

Estimation of maize genetic parameters under improvement by recurrent reciprocal selection

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Abstract

In the development of trilineal corn hybrids it is required to know the genetic parameters of the populations that are used to derive their parent lines. In this study, the additive variance was estimated directly from the genotype component of the Anova in the random evaluation of 182 S1 lines derived from the 'P' population (producers). This participates in a heterotic pattern P x A (farmers) in continuous improvement through the method of reciprocal recurrent selection (SRR). In 2014 the lines were evaluated in Xalisco, Compostela and Santa Maria del Oro, Nayarit. The combined Anova detected significant differences between the lines for most of the variables studied. High estimates of additive variance resulted for grain yield and other agronomic characteristics. High estimates of heritability in the strict sense were observed due to high estimates of additive variance. The grain yield showed a high heritability of 0.63, similar to most of the estimates studied in corn. A high heritability was observed in all the characters of the performance components. Heritability estimates varied from 0.54 to 0.87 and are in the similar ranges that have been observed in most studies conducted in corn. The values are adequate to have progress in the evaluated characters of the population P; which will allow for the case of the development of trilinear hybrids to find simple intra-cross combinations that can be used as simple female crosses in the production of grain and seed.

Keywords: heritability, trilinear maize hybrids, additive genetic variability.

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Introduction

The best type of improved seed for the cultivation of corn in Mexico is the trilinear hybrid. More than 50% of the improved maize seed that is grown in Mexico is of the trilinear hybrid type (Luna *et al.*, 2012). It has good grain yield and its seed production makes it advantageous and with good economic benefits because the seed that is harvested comes from a simple cross. It is recognized that a simple cross, having only two parents, mainly exploits hybrid vigor (Tiessen, 2012). Which is why there are good seed productions in the field. This good production not only benefits the company that markets it, but also the farmer who produces it in the field. Better profits are obtained as they have higher production because the improved seed producer receives an added value.

However, the simple cross used as a female has to be combined with a progenitor line used as a male to form the trilinear hybrid. The hybrid thus formed already has three progenitors and there is a tendency to lose hybrid vigor (Preciado and Terron, 1997; Luna *et al.*, 2012). Plant breeders, then, look for combinations of lines that assure good performance both in the simple female cross and in the trilinear hybrid that is formed when crossing with another line that functions as a male parent.

The current strategy of the plant breeder is to develop trilinear maize hybrids that have a simple cross that is productive in seed production and at the same time, that conserves its heterosis in grain production. This can be achieved by identifying related lines derived from a population, but still have good production when crossing them. This type of simple crosses is crossed with a male line derived from another population unrelated to the first. The lines of the simple cross used as a female would behave as 'sister lines'. Thus, the trilinear hybrid would have a production similar to a modified hybrid.

The selection and identification of this type of progenitor lines of corn hybrids is made with the use of several breeding methods and the use of improved populations or with good attributes of agronomic quality and combinatorial aptitude. In this sense, one of these methods is reciprocal recurrent selection (SRR), which simultaneously improves two heterotic populations and is widely used in corn (Comstock, 1949, Hallauer and Miranda, 1981). The method is cyclical and systematic; in each advance cycle, it not only improves each of the two populations on their own, but also improves the heterotic pattern of the populations. On the one hand, varietal hybrids of any advance cycle can be developed, which have been developed and commercially released (Valdivia *et al.*, 2014). On the other hand, they are also appropriate to be included in selection programs with the participation of farmers looking to develop their own seed (Valdivia *et al.*, 2007). In addition, it is expected that in each advance cycle, the improved populations will be excellent sources for the development of lines of high genetic and agronomic quality.

As a premise, the breeder should know the genetic behavior of populations under continuous improvement to predict and design breeding strategies in order to identify elite lines for the formation of trilinear corn hybrids, mainly genotypic variation of populations and their heritability. The estimation of the additive variance is the most important parameter in the estimation of heritability.

