Article

Genetic behavior for yield components in a dwarf maize population

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Abstract

Yields components are important variables to make indirect selection towards productivity. In maize, yield is correlated with ear length, hectoliter weight and grain size. This research analyzed the results of a diallel that underwent yield trials in two locations during 2016, formed with five lines representative of a dwarf maize population. The above to estimate the genetic effects and heritability of yield through three components of yield, in order to outline the improvement strategy to be used in each component. Genetic analysis was performed using the Griffing's Method III Model II. The results showed that the variance of the additive type governs the behavior of the ear length and yield variables. The type of non-additive gene action is responsible for the phenotypic behavior of hectoliter weight, while the reciprocal effects (maternal and non-maternal) are the ones that most influence phenotypic expression of grain depth. In addition, high heritability values were found with an estimated of 0.56 for ear length and 0.58 for yield, while for hectoliter weight and grain depth the heritability found is low 0 and 0.07, respectively. It is suggested that the full-sib improvement scheme be used for ear length and yield, for hectoliter weight and grain depth it is preferable to use selfed progenies.

Keywords: diallel analysis, genetic effects, heritability.

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Introduction

Mexico is an important participant in global maize production, ranking 8th with a production of 27 228 242 t on an area of 7 157 586 ha. However, it is in deficit in maize production, which imposes the need to acquire significant quantities in the foreign market, it imports 17 million tons of maize annually due to the low yield of this cereal at the national level, which is 4.07 t ha^{-1} (SIAP, 2020).

The increase of agricultural production directs research to achieve production in greater quantity per unit area. Because of this, the use of dwarf maize emerges as an alternative that confers the advantages of: accommodating more plants per hectare without reducing the size of the ear, which will allow the farmer to obtain higher yield per unit area, better use of solar energy by having the vertical arrangement of its leaves above the ear, a great adaptation to the mechanization of the crop since its low size improves the ease of access of machinery for the application of agrochemicals such as foliar nutrients, herbicides, chemical control of pests and diseases, etc., increased tolerance to lodging due to its low height and good root system; response in the hyper-density planting, in addition, it adapts easily to the different localities of the subtropical regions tolerating the occasional limitations of non-availability of water.

In maize cultivation, it is common that when performing improvement practices directly for yield, other variables that are positively correlated with this variable are also improved, such as ear length, hectoliter or volumetric weight and grain depth, these variables are known as yield components. These characteristics are important, because by improving them directly or indirectly they increase productivity per unit surface.

Ear and grain yield correlate positively with variables comprising yield components; particularly, the best yield expression is given by having a longer ear length (Wong *et al*., 2007; Diaz *et al*., 2009; Pecina *et al*., 2011). On the other hand, Arellano *et al*. (2010) report high correlation values with hectoliter weight, while Borrás and Otegui (2001) mention that the grain size, the larger, allows a greater expression in yield.

Maize is currently required to maintain its production capacity to the maximum, for this it is desirable to know the type of gene action that governs each character and thus, to more easily incorporate agronomic characteristics that offer a competitive advantage. In this sense, it is necessary to characterize phenotypes through techniques that allow to determine the genetic effects involved in the study materials (Wong *et al*., 2007).

Diallel analysis is a tool that allows to estimate the amount of additive variance and dominance variance in the behavior of variables; as well, to estimate the effects of combinatorial aptitude, reciprocal and maternal effects of the progenitors, also allows to know the heterosis of the crosses and the heritability of the character (De León *et al*., 2005; Coutiño *et al*., 2010).

Heritability (h^2) is considered to be the fundamental parameter for selection, since it determines the amount of total variation found in a characteristic that is attributed to the direct effect of genes (additive variance); that is, inheritance (Ruales *et al*., 2007).

In this research work, based on a diallel analysis between five representative lines of a dwarf maize population, general combinatorial aptitude, specific combinatorial aptitude, reciprocal effects, maternal effects and non-maternal effects were estimated to generate knowledge of what type of gene action is the one that controls each component of yield and heritability, to define which improvement strategy to use for the next generation of improvement.

