4										
	PB2	202.5	3416	0.125	77	-0.04	80	0.01	210	-0.36	77.4
	x PB5										
	PB2	-85.2	5290	0.542	79	0.61	82	-0.004	210	0.07	77.7
	x PB6										
	PB3	-292	5125	0.722 [*]	78	0.72	81	0.07	220	-0.78	75.6
	x PB4										
	PB3	-414.3 ^{**}	4412	-0.167	78	-0.19	81	-0.01	210	0.09	78.6
	x PB5										
	PB3	343.8 [*]	6945	0.306	79	0.52	82	0.02	214	0.015	76.1
	x PB6										

Type of cross	CPP	Yield		MF		FF		PH		VW	
		SCA	(kg ha ⁻¹)	SCA	days	SCA	days	SCA	cm		SCA
	PB4 x PB5	-749.5 ^{**}	4346	-0.278	77	0.11	80	0.08 [*]	240	1.16	79.9
	PB4 x PB6	96.3	5848	-0.67 ^{**}	78	-0.88 [*]	81	0.007	210	-0.31	79
	PB5 x PB6	483.8 [*]	5279	0.111	77	0.3	80	-0.009	204	-0.71	78.3
RC	PB2 x PB1	248.7	4167	0.694	75	-0.28	79	0.02	213	0.46	76.7
	PB3 x PB1	274.4	6435	-0.389	76	-0.9 [*]	79	0.01	212	1.12	77.2
	PB4 x PB1	644.9 ^{**}	6169	-0.667	76	-0.9 [*]	79	0.01	210	0.92	77.1
	PB5 x PB1	1875.5 ^{**}	4817	0.194	77	-0.81	79	0.12 [*]	210	1.13	78.1
	PB6 x PB1	314.3	5870	0.917 [*]	76	1.28 ^{**}	79	-0.006	210	-2.04 [*]	77.2
	PB3 x PB2	-1169 ^{**}	4530	0.444	77	0.36	80	-0.04	205	-0.41	76.4
	PB4 x PB2	-981.04 ^{**}	4687	0.194	78	0.58	81	0.01	222	-0.18	75.2
	PB5 x PB2	-700.6 ^{**}	3394	0.222	77	0.25	80	0.02	201	-0.36	77.3
	PB6 x PB2	-290.5	5879	1.31 ^{**}	77	1.8 ^{**}	80	-0.004	211	0.26	78.2
	PB4 x PB3	219.3	5498	-0.25	77	-0.44	79	-0.02	202	0.19	76.5
	PB5 x PB3	509.2 ^{**}	2801	0.333	77	0.4	80	0.04	200	0.65	77.4
	PB6 x PB3	533 ^{**}	6493	0.75	76	1.36 ^{**}	77	0.02	220	-1.8	74
	PB5 x PB4	772.2 ^{**}	4287	-0.278	77	0.14	80	0.21 ^{**}	200	1.24	79.3
	PB6 x PB4	-322.1	6076	1.278 ^{**}	79	1.92 ^{**}	81	-0.05	206	2.5 ^{**}	77.3
	PB6 x PB5	-398.3	6271	-0.689	78	-0.6	80	-0.008	210	0.47	79.4

^{**}, ^{*} = $p \leq 0.01$ and $p \leq 0.05$; MF= male flowering; FF= female flowering; PH= plant height; VW= volumetric weight; CPP= crosses per population; DC= direct cross; RC= reciprocal cross; SCA= specific combining ability.

The cross with the highest SCA did not produce the best yield since it was the product of crossing two parents of low GCA, but the crosses with the highest yield had an intermediate SCA, being the result of crossing two parents of high GCA (Escorcia-Gutiérrez *et al.*, 2010), stability in the evaluation environments, Guerrero-Guerrero *et al.* (2011); Manjarrez *et al.* (2014); López-López *et al.* (2021) reported that a single cross is high-yielding when its parents have high GCA or at least one of them has it, but they presented positive high effects of SCA.

On the other hand, eight reciprocal crosses (Table 5) showed differences ($p \leq 0.01$), with yields ranging from 2 801 to 6 493 kg ha⁻¹. The reciprocal cross with the greatest effect of SCA for yield was PB6 x PB3. The direct cross PB3 x PB6 and the reciprocal cross (PB6 x PB3), which presented

a highly significant difference, both single crosses, presented the highest yield (6 945 and 6 493 kg ha⁻¹); these crosses are the result of the cross between two parents of high GCA of the same genealogy.

For the days to male flowering of the crosses, only one presented a significant difference ($p < 0.01$); when used as a female parent, the PB6 population added additive effects in several parents, but its flowering fluctuated between 76 and 79 days. Regarding the volumetric weight, the presence of the parents PB1, PB4, PB5, and PB6 increases the density of the grain, which is directly related to the grain hardness of its progeny (77.2 to 79.9 kg hl⁻¹) despite the fact that, in the SCA, both in direct and reciprocal crosses did not have any significance.

The reciprocal cross PB6 x PB4 was highly significant (2.5) but maintains the average value shown by the crosses. Reciprocal effects (RecE) are a relevant factor in the genetic improvement of corn, so the expression of these effects through the genetic diversity of the parents must be considered (Khehra and Bhalla, 1976).

Conclusions

In the popcorn corn materials evaluated, the effects of general combining ability (additive effects) were more important than those of specific combining ability for yield, male flowering, and volumetric weight. Maternal and reciprocal effects were found in the crosses, so the traits evaluated are determined by nuclear and cytoplasmic inheritance, which allows crossing parents directly and reciprocally for the development and use of PB6 x PB3 and PB3 x PB6, which stood out with the greatest effect of SCA.

The use of parents of contrasting GCA (high and low) allowed their progeny to express favorable yields. Popcorn populations with high GCA effects can be used to develop synthetic varieties or drive more breeding cycles, while crosses with high SCA levels can be used to generate single-cross hybrids.

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