At the Autonomous University of Nayarit (UAN) a program of genetic improvement in corn is carried out based on the method of reciprocal recurrent selection (SRR). Two heterotic populations were formed in the decade of the 1990s and have been improving by the SRR method. With support from Nayarit farmers through the 'producer-experimenter' method (Valdivia *et al.*, 2007), recognized as participatory genetic improvement. The populations are 'P' and 'A', mostly with the conformation of P x A in the generation of progenies. Populations that originated in a diallelic study with the best corn planted at the time of the 1990s. In this context, the objective of this research work was to estimate the genetic parameters of the additive variance and heritability focused on the population 'P', as a source to derive progenitor lines of the simple cross that is used as a female in the trilinear hybrids.

Materials and methods

Location of the experiment

The present investigation was carried out in three sites. Compostela, Nayarit that is geographically located at 20° 52' north latitude and 105° 22' west longitude. Xalisco, Nayarit, at 21° 22' north latitude and 104° 24' west longitude. Santa Maria del Oro, Nayarit at 21° 09' north latitude and 104° 23' west longitude.

Genetic material

The 'P' and 'A' heterotic populations were formed under a diallel crossing scheme. The genotypes were separated by specific combinatorial aptitude. Once the heterotic pattern was formed, the two populations were improved by the SRR method. In the first two cycles of selection, half-sibling progenies were used. From the third cycle, progenies of self-fertilized S₁ lines were used (Valdivia *et al.*, 2014). In this third cycle, different S₀ plants were randomly identified from the 'P' population, in total 182 S₁ lines were achieved. The developed progenies were used in the estimation of genetic parameters. Thus, the lines are a representative sample of the population 'P' and considered in Hardy-Weinberg equilibrium.

Evaluation of experiments

The 182 S₁ lines were evaluated in experiments planted on July 5, 7 and 9, 2013 at the sites of Santa Maria del Oro, Compostela and Xalisco, Nayarit. An experimental design of duplicated lattice 10 x 10 distributed in plots of a furrow of 4 m in length was used. The handling of the experiments was carried out according to the production technology recommended by the National Institute of Forestry, Agriculture and Livestock Research (INIFAP).

Data obtained

Agronomic characteristics data were recorded; grain yield (RENDG) (kg ha⁻¹), days to female flowering, ear height (cm), percentage of ear rot (PM), ear length (LM), ear diameter (DM) (cm), number of rows per corn (NH), number of grains per row (GH), total number of grains per ear (NG) and grain size (TG).

Statistical and genetic analysis

A combined analysis was performed under a completely randomized block design; the lattice design was not more efficient compared to that of randomized complete blocks. The agronomic characteristics that were significant ($p < 0.05$) were used to estimate the components of variance. The comparison between means was not necessary for this study. The appropriate Anova for the estimates is presented in Table 1.

Table 1. Variance analysis of S1 lines of maize repeated in three environments.

Source	Degrees of freedom	Medium squares (CM)	Hope of CM
Environments (E)	a-1		
Repetitions/E	a (r-1)		
Lines S ₁	n-1	M4	$\sigma^2 + r \sigma^2ga + re \sigma^2g$
A x Lines S ₁	(a-1)(n-1)	M3	$\sigma^2 + r \sigma^2ga$
Error	a(r-1)(n-1)	M2	σ^2
Totals	arn-1		

a, r, n= refer to the number of environments, repetitions within environments and lines, respectively.

Estimates of genetic variability

Data were taken per plot and their means were analyzed ordinarily in three environments. Direct tests of 'F' and estimates of variance components were made from the mean squares obtained from the Anova, model II is appropriate for this analysis because the data is a random sample representative of the population 'P'. The components of variance are used to transfer the data in the estimates of genetic variance. Because there is only one equation, the assumption of non-dominance is considered and the gene frequencies are considered as $p = q = 1$; thus, the variance component of the lines provides a direct estimate of the additive variance. With the additive variance, the heritability and the standard error of heritability were estimated (Hallauer and Miranda, 1981).