Materials and methods

Genetic material

This research used direct and reciprocal crosses between five lines of dwarf maize with advanced degree of endogamy, representative of the dwarf maize population and belonging to the improvement program of the Mexican Maize Institute (IMM) Dr. Mario E. Castro Gil of the Universidad Autónoma Agraria Antonio Narro (UAAAN). The lines evaluated were: LE1=dwarf line 1; LE2= dwarf line 2; LE3= dwarf line 3; LE4=dwarf line 4 and LE5=dwarf line 5.

Mating design

The mating system used was Griffing’s Method III (1956), which allowed direct and reciprocal crosses to be generated from p parent lines, originating p (p-1) different genotypes. The crosses of the diallel between the dwarf lines were carried out in the direct field of the Mexican Maize Institute, obtaining the required crosses.

Conditions of development

The performance test was conducted under a random block design with two repetitions per environment, in the first environment it was sown on March 3 and in the second environment it was sown on April 16, both located in the town of Buenavista, Saltillo, Coahuila, at a northern latitude of 25° 20’, west longitude 101° 01’ and an altitude of 1 750 m, during 2016. The experimental unit consisted of a furrow 3.84 m long, where 33 seeds spaced at 11.6 cm were sown, the row spacing was 0.8 m.

During agronomic management, a fertilization was performed at a dose of 240-100-100 corresponding to the units of nitrogen (N), phosphorus (P) and potassium (K) respectively, applying half of the nitrogen and all phosphorus and potassium at sowing time, the rest of the fertilization was applied in the first crop. Weed control was performed chemically by applying the active ingredient (atrazine) under the trade name Gesaprim Calibre 90 of the company Syngenta. For pest control, the product Proclaim 5 GS was applied, with active ingredient (emamectin benzoate) from Syngenta, in addition, the product Topgard 75 WP with active ingredient (cyromazine 75%) from the enterprise Koor Intercomercial, SA., was applied.

Yield components

Yield components were determined with the average value of 10 representative ears, obtained from each experimental unit, the variables evaluated were: the ear length was obtained from the distance from the base to the apex of the top ear (cm). Hectoliter weight, which was obtained from a sample of 250 g per plot, was estimated with the device mini GAC plus of the company Dickey-John sinc, 1966, the information was reported in volume. Grain depth was obtained with a precision Vernier (Steren, HER-411), this data was generated from the central diameter of the ear minus the diameter of the cob divided by two (cm). Yield was reported in t ha^{-1} of ear and adjusted to 15.5% humidity.

Statistical and genetic analysis

The analysis of genetic components and the estimation of heritability was carried out through two environments by means of Griffing's Method III model II (1956), with the computational routine Diallel-SAS05, proposed by Zhang *et al*. (2005). Whose genetic model is presented below: $Y_{ijklm} = \mu + A_i + R_{j(i)} + g_k + g_l + s_{kl} + m_m + Ag_{ik} + Ag_{il} + As_{ikl} + Am_{im} + \mathscr{E}_{ijklm}$. Where: Y_{ijklm}= response variable; μ= effect of the general mean; A_i= effect of the *i*-th environment; $R_{j(i)}$= effect of *j*-th repetition within the *i*-th environment; g_k= effect of the general combinatorial aptitude of father *k*; g_l= effect of the general combinatorial aptitude of father *l*; s_{kl}= effect of specific combinatorial aptitude of parents *k* and *l*; m_m= reciprocal effect; Ag_{ik}= effect of the interaction between the *i*-th environment and the general combinatorial aptitude of father *k*; Ag_{il}= effect of the interaction between the *i*-th environment and the general combinatorial aptitude of father *l*; As_{ikl}= effect of the interaction between the *i*-th environment and the specific combinatorial aptitude of the parents *k* and *l*; Am_{im}=effect of the interaction between the *i*-th environment and the reciprocal effect and; $\mathscr{E}_{ijklm}$= experimental error.

The contribution rate of the effects of general combinatorial aptitude (ANG), specific combinatorial aptitude (ACE), reciprocal effects (EREC), maternal effects (EMAT) and non-maternal effects (ENMAT) was calculated based on the proportion of the sum of squares of the source, with respect to the total sum of squares.

