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Yield prediction and inbreeding of maize synthetics generated with lines and single crosses.
Classic probability

Predicción de rendimiento y endogamia de sintéticos de maíz generados con líneas y cruzas simples.
Probabilidad clásica

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ABSTRACT

To reduce costs and labor associated with predicting the genotypic mean (*GM*) of a synthetic variety (SV) of maize (*Zea mays* L.), breeders can develop SVs from *L* lines and s single crosses ($Syn_{L,SC}$) instead of *L*+2*s* lines (Syn_L). The objective of this work was to derive and study formulae for the inbreeding coefficient (*IC*) and *GM* of $Syn_{L,SC}$, Syn_L, and the SV derived from (*L*+2*s*)/2 single crosses (Syn_{SC}). All SVs were derived from the same *L*+2*s* unrelated lines whose *IC* is F_L, and each parent of a SV was represented by *m* plants. An *a priori* probability equation for the *IC* was used. Important results were: 1) the largest and smallest *GM*s correspond to Syn_L and $Syn_{L,SC}$, respectively; 2) the GM predictors with the largest and intermediate precision are those for Syn_L and $Syn_{L,SC}$, respectively; 3) only when F_L=1, or *m* is large, Syn_L and Syn_{SC} are the same population, but only with Syn_{SC} prediction costs and labor undergo the maximum decrease, although its prediction precision is the lowest. To determine the SV to be developed, breeders should also consider the availability of lines, single crosses, manpower and land area; besides budget, target farmers, target environments, etc.

RESUMEN

Para reducir costos y trabajo para predecir la media genotípica (*GM*) de una variedad sintética (SV) de maíz (*Zea mays* L.), se puede desarrollar SVs con *L* líneas y *s* cruzas simples ($Syn_{L,SC}$) en lugar de *L*+2*s* líneas (Syn_L). El objetivo de este trabajo fue derivar y estudiar fórmulas para el coeficiente de endogamia (*IC*) y la *GM* del $Syn_{L,SC}$, Syn_L y de la SV derivada con (*L*+2*s*)/2 cruzas simples (Syn_{SC}). Las SVs fueron generadas con las mismas *L*+2*s* líneas no emparentadas, con *IC* igual a F_L. Cada progenitor se representó por *m* plantas. Se usó el concepto de probabilidad *a priori* para derivar fórmulas para *IC*. Resultados importantes fueron: 1) las *GM*s mayor y menor corresponden a Syn_L y $Syn_{L,SC}$, respectivamente, 2) la mayor mayor e intermedia precisiones para estimar *GM*, respectivamente, se obtienen con Syn_L y Syn_{SC}, y 3) solo cuando F_L=1 o *m* es grande, Syn_L y Syn_{SC} son la misma población, pero Syn_{SC}, requiere menos trabajo y costos para la predicción aunque esta es menor. Para determinar qué SV desarrollar, se debe considerar también la disponibilidad de líneas, cruzas simples, mano de obra y área experimental; además de presupuesto, y ambientes y usuarios potenciales, etc.

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Keywords

low-input agriculture • plant breeding • genotypic stability • random mating population • identical by descent genes

Palabras clave

agricultura marginal • mejoramiento genético vegetal • estabilidad genotípica • población en apareamiento aleatorio • genes idénticos por descendencia

INTRODUCTION

A synthetic variety (SV) of a crop species as maize (*Zea mays* L.) is the population resulting from the random mating of *m* plants from each of *p* selected parents. It has the advantages of exploiting the natural system of this cross-fertilizing species and having large genetic variability and an important proportion of heterozygosity that accounts for grain yield and a broad stability across environments, including low-input agriculture. Further, this mating system must produce stability in its genotypic array across the subsequent generations, which means that: 1) the farmers do not have to buy seed of the SV each cycle, except for the first one, and 2) the SV does not undergo inbreeding depression. Besides that these two advantages of a SV are not shown by hybrids, these varieties have been vulnerable to destructive diseases such as *Helminthosporium maydis* (11). Hybrids, however, show large heterotic effects.