Estimation of the genotypic variance σ^2g

The genotypic variance, σ^2g , is the portion of the total variation explained by the effect of the genotypes in their evaluation in different environments. It is the component of variance that is transferred to estimate the genetic component of the variance. For the case of S₁ lines, it gives a direct estimate of the additive genetic variance (σ^2A). This occurs under the assumption that the dominant and epistasis effects are minimized with inbreeding; as well as, it is assumed that the reference population, from which the lines under study were developed, is in Hardy-Weinberg equilibrium; thus, the gene frequencies are $p = q = 0.5$.

$$\sigma^2g = (M4 - M3)/ra$$

Where: M4 and M3= are the mean squares (CM) of the line variation factors and of the interaction, A x L, respectively; r and a= are the number of repetitions and environments, respectively.

Estimation of the phenotypic variance (σ^2_f)

The phenotypic variance, (σ^2_f), explains the total variation between the genotypes evaluated in different environments. It is calculated by the formula.

$$(\sigma^2_f) = ((\sigma^2/ra) + (\sigma^2_{ga/a}) + (r \sigma^2_g))$$

Where: σ^2 = is the variance of the Anova or CME error; $\sigma^2_{ga/a}$ = is the variance of the interaction lines by environments; σ^2_g = is the genotypic variance.

Estimation of the variance interaction (σ^2_{ga})

It is the component of variance of the interaction of lines by the environment and is estimated in the following way.

$$\sigma^2_{ga} = (M3 - M2)/r$$

Where: M3 and M2= are the CM of the interaction variation factors, A x L and CM of the error, respectively; r= is the number of repetitions.

Estimation of the additive variance (σ^2_A)

The additive variance, (σ^2_A), is due to the average effects of alleles in the same locus, they are additive effects that are inherited and transferred from generation to generation, from parents to children. As the level of inbreeding of the S₁ lines, tested is the same, it facilitates their analysis and translation in the additive variance. Based on the implied assumptions mentioned above. Thus, the variance component of the Anova gives a direct estimate of the additive variance, $\sigma^2_g = \sigma^2_A$.

Estimation of heritability (h^2)

With the information of the genetic components of variance, we proceeded to estimate the heritability in narrow sense. Its formula is: $h^2 = \sigma^2_A / \sigma^2_f = \sigma^2_A / ((\sigma^2/ra) + (\sigma^2_{ga/a}) + (r \sigma^2_g))$.

Where: h^2 = heritability in the narrow sense; σ^2_A = additive variance; σ^2 = error variance; $\sigma^2_{ga/a}$ = variance of the interaction lines by environment; σ^2_g = genotypic variance.

Estimation of the standard error of heritability (SE)

You can also have an estimate approximation of the standard error of heritability.

$SE(h^2) = SE(\sigma^2_g) / \sigma^2/ra + \sigma^2_{ga/a} + \sigma^2_g$, which can be calculated by using the CMs of the ANOVA. Where= $SE(h^2) = ((2/(ra)^2) * ((M4)^2 / (n+1)) + (M3)^2 / ((e-1) * (n-1) + 2))^{0.5}$

Where: σ^2_g = genotypic variance; σ^2 = error variance; $\sigma^2_{ga/a}$ = variance of the interaction lines by environment.

Calculation of the estimates

The genotypic variance for grain yield was estimated by the formula:

$$\sigma^2_g = (M4 - M3) / ra = (6\ 872\ 436 - 2\ 513\ 714) / (2 * 3) = 726\ 454$$

Where: M4 and M3= are the CM of the line variation factors and the interaction A x L, respectively; r and a= are the number of repetitions and environments, respectively.