From the expectation of mean squares (Table 1), σ_A^2, σ_D^2, σ_F^2 and the heritability in narrow sense were calculated. Where: $\sigma_A^2 = 2\sigma_{acg}^2$; $\sigma_D^2 = \sigma_{ace}^2$; $\sigma_F^2 = (2\sigma_{acg}^2) + (\sigma_{ace}^2) + (2\sigma_{erec}^2) + (2\sigma_{acg\ x\ amb}^2/_{amb}) + (\sigma_{ace\ x\ amb}^2/_{amb}) + (2\sigma_{erec\ x\ amb}^2/_{amb}) + (^{error}/_{rep} * amb)$. $h^2 = \frac{\sigma_A^2}{\sigma_F^2}$

Table 1. Description of the genetic analysis combined through environments of Griffing's Method III Model II.

Source of variation	gl	CM	ECM
Environment (Amb)	a-1		
Repetitions (Rep)/Amb	a(r-1)		
Hybrid (Hib)	p(p-1)-1	M_h	$\sigma_e^2 + r\sigma_{hy}^2 + ra\sigma_h^2$
ACG	p-1	M_g	$\sigma_e^2 + 2r\sigma_{sy}^2 + 2ra\sigma_s^2 + 2r(p-2)\sigma_{gy}^2 + 2ra(p-2)\sigma_g^2$
ACE	p(p-3)/2	M_s	$\sigma_e^2 + 2r\sigma_{sy}^2 + 2ra\sigma_s^2$

Source of variation	gl	CM	ECM
EREC	p(p-1)/2	M_r	$\sigma_e^2+2r\sigma_{ry}^2+2ra\sigma_r^2$
EMAT	p-1	M_m	$\sigma_e^2+2r\sigma_{ny}^2+2ra\sigma_n^2+2rp\sigma_{my}^2+2rap\sigma_m^2$
ENMAT	(p-1)(p-2)/2	M_n	$\sigma_e^2+2r\sigma_{ny}^2+2ra\sigma_n^2$
Hib x Amb	p(p-1)(a-1)	M_{hy}	$\sigma_e^2+ r\sigma_{hy}^2$
ACG x Amb	(p-1)(a-1)	M_{gy}	$\sigma_e^2+2r\sigma_{sy}^2+2r(p-2)\sigma_{gy}^2$
ACE x Amb	p(p-3)(a-1)/2	M_{sy}	$\sigma_e^2+2r\,\sigma_{sy}^2$
EREC x Amb	p(p-1)(a-1)/2	M_{ry}	$\sigma_e^2+2r\sigma_{ry}^2$
EMAT x Amb	(p-1)(a-1)	M_{my}	$\sigma_e^2+2r\sigma_{ny}^2+2rp\sigma_{my}^2$
ENMAT x Amb	(p-1)(p-2)(a-1)/2	M_{ny}	$\sigma_e^2+2r\sigma_{ny}^2$
Error	[p(p-1)][a(r-1)]	M_e	σ_e^2

gl= degrees of freedom; ACG= general combinatorial aptitude; ACE= specific combinatorial aptitude; EREC= reciprocal effects; EMAT= maternal effects; ENMAT= non-maternal effects; CM= mean squares; ECM = expectation of mean squares.

Results and discussion

The results for the source of variation of the environments (Table 2) were detected significance ($p\leq 0.05$) in the ear length variable and in the hectoliter weight ($p\leq 0.05$). Suggesting that the average behavior of environments was not statistically the same, this is attributed to the fact that the climatic and edaphic conditions and that agronomic management was different. Hermes *et al*. (2017) points out that the main components of variability when trials are performed through environments in the same year are: climate, rainfall, altitude, geographical location and type of soil.

Table 2. Mean squares of genetic analysis of 20 F_1 hybrids formed from 5 lines, considering direct and reciprocal crosses evaluated in two environments during 2016.