Normally, the development of a synthetic variety (SV) of a crop species such as maize (*Zea mays* L.) includes the field evaluation of *p* pure lines and their $p(p - 1)/2$ direct crosses. The data produced is then used according to a prediction equation to estimate the genotypic mean of each of the $2^p - (p + 1)$ SVs that can be derived.

Furthermore, a prediction equation (1) and evidence from reality imply an inverse relationship between genotypic mean (*GM*) and inbreeding coefficient (*IC*). This equation, however, also requires field evaluation of the *p* parents and their $p(p - 1)/2$ crosses. Moreover, when *p* is large, the available resources might not be enough, and an alternative approach should be applied instead.

A partial solution to the problem of limited resources to derive SVs that is more flexible than the use of parents that are exclusively single crosses (5), double crosses (6) or a mixture of single and double crosses (4), is the use of *L* lines and s single crosses as potential parents of a SV. It is based on $L + 2s$ unrelated initial lines whose *IC* is F_L (the s single crosses are derived from 2*s* lines).

Besides more flexibility, this synthetic variety ($Syn_{L,SC}$) relative to the conventional SV derived from L+2*s* lines, implies a decrease in *s* parents thereby reducing the number of possible SVs. This $Syn_{L,SC}$ was already studied (7), but it was restricted to pure initial lines (F_L=1) and did not include the estimation of the genotypic mean. The hypothesis is that when the initial lines are not pure (F_L< 1), the *GM*, *IC*, and the precision of the estimation of the genotypic mean of the $Syn_{L,SC}$ may undergo a change due to the decrease in the number of parents.

Moreover, the derivation of the *IC* of a SV has been based on the known coancestries of the individuals produced by randomly mating the parents, usually a set of pure and unrelated lines (3), or on the genotypic array of the SV where each genotype is substituted for the probability of identity by descent of the two genes forming the substituted genotype (5).

The procedure proposed here to derive the *IC* considers that the two genes of each genotype of a SV can be visualized as the result of a random sample with replacement of size two from the set whose elements are the genes of the gametic array of the parents. This consideration in turn makes it possible to visualize the derivation of the *IC* of the SV as a random experiment where the calculation of the probability of the occurrence of an event can be based on an *a priori* model. Thus, it would be interesting to see how useful this approach could be to derive the *IC* of $Syn_{L,SC}$.

Under this context for $Syn_{L,SC}$, a work was planned to study the SVs derived from L lines and s single crosses, including the cases: 1) $L > 0$ and $s = 0$ (Syn_L), and 2) $L = 0$ and $s>0$ (Syn_{SC}). The objectives were to determine and analyze general ($F_L \leq 1$) formulae for the *IC* and *GM* of the $Syn_{L,SC}$, Syn_L, and Syn_{SC}.

METHODS AND THEORETICAL FRAMEWORK

In this study, the concepts of gametic array (*GA*) and genotypic array (*GEA*) of a diploid population under random mating were used in the context of the Hardy- Weinberg law. If in a population the frequency of the gene A_i is p_i (i=1, 2, …, *a*), these concepts are defined as:

$$GA = \sum_{i=1}^{a} p_i A_i \quad \text{and} \quad GEA = \sum_{i=1}^{a}\sum_{j=1}^{a} p_i p_j A_i A_j$$

Since a SV is the progeny generated by randomly mating its parents, the inbreeding coefficient of the variety can be visualized as the probability that two random genes taken with replacement from the set whose elements are the genes of the gametic array of the parents are identical by descent (*IBD*).

In particular, if the parents of a SV are L lines and s single crosses and each parent is represented by m individuals, according to the one-locus model of a diploid species, the genes of the gametic array of the SV can be visualized as a set whose elements are the $2mL + 2ms$ genes contributed by the mL and ms individuals that represent the L lines and s single crosses, respectively.

Thus, the calculation of the probability that two random genes taken with replacement are *IBD* can be explicitly made based on the classical definition of probability.