The variance of the interaction (σ^2_{ga}) was estimated with the following formula.

$$\sigma^2_{ga} = (M3 - M2) / r = (2\ 513\ 714 - 2\ 144\ 502) / 2 = 163\ 451$$

Where: M3 and M2= are the CM of the variation factors of the interaction, A x L and CM of the error, respectively; r= is the number of repetitions.

The phenotypic variance is the total variation and is estimated with the formula:

$$\sigma^2_f = (2\ 144\ 502 / (2 * 3)) + (184\ 606 / 2) + 726\ 454 = 1\ 145\ 406$$

The estimation of the heritability is done with the data of the estimates of the genetic components of variance. Heritability was estimated in a narrow sense because there was a direct estimate of the additive variance:

$$h^2 = 726\ 454 / 1\ 145\ 406 = 0.634$$

You can also have an estimate approximation of the standard error of heritability.

$$SE(h^2) = \{SE(\sigma^2_g)\} / \{(\sigma^2 / re + \sigma^2_{ge}/e + \sigma^2_g)\}$$

$$SE \sigma^2_g = \{2 / (2 * 3)^2 * [(6\ 872\ 436^2) / (100 + 1)) + (2\ 513\ 714^2) / ((3 - 1) * (100 - 1) + 2)]^{0.5}\}$$

$$SE \sigma^2_g = \{(0.0556) * [(467\ 627\ 490\ 833 + 31\ 912\ 567)]^{0.5}\} = 983\ 265$$

$$SE(h^2) = 983\ 265 / 1\ 145\ 406 = 0.85$$

Results and discussion

Variance analysis

In the Table 2 shows that the yield of grain and all other variables of plant and ear were significantly different ($p < 0.05$). Thus, all the variables that were significant were used to estimate the components of variance.

Table 2. Mean squares of the analysis of variance of the evaluation of 182 S₁ lines of corn in three environments of Nayarit.

SV	DF	Average squares											
		REND	FF	AM	PM	LM	DM	NH	GH	NG	TG		
Ambient (A)	a - 1	2											
Repetitions /A	a (r-1)	3											
Lines S ₁	n-1	99	6 872 436	23.9	519	2.5	10.2	0.38	8.3	63	20.5	0.18	
A x L	(a-1)(n-1)	198	2 513 714	13.8	158	909	2.4	0.1	1.5	18	5.87	0.05	
Error	a(r-1)(n-1)	297	4 395 987	10.7	141	766	2	0.09	1.5	15	5.46	0.04	
Total	arn-1	599											
	Pr>F		**	**	**	**	**	**	**	**	**	**	
	Media		5908	67.2	81	11.4	13.1	4.3	16	27	406	1.61	
	CV		24.8	4.9	14.7	24.4	10.8	7.1	8.4	14	18.2	13.3	

** = significance at 0.05; SV = source of variation; DF = degrees of freedom; R END= grain yield (kg ha⁻¹); FF= days to female flowering; AM= ear height (cm); PM= percentage of pod rot; LM= length of ear (cm); DM= ear diameter (cm); NH= number of rows per ear; GH= number of grains per row; NG= total number of grains per ear; TG= grain size.

The grain yield variable was significant, so we proceeded to estimate the components of variance (Table 3). The components of variance allowed estimates of the different genetic parameters. The genotypic variance (σ^2_g) gave a direct estimate of the additive variance (σ^2_A) of 726 454, enough genetic variation to improve the grain yield in the 'P' population, as well as to develop lines that when combined with each other will show good yields in the simple crosses that can be formed (Maphumulo *et al.*, 2015). Thus, the seed production of that simple cross as a female of the trilinear hybrid will achieve good seed production. The heterosis can be maintained and even improved when it intersects with the male parent line from another population, such as 'A', as used in the SRR scheme with the heterotic populations 'P x A'.

Table 3. Estimation of variance components for grain yield in 182 S₁ lines of corn in Nayarit.