Sources of variation	gl	Ear length (cm)	Hectoliter weight (vol)	Grain depth (cm)	Yield (t ha^{-1})
Environments (Amb)	1	11.777 *	149.331 **	0.499	1.2
Repeats (Rep)/Amb	2	18.855 **	53.839 **	0.983	37.787 *
Hybrids (Hib)	19	6.157 *	8.374 *	0.498	35.296 **
ACG	4	19.543 **	8.38	0.549	110.51 **
ACE	5	1.63	15.229 **	0.486	8.882
EREC	10	3.066	4.944	0.484	18.417
EMAT	4	2.961	4.644	0.561	27.731 *
ENMAT	6	3.137	5.145	0.433	12.208
Hib x Amb	19	2.573	6.835 *	0.56	12.688
ACG x Amb	4	6.416	8.798	0.65	15.667
ACE x Amb	5	1.444	5.203	0.602	10.141
REC x Amb	10	1.6	6.866	0.504	12.772

Sources of variation	gl	Ear length (cm)	Hectoliter weight (vol)	Grain depth (cm)	Yield (t ha^{-1})
EMAT x Amb	6	3.09	10.748	0.561	14.073
ENMAT x Amb	6	0.607	4.278	0.519	11.905
Error	38	2.473	3.593	0.519	9.161
Total	79				
Coefficient of variation		10.442	2.678	58.543	16.956
Mean		15.06	70.766	1.231	17.855

*, **= significant to ($p\leq$ 0.05) and ($p\leq$ 0.05) respectively; gl= degrees of freedom; ACG= general combinatorial aptitude; ACE= specific combinatorial aptitude; EREC= reciprocal effect; EMAT= maternal effect; ENMAT= non-maternal effect.

For the source of hybrid variation, the significance was detected in the variables of ear length, hectoliter weight ($p\leq$ 0.05) and yield ($p\leq$ 0.05). The above attributable to the fact that hybrids exhibited variability in these characters, indicating that at least one is different from the rest, for grain depth no significance was found, this is attributed to the low selection intensity that has been put to this characteristic. Abbott and Pistorale (2011) also mention that the wide range of climate and edaphic environments can cause differential responses in the genotype behavior.

The breakdown of the mean squares of hybrids in ACG and ACE effects shows that the effects in ACG are not statistically equal to zero, with a significance of ($p\leq$ 0.05) for ear length and yield variables. These differences found in ACG can be attributed to the genetic basis from which the progenitors were derived, which have gone through several cycles of recurrent selection.

By not detecting significance in hectoliter weight and grain depth it is suggested that it is necessary to promote variability for these characters and thus, to increase the variance. Luna *et al*. (2013) and Haochuan *et al*. (2014) mention that having broad knowledge of the genetic basis of germplasm and the type of gene action of the most economically important characteristics, such as yield, this allows to maximize genetic variance and, in this way, to increase and fix the frequency of favorable alleles in the population.

Regarding ACE, significance was detected for hectoliter weight ($p\leq$ 0.05), indicating that there is a dominance effect; that is, the non-additive genetic variability for this character was important. Kamara *et al*. (2020) indicate that the significant effects of ACG and ACE imply that both additive and non-additive effects are involved in the governing of characteristics.

The practical aspect of genetic improvement of maize by hybridization is based on the development of inbred lines and the evaluation of their ACG and ACE for the obtaining of high-yield commercial hybrids. In this regard, Bernardo (2001) mentions that the behavior of the lines *per se* do not provide a good measure of their value in hybrid combinations. On the other hand, Lobato *et al*. (2010) indicate that the development of simple, fast and appropriate methodologies for evaluating new lines has been a problem in the generation of hybrids with high productive potential.

ACG and ACE

Table 3 presents in detail, per progenitor, the effects of ACG for the evaluated characters, in which the following can be discussed to make complementary crosses within the same heterotic group: line LE01 can be good donor in ear length and yield, since significance ($p \leq 0.05$) was detected in both variables. Line LE02 shows favorable values ($p \leq 0.05$) for yield.

The LE03 line has positive effects for hectoliter weight and grain depth, although they are not significant. The LE05 was no significant, yet positive values for ear length and yield are observed.

In the effects of ACE (Table 3), only 10% have significant values. The low detected effects of ACE are attributed to the fact that lines belong to the same heterotic group, this is of utmost importance to the program since heterosis can be exploited according to De León *et al*. (2005), when crossing with the complementary heterotic group of normal height with tropical background.

