

Genetic parameters and yield potential of polyembryonic maize genotypes

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Abstract

In the context of the mutants, polyembryony in maize (PEm) has agronomic potential; therefore, the inclusion of the PEm in new varieties may be useful when considering the ascending demand for food. The objective of this study was to develop new genotypes with high productivity potential, superior to in local area, and useful for family and extensive agriculture. In this work, single crosses were carried out between three pure lines and the high frequency polyembryonic populations. The resulting F1 were advanced to the third generation (G3) and the genotypes obtained from this last generation were used as progenitors of a mating plan, according to the Griffing method 4. The resulting crosses were evaluated in a yield test measuring common characteristics of economic importance (Days to Male Flowering (MF), Plant Height (PH), Cob Height (CH), *Fusarium* Rotten cobs, Cobs (CFUS), Yield (YLD), and analyzed with the computer routine DIALLEL-SAS05. The results allowed to indicate that both the source of variation Genotypes as additive effects (GCA) presented significance for all variables, while non-additive (SCA) were significant only in the variables of cob sanity ($p \leq 0.01$) and productivity ($p \leq 0.05$). In this regard, most of the variables showed a greater contribution of the effects of General Combining Ability (GCA) compared to Specific Combining Ability (SCA). In addition, it was observed that the crosses were superior in all the variables evaluated with respect to BAP and NAP, and statistically similar in some cases with respect to hybrids. This means that this type of segregant polyembryony crosses can compete with other materials evaluated in the region. The estimation of GCA and SCA generated information on the potential of the studied parents and their crosses and are worthy of being taken into account in the formation of varieties.

Keywords: Diallelic, Polyembryony, Yield test, *Zea mays*.

Abbreviations: GCA_General combining ability; SCA_Specific combining ability; PEm_Polyembryony in maize; AP+_positive preferential mating.

Introduction

The knowledge of genetic variation of a population of interest, is indispensable in the breeding programs of any cultivated species, in this case, maize. The mutation produces phenotypic differences between individuals that is essential to allow plants to adapt to a physical and biological environment in continuous change, which can be used in breeding programs (Nogué et al., 2016).

In studies on mutants in maize, either for applications in genetic improvement or for studies of domestication, or in recent topics related to genomics, there is a record of a large number of characteristics or treatments of economic importance. Polyembryony in maize (PEm) is the condition where the germinating seed manifests two or more plumules

simultaneously, which are maintained until the end of life cycle of the plant (Webber, 1940).

Espinoza et al. (1998) reported that the base germplasm was observed in the Instituto Mexicano del Maíz of the Universidad Autónoma Agraria Antonio Narro (IMM-UAAAN). The mixture of seeds extracted from twin plants, which had a frequency of less than 1.5% of a group of related progenies of the "square stem" type, whose characteristic was given by two identical and intimately linked plants. The next generation of the base population presented normal, twin and square stem plants. From 1992, the germplasmic base of the PEm, was divided into two groups: one for dwarf size (BAP) and another for normal size (NAP), with a reproductive management within each group of fraternal crosses with pollen mixture.

The inheritance of the polyembryonic character in corn is controlled by two duplicated recessive epistatic loci, where the normal condition of the plant is presented with only the presence of a dominant allele. This condition can also present incomplete penetrance of up to 50%, which means that the PEm is not phenotypically expressed in all the screens (Rebolloza et al., 2011).

Crosses between populations of high polyembryony (NAP and BAP) by exotic material of different origin, regularly produce F_1 phenotypic normal progenies, which indicates the "recessive" nature of the PEm, and the dominant "normal" condition the exotic sources. The recovery of the PEm can be obtained from generation F_2 (crosses plant to plant, within each segregating group), or the RC_1 of $F_1 \times$ NAP or BAP, which present progenies that manifest the PEm in proportions of 15:1 and 12:4, respectively (González et al., 2011).

Different methods have been proposed for the analysis of mating designs for the purpose of genetic studies. Sprague and Tatum (1942) proposed the method that includes the diallel crosses and that originated the concepts of General Combining Ability (GCA) and Specific Combining Ability (SCA). In the genetic mating systems called diallel, all possible crosses between several genotypes are carried out (Hayman, 1954; Kempthorne, 1956). This has been successfully applied by plant breeders, both in the use of lines and populations, with the purpose to estimate effects of GCA and SCA, reciprocal effects (RE), components of variance, levels of heterosis and heritability (Griffing, 1956; Gardner and Eberhart, 1966).