Since the initial L+2s lines were assumed to be unrelated (without parentage) and their inbreeding coefficient was F_L ($0 \leq F_L \leq 1$), the contributions to the inbreeding coefficient of the $Syn_{L,SC}$ can occur only when two sampled genes trace back to the same individual (as a selfpollination) and to two individuals from the same line or single cross (as an intraparental cross).

The prediction equation, based on a decomposition of the genotypic array of the SV into subpopulations that, once evaluated in the field, produce data that enable the breeder to develop unbiased estimators of the genotypic mean of the SV, was considered as well.

With respect to the prediction of the genotypic mean of the $Syn_{L,SC}$ based on experimental data only, let $A_{pi1}A_{pi2}$ be the genotype of the *p-th* individual that represents parent *i*.

Consider a random sample of size two with replacement taken from the 2*m* (*L* + *s*) genes of the gametic array, the probability that the obtained genes are those that integrate the ordered genotype $A_{pik}A_{qjl}$ is $1/[2m(L+s)]^2$ (p, q = 1, 2, 3, …, m; i, j = 1, 2, 3, …, $L + s$; k, l = 1, 2). In addition, if $Y_{pik,qjl}$ is the genotypic value of $A_{pik}A_{qjl}$, the expected genotypic mean of the SV derived from L lines and s single crosses ($MSyn_{L,SC}$) must be expressable as:

$$MSyn_{L,SC} = \sum_{p=1}^{m}\sum_{q=1}^{m}\sum_{i=1}^{L+s}\sum_{j=1}^{L+s}\sum_{k=1}^{2}\sum_{l=1}^{2} Y_{pik,qjl} / [2m(L+s)]^2 \qquad [1]$$

It should be noted that if in equation 1 $Y_{pik,qjl}$ is substituted for $A_{pik}A_{qjl}$, the equation becomes the genotypic array of the $Syn_{L,SC}$, whose gametic array is:

$$\sum_{p=1}^{m}\sum_{i=1}^{L+s}\sum_{k=1}^{2}[2m(L+s)]^{-1}A_{pik}$$

RESULTS

Inbreeding coefficients

Each genotype of the genotypic array of the $Syn_{L,SC}$ can be visualized as formed by two random genes taken with replacement from the set of the 2*m*(*L*+*s*) genes of the gametic array of the parents of the SV. Two sources of the inbreeding coefficient of the $Syn_{L,SC}$ ($FSyn_{L,SC}$) are the *Lm* selfpollinations of the *L* lines and their *Lm*(*m*-1) intraparental crosses; in each case, the frequency of the genotypes generated by two *IBD* genes is expected to average $(1+F_L)/2$. Thus, the contribution of the *L* lines to the $FSyn_{L,SC}$ is:

$$\frac{[4Lm + 4Lm(m-1)](1+F_L)/2}{[2m(L+s)]^2}$$

Similarly, the two remaining contributions to the $FSyn_{L,SC}$ are from the *sm* selfpollinations of the parental single-cross hybrids and their *sm*(*m*-1) intraparental crosses. Since the frequencies of genotypes formed with two *IBD* genes are expected to average 1/2 and (1+F_L)/2, respectively, the two contributions of the s single crosses to $FSyn_{L,SC}$ were:

$$\frac{4sm(1/2)}{[2m(L+s)]^2} \quad \text{and} \quad \frac{4sm(m-1)[(1+F_L)/2]}{[2m(L+s)]^2}$$

In summary, $FSyn_{L,SC}$, the sum of all three previous contributions, reduces to:

$$FSyn_{L,SC} = \frac{m(1+F_L)[2L+s]+2s[1-(1+F_L)/2]}{4m(L+s)^2} \qquad [2]$$

When all parents of the SV are only lines ($L > 0$ and $s = 0$), the inbreeding coefficient ($FSyn_L$) reduces to:

$$FSyn_L = \frac{1+F_L}{2L} \qquad [3]$$

For $F_L = 1$, equation 3 becomes $FSyn_L = 1/L$.

When $L = 0$ and $s > 0$, according to equation 2, the inbreeding coefficient of the resulting SV ($FSyn_{SC}$) is:

$$FSyn_{SC} = \frac{1+F_L}{4s} + \frac{1-F_L}{4ms} \qquad [4]$$

For F_L=1, Equation 4 becomes $FSyn_{SC} = 1/(2s)$, as showed in other study (7).