Table 3. Estimation of ACG and ACE effects, obtained through the diallel design of Griffing's method III, model II in four agronomic variables of 10 crosses in F_1.

Variables	Ear length (cm)	Hectoliter weight (vol)	Grain depth (cm)	Yield (t ha^{-1})
ACG				
LE01	1.299 **	-0.018	0.186	2.005 **
LE02	-0.182	-0.788	-0.082	1.3488 **
LE03	-0.977 **	0.841	0.129	-2.4074 **
LE04	-0.605	0.166	-0.062	-1.6149 **
LE05	0.466	-0.201	-0.172	0.6684
ACE				
LE01xLE02	0.643	1.177	-0.106	-0.3804
LE01xLE03	-0.222	-0.027	0.388 *	1.662 **
LE01xLE04	-0.241	-0.102	-0.123	-0.4429
LE01xLE05	-0.179	-1.048	-0.159	-0.8387
LE02xLE03	-0.046	0.506	-0.141	-0.7979
LE02xLE04	-0.448	-1.831 *	0.104	0.652
LE02xLE05	-0.149	0.148	0.143	0.5262
LE03xLE04	0.314	0.277	-0.122	-0.6684
LE03xLE05	-0.046	-0.756	-0.125	-0.1712
LE04xLE05	0.374	1.656 *	0.141	0.4837

*, **=significant at ($p \leq 0.05$) and ($p \leq 0.05$) respectively; LE01= dwarf line 01; LE02= dwarf line 02; LE03= dwarf line 03; LE04= dwarf line 04; LE05= dwarf line 05; ACG= general combinatorial aptitude; ACE= specific combinatorial aptitude.

In research conducted by Reyes *et al*. (2004), it was mentioned that crosses with greater ACE are expected to result when crossing at least two different lines, regardless of their ACG effects. In the present study, it was found that progenitors with low or negative effects of ACG produced good crosses. Similar results were obtained by Guillen *et al*. (2009) when crossing parents with negative ACGs and obtaining crosses with positive ACE values.

When observing the behavior of crosses, significance is shown in ACE for the cross LE01x LE03 in grain depth at ($p\leq 0.05$) and at ($p\leq 0.05$) for performance (Table 3), being this progeny of the lines that presented significance for ACG both positive and negative; this result produced the most outstanding cross for these yield components.

The cross that presented a positive value with a significance of ($p\leq 0.05$) is LE04xLE05 (Table 3). This is of utmost importance, as the hectoliter weight of the grains is one of the parameters that determine yield; in addition to contributing directly to grain health, speed of drying and resistance to fungal attack, the latter characteristic is of importance to the health problem of this cereal, since it directly affects yield. Olán *et al*. (2012) mention that hectoliter weight is an important characteristic for its significant relationship to yield, because it is related to health, shape, grain size, among others.

Exploring reciprocal effects is important for making right decisions about the use of lines as a male or female progenitor. The separation of reciprocal effects in maternal or extranuclear effects, but genetic in nature and non-maternal or epigenetic in nature indicates what factors are involved in the expression of a character as reciprocal effects (Hernández *et al*., 2018).

EREC, EMAT and ENMAT

According to the information presented in Table 2, the source variation of reciprocal effect, in general, showed no significance for the variables studied, indicating that the use of crosses could be done in both ways (direct or reciprocal) without having significant changes in the behavior of the offspring. Kang *et al*. (1999) report that the division of reciprocal effect (EREC) into maternal (EMAT) and non-maternal (ENMAT) effects in diallel analysis is useful in determining whether maternal or extranuclear factors are involved in the expression of a character. These cytoplasmic effects present in reciprocal crosses influence some characteristics; in addition, reciprocal effects can be widely extended and phenotypic expression of characters may be due to genetic and cytoplasmic effects.

In Table 4, it can be specifically observed that the cross LE03xLE01 has significance at $p\leq 0.05$ for EREC, this cross shows a reduction in grain depth by changing the participation of the order of the progenitors, indicating that for these variables it is better to use the cross of the form LE01xLE03 to have offspring with greater grain depth.

Table 4. Estimation of reciprocal, maternal and non-maternal effects, obtained through the diallel design of Griffing's method III model II of four agronomic variables in 10 crosses in F_1.