The knowledge of the combinatorial effects of parents are essential, through which breeder obtains information on the gene action in quantitative characters of agricultural importance. This allows establishing improvement schemes to select genotypes with good average behavior in a series of crosses and to identify combinations specific hybrids in the selection of superior genotypes (Gardner and Eberhart, 1966; Ávila et al., 2009). In this work, the following objectives were proposed: (1) to test the agronomic-productive capacities of combinations of different germplasm sources that include polyembryony and (2) to obtain the genetic parameters of General Combining Ability (GCA) and Specific Combining Ability (SCA).

Results and discussion

Components of the genetic variance of diallel cross by Griffing method 4

The effects of combining ability for six variables of interest are presented in Table 2. In this research, we found that both genotypes and additive effects had significance ($p \leq 0.01$) for all variables except CFUS that showed significant differences ($p \leq 0.05$) in the GCA variation source, while non-additive effects showed high significance ($p \leq 0.01$) for the variables RC, CFUS and differences ($p \leq 0.05$) for YLD. This means that genotypes have a different capacity to transmit their characteristics to the offspring and present a different performance in specific hybrid combinations. Therefore, it is possible to detect the best segregating genotypes of the PEm,

and those crosses that show the best SCA values for the possible formation of varieties or hybrids.

Regarding the components of genetic variance, it is observed that for all the studied variables the additive variance was manifested to a greater degree than the variance of dominance with the exception of PH and CFUS, which could have influenced the heritabilities, presenting values from intermediate to high. The predominance of additive variance may favor the improvement of selection efficiency in segregating populations (Bocanski et al., 2009).

Contribution of the variance of additive and non-additive effects

Table 3 shows the estimation of the contribution ratio of the effects of GCA and SCA according to the sum of squares of the analysis of variance of Griffing method 4. The variables MF, HP, HC, RC and YLD presented higher values in the effects of GCA, which indicates that the additive gene action was involved in these variables in a prevalent manner. These results agree with what was said by Moll and Robinson (1967) who pointed out that the additive genetic variance is at least twice as large as the variance of dominance in maize populations. On the other hand, Beyene et al. (2017) mentioned that the action of the additive gene is more important than the action of the non-additive gene when the effects of GCA are greater than the effects of SCA. In addition, its importance lies in the fact that its characteristics are inherited from the parents for its progeny, determinants of the genetic properties of the population and the response to selection (Silva et al., 2018).

General Combining Ability (GCA)

The punctual data of General Combining Ability are presented in Table 4, where it can be observed that the segregating genotypes B and E stand out according to the agronomic characteristics of interest, contributing precocity in the MF variable, and reducing the RC in addition to increasing the HP. In the yield variable, genotype B and E contributed 1.96 t and 0.6 t above the mean, respectively. This is reflected in most of the crosses where these genotypes are involved, surpassing the general average, which means that the genotypes have a different capacity to transmit their characteristics to offspring. The segregating genotypes A and C have significant negative effects in HP, HC and YLD, which can influence any other genotype after crossing. This reduces the height and obtain lower yield values as mentioned by Márquez (1998), who reported that genetic value of the lines determine the degree of behavior that the crosses will present.

Specific Combining Ability (SCA)

The effects of SCA for six variables are presented in Table 5. The crosses BA and CE were considered as the best hybrid combinations since they contributed greater precocity, presenting negative values in MF, low bearing in HP, reduction of RC. This favored 1.01 t ha⁻¹ to YLD, which is probably due to genetic differences between the exotic genotypes and their

Table 1. Genotypes used in this field experiments.

Inbred lines			Pol.	Initial crosses	
Lines	Pedigree	Origin		ID	Cross
1	G32-C19-HS32-1-#-2-B-#*3-3-B	CIMMYT	NAP	A	NAP x CML-78
2	AN-7	UAAAN	BAP	B	NAP x AN-7
3	AN-255-18-19	UAAAN		C	BAP x CML-78
				E	NAP x AN-255-18-19

Pol.: Reference population to polyembryony (Espinoza et al., 1998), CIMMYT: International Center for Maize and Wheat Improvement, UAAAN: Universidad Autónoma Agraria Antonio Narro

Table 2. Mean squares of the analysis of variance of a diallel under Griffing method 4 for six crosses.