Table (page 80) shows the inbreeding coefficients of several $Syn_{L,SC}$ classified into four sets. All SVs in a set were derived from a particular group of lines, each participating in a SV only once, either as a parent of the SV, or as a parent of a parental single cross.

The numbers of lines in a set were 4, 6, 8, and 10, determined according to results found for the optimum number of parents of synthetic maize varieties (2).

The differences among the SVs in a set were the number of lines used to derive the single crosses that, in addition to the remaining lines of the set, were parents of a SV. For each SV, 15 inbreeding coefficients were calculated (all possible combinations between 5 values of *m* and 3 of F_L).

Table. Inbreeding coefficients (X1000) of the synthetic varieties (SVs) of four sets, each developed from a particular set of unrelated parental lines whose inbreeding coefficient is F_L. Each SV is derived from *L* lines and *s* single crosses, and each parent is represented by *m* individuals. In a set each line participates only once in each SV, either as a parent itself or as a parent of a single cross that is a parent of the SV.

Tabla. Coeficientes de endogamia (x1000) de las variedades sintéticas (SVs) de cuatro conjuntos, cada uno desarrollado a partir de un grupo particular de líneas cuyo coeficiente de endogamia es F_L. Cada SV tiene como progenitores *L* líneas y *s* cruzas simples, cada uno representado por *m* individuos. En cada conjunto cada línea participa una vez en cada SV, como progenitora o para formar una cruza simple progenitora de la SV.

		F_L = 0.500					F_L = 0.750					F_L = 0.875				
		m					*m*					*m*				
L	*s*	10	20	50	100	200	10	20	50	100	200	10	20	50	100	200
4	0	188	188	188	188	188	219	219	219	219	219	234	234	234	234	234
2	1	210	209	209	208	208	244	243	243	243	243	261	261	260	260	260
0	2	194	192	189	188	188	222	220	219	219	219	236	235	235	235	234
6	0	125	125	125	125	125	146	146	146	146	146	156	156	156	156	156
4	1	136	135	135	135	135	158	158	158	158	158	169	169	169	169	169
2	2	142	141	141	141	141	165	164	164	164	164	176	176	176	176	176
0	3	129	127	126	125	125	148	147	146	146	146	157	157	156	156	156
8	0	94	94	94	94	94	109	109	109	109	109	117	117	117	117	117
6	1	100	100	100	100	100	116	116	116	116	116	124	124	124	124	124
4	2	105	105	104	104	104	122	122	122	122	122	130	130	130	130	130
2	3	107	106	105	105	105	123	123	123	123	123	132	131	131	131	131
0	4	97	95	94	94	94	111	110	110	110	109	118	118	117	117	117
10	0	75	75	75	75	75	88	88	88	88	88	94	94	94	94	94
8	1	79	79	79	79	79	92	92	92	92	92	98	98	98	98	98
6	2	82	82	82	82	82	96	96	96	96	96	103	103	103	103	103
4	3	85	85	84	84	84	99	98	98	98	98	105	105	105	105	105
2	4	85	84	84	83	83	98	98	97	97	97	105	104	104	104	104
0	5	78	76	75	75	75	89	88	88	88	88	94	94	94	94	94

Genotypic mean

Let M_{RMP} and M_{CP} stand for the mean of the *L* + *s* progenies generated by randomly mating the *m* individuals that represent each parent in isolation (*RMP* populations), and the progenies produced by all direct crosses among the *L* + *s* parents, respectively. From a decomposition into two sets of progenies related with M_{RMP} and M_{CP}, equation [1] can be rewritten as:

$$MSyn_{L,SC} = \frac{(2m)^2(L+s)}{[2m(L+s)]^2} M_{RMP} + \frac{(2m)^2(L+s)(L+s-1)}{[2m(L+s)]^2} M_{CP} \qquad [5]$$

$$= M_{CP} - [M_{CP} - M_{RMP}]/(L+s)$$

Equation 5 (page 80) is a particular case of a prediction formula (10). Clearly, the same approach can be used to derive the *GM* of Syn_L ($MSyn_L$) and Syn_{SC} ($MSyn_{SC}$). For example, analogically:

$$MSyn_L = M'_{CP} - [M'_{CP} - M'_{RMP}]/(L+2s)$$

Where M'_{CP} is the mean of the (L+2s)(L+2s-1)/2 direct crosses of the lines and M'_{MRP} stands for the mean of the L+2s populations produced by the random mating of the *m* plants of each of the parental lines.