Source of variation	Degrees of freedom	Average squares (CM)	Hope of CM
Environments (A)	a-1	2	87.347.048
Repetitions /A	a(r-1)	3	26.810.443
Lines S ₁	n-1	181	6.872.436 M4
A*Lines S ₁	(a-1)(n-1)	362	2.513.714 M3
Error	a(r-1)(n-1)	543	2.144.502 M2
Total	arn-1	109*1	

The phenotypic variance (σ^2_f) or estimated total variation was $(2\ 144\ 502/(2*3)) + (184\ 606\ 2) + 726\ 454 = 1\ 145\ 406$. Component of variance used in estimating heritability. It was estimated in a narrow sense (h^2) because we had a direct estimate of the additive variance: $726\ 454/1\ 145\ 406 = 0.634$. The approximate estimate of the standard error of heritability SE (h^2) was $983\ 265/1\ 145\ 406 = 0.85$. With the calculated data of the standard error implies that the estimated heritability of 0.634 for grain yield can have a variation of 0.85.

The narrow-sense heritability shows a high value to be a characteristic of grain yield. It indicates that 63% of the variation found is genetic and highly heritable. The trilinear hybrids that are developed, on the part of the population 'P', will be of sufficient genetic quality for the environmental and management conditions where the lines studied were evaluated. In the literature, the ranges that have been obtained, on average, in many studies vary from 0.2 to 0.5 and assuming no epistatic effects (Hallauer and Miranda, 1981). They correspond, mostly, to estimates obtained with genetic designs and before the 1980s. Although genetic designs are more appropriate for estimating the genetic variance of populations, they are procedures that require more time, effort and financing. Also after several cycles of selection, estimates may not be valid for predicting genetic gains due to expected changes in the frequency of genes with selection (Lamkey and Hallauer, 1987).

Consequently, the variability between S_1 lines selected at random is a method that can be conveniently used to estimate the genetic variability of a reference population (Hallauer and Miranda, 1981). On the contrary of a formal genetic design, it is fast, little effort and money because it is part of the population improvement that is done with recurrent selection methods.

High heritability estimates that were estimated for performance in this study with the evaluation of 182 S_1 lines, could be explained in several ways. That some assumptions, such as no dominance effects, no epistasis, lack of balance of Hardy-Weinberg. It is recognized that with the additive variance there is a possible bias of dominance effects of 1/4 magnitude of dominance variance (Cockerham and Matzinger, 1985). Lamkey and Hallauer (1987) compared estimates of heritability and other genetic parameters for maize grain yield with the use of variances between progenies with data from 121 experiments obtained from seven recurrent selection programs. Found 68% heritability estimates for full siblings, 58.5% for half siblings, 79.8% for S_1 lines, 77.3% for S_2 lines, 53.3%, in test crosses with a line as a tester, 62.7% with test crosses with a tester of broad genetic base and 54.9% with complete reciprocal siblings (SRR). The possible presence of dominant effects was the explanation given for the high estimates of heritability found.

On the other hand, in recent years' studies have been made to estimate genetic parameters that include genotypic variances and heritability for corn grain yield. Three categories of heritability in the broad sense (H^2) are considered (Khan *et al.*, 2018); from 0% to 30%, low, from 30% to 60%, moderate; and more than 60%, high. The studies show different situations in H^2 values, grain yield combinations and agronomic characteristics in terms of high, moderate and low H^2 . Low heritabilities have been reported for grain yield and high heritabilities for agronomic traits (Ali *et al.*, 2010; Olakojo y Olaoye, 2011; Wuhaib *et al.*, 2017). Also, moderate and low heritabilities for grain yield (Sujiprihati *et al.*, 2003; Bekele and Rao, 2013; Ullah *et al.*, 2015). The majority of these studies of heritability in a broad sense find moderate and high estimates of heritability for maize agronomic traits and grain yield (Aminu *et al.*, 2012; Vashista *et al.*, 2013; Rahman *et al.*, 2016; Mieso, 2017). Khan *et al.* (2018) found moderate heritabilities in a broad sense for grain yield and agronomic characteristics. Bello *et al.* (2012) found high heritabilities in yield and agronomic characters. High H^2 than the narrow sense heritabilities in agronomic characteristics (Tengan *et al.*, 2012).