SV	DF	MF	HP	HC	RC [‡]	CFUS [‡]	YLD
REP	2	5.06	14.9	46.77	0.97	13.94	0.26
GEN	5	10.32	** 1267.52	** 439.23	** 290.47	** 92.8	** 10.84
GCA	3	16.72	** 2051.41	** 729.65	** 362.29	** 42.82	* 14.92
SCA	2	0.72	91.69	3.6	182.76	** 167.77	** 4.73
ERROR	10	1.26	33.78	26.94	10.5	6.22	1.27
CV		1.41	2.89	4.57	17.13	9.88	8.98
R ²		83	95	89	93	89	81
MEAN		79.4	201.2	113.7	12.5	18.8	12.5
σA		4.59	653.24	242.02	82.31	-67.48	3.40
σD		-0.18	653.24	-7.78	78.48	93.88	1.15
h ²		0.95	0.50	1.00	0.50	-2.26	0.68

*, ** Significant at the probability levels ≤ 0.05 and ≤ 0.01 , SV: Sources of variation, REP: Repetitions, GEN: Genotypes, DF: Degrees of freedom, MF: Male flowering, HP: Plant height, HC: Cob height, RC: Rotten cobs, CFUS: *Fusarium* cobs, YLD: Yield, ‡ Variable data with Arco-Seno transformation.

Table 3. Percentage of contribution of additive and non-additive effects for six variables.

EFFECT	MF	HP	HC	RC	CFUS	YLD
GCA	97.2	97.1	99.7	74.8	31.5	82.6
SCA	2.8	2.9	0.3	25.2	68.5	17.4

MF: Male flowering, PH: Plant height, HC: Cob height, RC: Rotten cobs, CFUS: *Fusarium* cobs, YLD: Yield.

Table 4. General Combinatorial Ability (GCA) of four segregant genotypes of polyembryony, estimated under Griffing method 4.

GEN	MF	HP	HC	RC	CFUS	YLD
B	0.58	25.27	** 15.10	** -11.46	** 4.73	** 1.96
A	0.42	-14.60	** -7.48	** 9.09	** 0.45	** -1.27
C	1.42	* -12.98	** -8.90	** -2.79	* -4.65	** -1.29
E	-2.42	** 2.31	1.27	5.16	** -0.54	0.60

*, ** Significant at the probability levels ≤ 0.05 and ≤ 0.01 , GEN: Genotypes, MF: Male flowering, HP: Plant height, HC: Cob height, RC: Rotten cobs, CFUS: *Fusarium* cobs, YLD: Yield.

Table 5. Specific combining ability (SCA) of six crosses obtained from crossing between four segregant genotypes of polyembryony, estimated under Griffing method 4.

CROSSES	MF	HP	HC	RC	CFUS	YLD
BA	-0.39	-2.24	0.36	-7.28	** 6.56	** 1.01
BC	0.28	-2.28	0.53	5.00	** -7.34	** -0.64
BE	0.11	4.51	* -0.89	2.28	0.78	-0.38
AC	0.11	4.51	* -0.89	2.28	0.78	-0.38
AE	0.28	-2.28	0.53	5.00	** -7.34	** -0.64
CE	-0.39	-2.24	0.36	-7.28	** 6.56	** 1.01

*, ** Significant at the probability levels ≤ 0.05 and ≤ 0.01 , MF: Male flowering, HP: Plant height, HC: Cob height, RC: Rotten cobs, CFUS: *Fusarium* cobs, YLD: Yield.

Table 6. Mean squares of the analysis of variance in the six genotypes resulting from diallel crosses and four controls.