Effects	Ear length (cm)	Hectoliter weight (vol)	Grain depth (cm)	Yield (t ha^{-1})
Reciprocal effects				
LE02xLE01	0.451	-1.013	-0.034	0.1962
LE03xLE01	0.655	0.588	-0.759 **	2.2925 **
LE04xLE01	-0.533	1.063	-0.05	0.02
LE05xLE01	0.945	0.45	0.078	0.24
LE03xLE02	0.32	-0.25	-0.085	0.4462
LE04xLE02	-0.2	-0.488	-0.046	-0.5462
LE05xLE02	-0.21	-1.05	0.028	-0.7912
LE04xLE03	0.983	0.375	0.049	-0.255
LE05xLE03	0.613	-0.1	-0.018	-0.3825
LE05xLE04	0.613	-1.388	0.085	0.175
Maternal effect				
LE01	0.304	0.2175	-0.153	0.5497
LE02	-0.108	-0.155	-0.014	-0.2175
LE03	0.124	-0.0125	0.175	-0.6752
LE04	0.091	-0.4675	0.0265	0.1912
LE05	-0.411	0.4175	-0.0345	0.1517
Non-maternal effect				
LE02xLE01	0.039	-1.385	0.1053	-0.571
LE03xLE01	0.475	0.358	-0.4308 *	1.0675
LE04xLE01	-0.745	0.378	0.1295	-0.3385
LE05xLE01	0.231	0.65	0.196	-0.158
LE03xLE02	0.552	-0.108	0.104	-0.0115
LE04xLE02	-0.001	-0.8	-0.0058	-0.1375
LE05xLE02	-0.512	-0.478	0.007	-0.422
LE04xLE03	0.95	-0.08	-0.0998	0.6115
LE05xLE03	0.078	0.33	-0.227	0.4445
LE05xLE04	0.204	-0.503	0.024	0.1355

*, **= significant at ($p \leq 0.05$) and ($p \leq 0.05$) respectively; LE01=dwarf line 01; LE02= dwarf line 02; LE03= dwarf line 03; LE04= dwarf line 04; LE05= dwarf line 05.

The yield variable has significance at $p\leq 0.05$ at the same cross; this indicates that, for the magnitude of the expression of a character in a cross, it is important to determine whether it is with the direct or reciprocal with which the most desirable expression of the character is obtained (Hernández *et al*., 2018). The non-maternal effects considered as epigenetic effects, according to Morange (2006), are the product of the interaction between the organism, its genetic material (including genes and non-coding materials) and the environment during development, so that the model allows to represent environmental influences on gene development and expression.

According to what Morange (2006) mentions in the previous paragraph, we can infer the importance of this effect for cross LE03xLE01 which has significance at $p\leq 0.05$ in the grain depth variable, as mentioned by King *et al*. (2007); Barca *et al*. (2014), these effects appear due to stress generated by drought, low temperatures, salinity, etc. There are no significant differences in maternal effect in any of the variables evaluated.

Finally, in Table 2, the sources of variation that address the interactions, it is highlighted that Hib x Amb in the variables cob length, degree depth and yield, showed no significance, the behavior of these variables does not change between environments; that is, the average value of variables remains stable across environments. Otherwise, for the hectoliter weight variable that had significant effects at ($p\leq 0.05$) indicating that this variable is not stable as it changes order across environments.

In ACG x Amb interactions, no significant differences were detected, that is, the estimation of ACG in the genotypes involved remain stable through environments, in this regard it will be mentioned here that if the interaction of ACG x Amb were significant, it would indicate the genotypic deviation expected of the parental values, caused by the environment, which is of interest to the plant breeder, since if this interaction is high (greater than the ACG), the heritability estimators are biased. The ideal would be that the value of ACG be the same for each genotype in the different environments; that is, the correlation between ACG and genotype be equal to one. Like the previous interaction those of ACE x Amb, EREC x Amb, EMAT x Amb, ENMAT x Amb, were also not significant, that is, the effects remain stable through environments.