Regarding the precision of the estimation of $MSyn_{L,SC}$, the variance (*Var*) of the experimental mean of the $Syn_{L,SC}$ ($\hat{M}Syn_{L,SC}$) for a single replication, if σ^2 is the experimental error variance, is Wricke & Weber (9):

$$Var\left(\hat{M}Syn_{L,SC}\right) = \left\{[2(L+s)-1]/(L+s)^3\right\}\sigma^2 \qquad [6]$$

Analogically,

$$Var\left(\hat{M}Syn_L\right) = \left\{[2(L+2s)-1]/(L+2s)^3\right\}\sigma^2$$

and

$$Var\left(\hat{M}Syn_{SC}\right) = \left\{[(L+2s)-1]/[(L+2s)/2]^3\right\}\sigma^2$$

DISCUSSION

According to table (page 80) and equations 2, 3 and 4 (page 79), the inbreeding values $FSyn_L$, $FSyn_{SC}$, and $FSyn_{L,SC}$ are always directly related with F_L. In addition, when $L > 0$ and $s > 0$, then: 1) the relationship between number of parents ($s + L$) and inbreeding coefficient of the $Syn_{L,SC}$ is inverse. This is so because an increase in the number of unrelated parents implies an increase in interparental matings whose progeny do not contribute to inbreeding, and 2) the $FSyn_{L,SC}$ values are larger than those of the Syn_L and Syn_{SC} that belong to the same set. Furthermore, equations 3 and 4 (page 79) imply that when *m* is large, or when the initial lines are fully inbred (F_L = 1), $FSyn_L = FSyn_{SC}$. This result was also found with the approach to derive formulae for *IC* based on coancestries (7).

An explanation of this is as follows: when F_L = 1, the formation of the single crosses does not imply losses of non-identical by descent genes, the gene frequencies in the set of single crosses and in the set of the lines are the same, and thus the inbreeding coefficients and the genotypic means of Syn_L and Syn_{SC} are the same as well. In fact, F_L = 1 the genotypic arrays of Syn_L and Syn_{SC} are the same. Otherwise, if the initial lines were not pure, it would be expected that $FSyn_{SC} > FSyn_L$ because the single cross parents would lose more *NIBD* genes (8).

It should be noted that whenever in the set of parents of a SV all or some have heterozygous individuals the gene frequencies that these parents contribute to their SV behave as random variables, and the magnitude of their variance may presumably be an indicator of the genetic stability of the SV. The truthfulness and utility of this assumption, however, deserves study.

For $0 \leq F_L < 1$, the two smallest inbreeding coefficients, although not necessarily equal, are $FSyn_L$ and $FSyn_{SC}$ (equations 2-3-4, page 79; table, page 80). This is at least partly because the gene frequencies in the initial lines are expected to be balanced in Syn_L and Syn_{SC}, whereas in $Syn_{L,SC}$ the frequency of a gene contributed directly from a line will probably double that of a gene of a line contributed *via* a single cross.

With balanced gene frequencies the random mating of the parents in each of Syn_L and Syn_{SC} may produce more heterozygous genotypes relative to those of the $Syn_{L,SC}$, and therefore $FSyn_{L,SC}$ will more likely be the largest. Furthermore, it has been found that if the parents of a SV were only lines the contribution of non-identical by descent genes to the Syn_L would be the largest (8), and consequently $FSyn_L$ would be the smallest, results that are consistent with those obtained in this article. Thus, independently of the F_L value, in terms of inbreeding and hence of genotypic mean, the two best SVs are Syn_L and Syn_{SC}.