SV	DF	MF	HP	HC	RC [‡]	CFUS [‡]	YLD
GEN	9	18.95	** 1300.57	** 611.45	** 326.93	** 202.95	** 24.63
REP	2	3.33	10.78	3.92	0.67	14.10	2.06
Error	18	1.37	37.56	43.59	9.98	6.89	2.19
CV		1.48	3.05	5.93	16.92	11.99	11.45
R ²		88	95	88	94	94	85
MEAN		79.1	200.7	111.4	12.7	15.4	12.9

*, ** Significant at the probability levels ≤ 0.05 and ≤ 0.01 , SV: Sources of variation, REP: Repetitions, GEN: Genotypes, DF: Degrees of freedom, MF: Male flowering, HP: Plant height, HC: Cob height, RC: Rotten cobs, CFUS: *Fusarium* cobs, YLD: Yield, ‡ Variable data with Arco-Seno transformation.

Table 7. Comparison of Tukey means ($\alpha = 0.05$), of the six genotypes resulting from diallel crosses and four controls.

GEN	MF	HP	HC	RC	CFUS	YLD
AC	81.3 ab	178.2 de	96.4 c	21.1 b	15.4 cd	9.6 e
AE	77.7 cd	186.7 d	108 bc	31.7 a	11.3 de	11.2 cde
BA	80 abc	209.7 b	121.7 ab	2.8 c	30.5 a	14.3 abcd
BC	81.7 a	211.3 b	120.4 ab	3.2 c	11.5 de	12.6 bcde
BE	77.7 cd	233.3 a	129.2 a	8.5 c	23.7 ab	14.7 abc
CE	78 bcd	188.3 cd	106.4 bc	7.6 c	20.1 bc	12.9 bcde
NAP	81.7 a	220 ab	134.2 a	27.7 ab	14.2 cd	10.1 de
BAP	81.7 a	164.5 e	90.8 c	20.3 b	21.1 bc	9.6 e
CAI	75.7 d	210 b	103.3 bc	2.7 c	4.8 ef	17.6 a
HER	75.3 d	205 bc	103.3 bc	1.4 c	1.4 f	16.8 b

GEN: Genotypes, MF: Male flowering, HP: Plant height, HC: Cob height, RC: Rotten cobs, CFUS: *Fusarium* cobs, YLD: Yield.

cross-breeding counterparts, the polyembryonic populations. Also, in those crosses of good SCA, it is observed that at least one of the progenitors presented high GCA. These results confirmed De la Cruz et al. (2003), who found that the highest yield crosses were formed by lines of different origin and genetically different.

Although the BE crosses had a negative but not significant value in the YLD variable, the contribution of the additive effects that these two genotypes present were favorably expressed in the yield. These results agree with Sánchez et al. (2017) and Escorcía et al. (2010) who mentioned that a single cross has high yield when the two progenitor lines present a high GCA, or that at least one line has high GCA and positive effects of SCA.

Valuation of the potential of diallel crosses

The diallel crosses were evaluated including reference populations to polyembryony and two hybrids, where the data obtained were subjected to analysis of variance to confirm the potential between the different genotypes in each of the variables involved. The results of the analysis of variance are shown in Table 6. It can be seen that the genotypes showed significance ($p \leq 0.01$) for all the variables. This indicates that the genotypes behave differently with respect to each variable and; therefore, at least one must be better than the rest in each group within a variable. The fact above can be verified by observing Tukey's mean comparison ($p \leq 0.05$) (Table 7). In general, the genotypes that showed a high HP concomitantly exhibited higher HC and high YLD. These agronomic characteristics are of great importance in the selection of the corn crop architecture (Li et al., 2017). These are indispensable in the increase of population density to maximize the use of fertilizer, humidity and incident photosynthetic radiation (Rao et al., 2014; Mock and Pearce, 1975). However, there is a high negative association between RC and YLD, so the first affects the second, reducing cob production. These data coincide with Mu et al. (2018) who mentioned that it is one of the most important maize diseases, which can severely reduce grain yield and quality. According to the desired agronomic characteristics (precocity, average size, good sanity, good yield) the diallel crosses showed superiority in all the variables evaluated when compared with the BAP and NAP populations, which are the reference to the PEm. In addition, they were

statistically the same in some cases with respect to hybrid high-yield controls. In these comparisons, BA and BE were detected as the best diallel crosses. This allows us to mention that the evaluation of GCA and SCA by diallel crossings was efficient in the classification of progenitors that could be useful to generate genotypes, hybrids and varieties with desirable characteristics in the improvement of crops (Rathore and Chauhan, 2017).