Genetic effects in percentage

It was considered important to explore the contribution of genetic effects in each of the variables studied because they are directly related to heritability and their genetic behavior (Table 5). The results indicate that the ACG contributed 66% to the sum of squares in the ear length variable, 21% for grain depth, 23% for hectoliter weight and 65% for yield, giving a clear idea that ear length and yield will have greater heritability compared among the variables studied, as seen in Table 6. These results are consistent with those found by Al-Naggar and Atta (2014); Kamara *et al*. (2020). The effect of ACE made a greater contribution in the expression of hectoliter weight by contributing 47%, this implies that this character is controlled mainly by non-additive or dominance effects.

Table 5. Percentage of contribution of gene action in four agronomic variables.

Variables	Ear length (cm)	Hectoliter weight (vol)	Grain depth (cm)	Yield (t ha^{-1})
ACG	66.82	21.06	23.17	65.91
ACE	6.96	47.86	25.61	6.62
EREC	26.21	31.08	51.22	27.46
EMAT	10.12	11.67	23.7	16.54
ENMAT	16.09	19.4	27.41	10.92

ACG= general combinatorial aptitude; ACE= specific combinatorial aptitude; EREC= reciprocal effect; EMAT= maternal effect; ENMAT= non-maternal effect.

The reciprocal effect has relevant effects for the grain depth variable, which is indicative that there are crosses in which the progenitors do not behave in the same way in the direct cross as in the reciprocal cross, attributable to the fact that there are extranuclear genes that influence the expression of this variable, as detected in the cross LE03xLE01 (Table 4).

The above means that the behavior of the crosses changes depending on the order of the male or female progenitors. When exploring the contribution percentages that the reciprocal effects have on the phenotype of the materials evaluated, it was observed that the non-maternal effect (ENMAT) is of greater importance in three of the variables. Sámano *et al*. (2009) reported that by combining lines between two non-genetically related groups of germplasm, the order of the participation of progenitors changes the genetic and phenotypic expression of F_1; that is, there are reciprocal effects.

Genetic variance and heritability

To better understand the presence of reproductive value in variables, heritability in narrow sense was calculated (Table 6), with this, it is possible to measure the degree of difference between populations due to the effect of genes. Additive variance was important for ear length and yield, which allowed it to have heritability of 0.569 and 0.581; by these values it is recommended to use full-sib recurrent selection improvement method. Al-Naggar and Atta (2017) mention that additivity is important in the heritability of grain yield and other agronomic traits.

Table 6. Components of genetic variance and heritability in four agronomic variables.

	Ear length (cm)	Hectoliter weight (vol)	Grain depth (cm)	Yield (t ha^{-1})
σ_A^2	1.907	-0.271	0.009	8.93
σ_D^2	0.023	1.253	-0.015	-0.157
σ_F^2	3.349	2.239	0.125	15.371
h^2	0.569	-0.121	0.073	0.581

σ_A^2= additive variance; σ_D^2= variance of dominance; σ_F^2= phenotypic variance; h^2= heritability.

Estimates of heritability for hectoliter weight and grain depth were -0.121 and 0.073, this indicates that the increase in favorable alleles for these components within populations is done at slow rates and therefore, genetic progress is much lower. In the hectoliter weight and grain depth variables, it is feasible to use improvement methods of inbred progenies in at least two selection cycles and thus, increase additive variance and purify the genetic load and, subsequently, continue with recurrent family selection. Silva *et al*. (2018) indicates that the most important function of heritability in genetic studies of quantitative characters is its predictive role in indicating the reliability of phenotypic value as a guide to reproductive value. Characters with high heritability can easily be fixed by family selection resulting in high genetic gain.

Conclusions

The effect of the additive type is important for the variables ear length and yield and effects of the non-additive type are responsible for phenotypic behavior of hectoliter weight. However, reciprocal effects play a very important role in phenotypic expression of grain depth, attributable to both maternal and non-maternal effects.

Estimated heritability for ear length and yield has a high value (0.569 and 0.581) respectively, while for hectoliter weight and grain depth the heritability is low (-0.121 equal to 0 and 0.073) respectively, suggesting that for the first two variables a full-sib improvement scheme will be very efficient and for the other two variables improvement is required under inbred progenies to try to elevate additive variance and improve heritability.

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