The magnitude of the decrease in the *GM*, of $Syn_{L,SC}$ however, also depends on how intense the inbreeding depression is in the genetical materials used. This disadvantage of $Syn_{L,SC}$, however, is ameliorated because this *SV* is more flexible, and reduces labor and costs. As already mentioned, relative to Syn_L, the use of $Syn_{L,SC}$ implies a decrease in the number of parents and this causes a decrease in the number of entries required for prediction. The resulting decrease is as follows: if the number of initial potential parents of a SV were *p*, with a decrease to *p*-1, the decrease in the number of entries to be prepared and evaluated in the field would be *p* [i.e., 1 *RMP*+(*p*-1) crosses].

Equation 6 (page 81) provides useful information to study the precision of the estimators of the genotypic means of the synthetics. For example, if $L + 2s = 12$ and $F_L < 1$, to estimate the mean of a Syn_L, 12 random mating populations (*RMP*s) must be generated and evaluated in the field (if $F_L = 1$, the formation and evaluation of *RMP*s would be substituted for the evaluation of the lines), in addition to the formation and experimental evaluation of the 66 direct crosses between the parents.

Alternatively, with 12 initial lines, 4 lines and 4 single crosses could be the parents of a $Syn_{L,SC}$. In this case the entries to be developed and then evaluated would be 36 (8 *RMP*s and 28 crosses between parents). But, although costs and labor are decreased, the precision of the estimation decreases as well. In the example, the variances of the estimations of the genotypic means of the SVs derived, one from 12 lines, and the other from 4 lines and 4 single crosses, are $0.0133\sigma^2$ and $0.0293\sigma^2$, respectively.

Theoretically, these results imply that in order for the two cases to have the same precision, the field evaluation of the entries for the $Syn_{L,SC}$ must use (0.0293)/ (0.0133) = 2.2 replicates per replicate used for Syn_L, although in terms of required experimental units these two cases would need about the same number: 79.2 (36x2.2) and 78 (12 *RMP*s and 66 direct crosses between parents, respectively).

Thus, although the genotypic mean decreases as the inbreeding coefficient becomes larger, the use of a mixture of lines and single crosses as parents of a synthetic variety enables the estimation of the genotypic means which, with limited resources, could not otherwise be possible (with Syn_L, for example).

Generalizing, *GM* and precision of estimation of *GM* (*PE*) undergo a reduction when a $Syn_{L,SC}$ is used instead of Syn_L. But whereas the labor and costs due to the use of $Syn_{L,SC}$ can be quantitatively measured, the magnitude of the effects on *GM* and *PE* due to the use of $Syn_{L,SC}$ are difficult to be assessed before making a decision relative to the choice of SV to be developed.

The effect of the increase in *IC* on *GM* depends on the size of the increase and on how sensitive the genetic material used is to inbreeding, whereas the magnitude of the *PE* depends on the number of entries under evaluation in the field, the number of replications, the experimental technique and the experimental materials. In addition to the previous considerations, the breeders should take into account the particularities of their breeding program (budget, number of single crosses and lines available, land area, labor capacity, target environments, target farmers, etc.).

CONCLUSIONS

From the equations derived for inbreeding coefficients (*IC*), genotypic means (*GM*) and precision of estimation of *GM* (*PE*), it is known that if a change from *p* to *p*-1 parents of a SV is made (when two lines are substituted for their single cross), then: 1) the number of entries that require field evaluation to predict performance of all possible SVs derived from the *p*-1 parents decreases by *p* units, 2) there is a loss of precision estimation of *GM* (*PE*), and 3) the *IC* increases and *GM* decreases.

While labor and cost reductions can be calculated, the effects on *GM* and *PE* depend, apart from a change of p entries and the number of replications (*PE*), on the genetic background of the parents (*GM*) and the experimental technique and materials used (*PE*).

In addition, maize breeders should consider the particularities of the breeding program to decide the type of SV to be developed (budget, flexibility of $Syn_{L,SC}$, labor capacity, experimental technique, target environments, target farmers, etc.).

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