Materials and methods

Genetic material

At the beginning of the experiment, a series of crosses was carried out between pure lines with proven combinatorial aptitude (called as exotic material, due to its non-polyembryonic condition) and the polyembryonic high frequency populations generated in IMM-UAAAN (They named NAP by its normal size and BAP for having a dwarf size (Espinoza et al., 1998) (Table 1). The F_1 generated, were taken to F_2 through plant-to-plant crosses (carnal brothers, or complete) within each group. The reproductive management of PEm plants from F_2 was through positive preferential mating (AP +) within each group, based on the polyembryonic condition. This means that only double plants were mated to rise to the third (G_3) and in this way maintain the same germplasm composition (exotic x NAP, or x BAP, in 50:50 dose). This was thought so, considering that the exotic sources in combination with the source populations of polyembryony, would contribute to improve the agronomic characteristics of the genotypic groups resulting from these processes.

Establishment of experiments

The present investigation was carried out in a series of experiments.

The first experimental works, where three segregant generations of the PEm (F_1 , F_2 , G_3) of the groups under study obtained, were carried out in the facilities of Universidad Autónoma Agraria Antonio Narro (UAAAN), in Buenavista, Saltillo, Coahuila, Mexico, located at coordinates $25^\circ 22' N$, $101^\circ 02' W$ and altitude of 1742 masl, presenting characteristics of dry, semi-warm climate, with average annual precipitation of 350-400 mm, average annual temperature of

19.8 ° C and clay loam texture soil with low contents of organic matter. The field experiments were carried out in two locations, the first in the experimental field of Instituto Nacional de Investigaciones, Forestales Agrícolas y Pecuarias (INIFAP) -Río Bravo, Tamaulipas with coordinates: 25 ° 57' N, 98 ° 01' O and altitude of 25 masl, whose climate is semi-arid subtropical warm, annual average precipitation of 653 mm, average annual temperature of 22.6 ° C and vertisol soil with clay texture. In this site, the experimental work consisted of developing a series of diallel crosses from four segregating genotypes of the polyembryony character which were in the third generation (G3), using the mating plan corresponding to Griffing method 4 (1956). This is because in this generation the genotypes had sufficient frequency of the character of the polyembryony to be able to make the crosses through AP+ and thus maintain the character. The second locality is located in the Buenavista Experimental Field, in the facilities of the UAAAN, in which a yield test of some of the crosses resulting from the diallel was carried out.

Variables evaluated

Days to male flowering (MF): Days passed from sowing to the development of 50% of dehiscent anthers; Plant height (PH): distance in centimeters from the base of the stem to the flag leaf; Cob height (CH): This length (cm) was determined from the base of the plant to the node where the main cob emerges; Rotten cobs (RC): Percentage of cobs with damage caused by different species of fungi with respect to the total cobs of corn harvested; Cobs with *Fusarium* (CFUS): Percentage of cobs that show damage by this pathogen, in relation to the total of cobs harvested; Yield (YLD): Is the estimated production per experimental plot reported in t ha⁻¹ of cobs at 15.5% humidity

Analysis of data

The diallel designs were analyzed with the computational routine DIALLEL-SAS05, proposed by Zhang et al. (2005). The yield trial data were analyzed through the analysis of variance according to the design used. In the cases where there were statistical differences, a Tukey multiple range means test was performed, $p \leq 0.05$.

Conclusion

The agronomic behavior of the segregating genotypes of polyembryony showed positive intermediate values when compared with the controls, who presented the extreme values, corresponding to the population of high polyembryony (the least qualified) and the commercial hybrid CAI (the most qualified), respectively. The estimation of General Combining Ability and Specific Combining Ability generated information about the potential of the four parents studied and their crosses, presenting superiority of additive effects, where B and E were the best genotypes, and BA, BE and CE turned out to be the best most outstanding crosses.

Acknowledgments

We would like to thank the Instituto Mexicano del Maíz (IMM) of the Universidad Autónoma Agraria Antonio Narro (UAAAN) for providing the genetic materials and the Consejo Nacional de Ciencia y Tecnología (CONACYT) for the scholarship for graduate studies awarded to the main author.

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