However, there is a misinterpretation in their estimates because they are evaluation studies of genotypes in normal experiments and few progenies. That is, they are of the order of model I or fixed effects. Surely the confusion has originated from the studies of researchers in molecular biology. Tiessen (2012) affirms that they are experiments that measure the repeatability or reliability or quality of the trials and not the heritability in a broad sense. It even suggests that the two terms are used interchangeably.

In the Table 4 presents the estimation of the components of variance, additive variance, heritability and the standard error of heritability for the agronomic characteristics measured in the 182 lines of the 'P' population. High values of additive variance were estimated for number of grains per ear, ear rot and ear height. Low estimates of additive variance were obtained in days of female flowering, ear length, ear diameter, number of rows per ear, grains per rows and grain size. Greater progress is to be expected in the highest estimates of additive variance in the selection of these characteristics in the 'P' population.

Table 4. Estimation of variance components for agronomic characteristics in 182 maize lines of the 'P' population evaluated in three sites in Nayarit.

Components	FF	AM	PM	LM	DM	NH	GH	NG	TG
$\sigma^2_g = \sigma^2A$	23.9	519	2508	10.2	0.38	8.3	62.9	2053	0.19
σ^2_{ga}	13.8	158	909	2.4	0.1	1.5	17.9	5871	0.05
σ^2	1.68	60	267	1.3	0.05	1.13	7.5	2444	0.02
$\sigma^2+r\sigma^2ga+\sigma^2g$	0.13	-10	63	0.39	0.01	0.03	0.4	152	0
$\sigma^2/ra+\sigma^2ga/a+\sigma^2g$	10.7	141	766	2	0.09	1.5	15.2	5452	0.05
h^2	0.48	0.748	0.642	0.738	0.723	0.814	0.739	0.718	0.718
SE h^2	3.51	80	415	1.76	0.06	1.39	10.17	3403	0.03

FF= days to female flowering; AM= ear height (cm); PM= percentage of pod rot; LM= length of ear (cm); DM= ear diameter (cm); NH= number of rows per ear; GH= number of grains per row; NG= total number of grains per ear; TG= grain size.

On the other hand, estimates of narrow-sense heritability are high; except for the days to feminine flowering. Most of the estimates of heritability found are similar to what has been reported in corn (Noor *et al.*, 2013; Ewool and Akromab, 2017). The observed variations are more genetic than environmental, which ensures that the transmissions of favorable genes for these characteristics are more inheritable.

Conclusions

Most of the estimated genetic parameters were favorable for the identification of progenitor lines of genetic quality. As well as the simple crosses that can form and that can be used as female parents in the production of seed of trilineal corn hybrids. The additive variance for grain yield was high estimated at 726 454. High values of the additive variance were estimated for number of grains per ear, ear rot, ear height, number of grains per ear. Agronomic characteristics that can be improved in the 'P' population within their program and may be

shorter term. Low estimates of additive variance were obtained in days of female flowering, ear length, ear diameter, number of rows per ear and grain size. Characteristics that can be improved in the population in the longer term.

The estimates of heritability in the strict sense in most of the characters studied showed high heritability. They varied 40% to 87%. The values are adequate to have progress in the evaluated characters of the 'P' population. Grain yield showed a heritability of 63%. This will allow, in the case of the development of trilineal maize hybrids, to find simple intracross combinations, that is, two lines or progenitors that combine well with each other, but function as relatives that can be used as simple female crosses and that when crossed with a line as a male parent, will maintain heterosis. By having two lines that function as related in the simple female cross, as if it were a single line, it represents a behavior of a modified simple hybrid.

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