General inbreeding coefficient of maize synthetics derived from three-way line hybrids

Coeficiente de endogamia general de sintéticos de maíz formados con híbridos trilineales

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SUMMARY

The scarcity of pure and unrelated maize inbred lines that possess high combining ability in Mexico has led breeders wishing to form single crosses to develop double-cross or three-way line hybrids (TWLHs) instead. However, some of the farmers who grow these hybrids cultivate their advanced generations later on. Although the resulting populations can be viewed as the synthetics that the random mating of the parental lines (SynL) of these hybrids would produce, there may be differences. The synthetic variety whose parents are t TWLHs (SynT) is interesting because the contributed gene frequencies of the three lines that are parents of a TWLH are not balanced and this may generate a difference between the inbreeding coefficients (ICs) of the SynL and SynT. Since an unbiased and general inbreeding coefficient of the SynT and a prediction formula for the synT genotypic mean (GM) are not yet known, the objective of this study was to derive formulae for these two important parameters of SynT.

To form the t TWLHs, it was assumed that 3t unrelated lines whose IC was F (0 ≤ F ≤ 1) were used. Unbiased and general formulae for FSynT and GM were derived for the first time. In particular, it was found that $FSyn_T = [3(1 + F)]/(16t)$. Since the inbreeding coefficient of the SynT derived from the same 3t lines is $(1 + F)/(6t)$, then $FSyn_T > FSyn_L$. These findings suggest that the genotypic mean of the SynL grain yield is larger than the SynT’s.

Index words: coancestry, genotypic mean, identity by descent, Zea mays L.

RESUMEN

La escasez de líneas puras no emparentadas y de aptitud combinatoria alta, en México, ha orientado a los mejoradores que desean formar cruzas simples al desarrollo de variedades híbridas trilineales (CTs) o de cruza doble. Sin embargo, de los agricultores que llegan a cultivar estos híbridos, algunos siembran las generaciones avanzadas de éstos en ciclos posteriores. Aunque las poblaciones resultantes pueden ser visualizadas como los sintéticos que produciría el apareamiento aleatorio de las líneas progenitoras de dichos híbridos, puede haber diferencias. El caso de la variedad sintética cuyos progenitores son t CTs (SinT) es interesante porque las frecuencias de los genes que aportan las tres líneas de cada progenitor no son balanceadas. Esto puede hacer que el coeficiente de endogamia (CE) del SinT difiera al del SinL. Como se desconocen fórmulas para predecir el CE insesgado y generalizado del SinT ($FSin_T$) y de su media genotípica (MG), el objetivo principal de este trabajo fue derivar fórmulas para estos dos importantes parámetros del SinT. Para la formación de las t CTs se supuso el uso de 3t líneas no emparentadas cuyo CE fue F (0 ≤ F ≤ 1). Se derivó fórmulas generales (0 ≤ F ≤ 1) e insesgadas para el $FSin_T$ y la MG. En particular, se encontró que $FSin_T = 3(1 + F)/(16t)$. Por otra parte, como el coeficiente de endogamia de la VS cuyos progenitores son las 3t líneas ($FSin_T$) es $(1 + F)/(6t)$, $FSin_T > FSin_L$. Estas diferencias implican que deba esperarse que el SinL tenga una media de rendimiento de grano mayor que la del SinT.
INTRODUCTION

In order to avoid the high seed cost of hybrid maize (Zea mays L.) varieties, some farmers in Mexico sow their advanced generations, or carry out other management strategies with existing hybrid varieties. This has contributed to the generation of a number of studies related to the formation of synthetic varieties with single-cross, three-way line cross or double-cross hybrids. Among other studies is one that deals with the theoretical aspects of synthetic varieties derived from single crosses as parents (Sahagún-Castellanos and Villanueva-Verduzco, 1997) and those that generated formulas for predicting the yield of synthetics that would be derived from double crosses (e.g.: Sahagún-Castellanos et al., 2005; Márquez-Sánchez, 2008). In particular, with regard to three-way line hybrids, which are commonly used in Mexico, the inbreeding coefficient and a formula to predict the yield of the synthetic produced by the random mating of three-way line crosses made with pure lines have been determined (Márquez-Sánchez, 2010).

The synthetic derived from three-way line hybrids (SynT) is interesting because the genetic participation of the three lines that form such a hybrid is not balanced; however, there are still gaps in our knowledge of their properties. For example, the study by Márquez-Sánchez (2010) did not include the case in which the parent lines have an inbreeding coefficient \( F \) \((0 \leq F \leq 1)\). In addition, the value that this author obtained for the contribution of intraparental coancestry to the SynT inbreeding coefficient is not convincing. In this regard, the hypothesis of this study is that this coancestry is overvalued. The value of \( F \) is important because it is related to the magnitude of the inbreeding coefficient of a SynT that can be derived from these lines. This in turn is linearly and inversely related to the genotypic means of some traits of economic interest (grain yield, for example) of this synthetic variety (Busbice, 1970).

RESULTS AND DISCUSSION

The genotypic array of the three-way line cross \((A_{1}A_{2}XB_{1}B_{2}) \times C_{1}C_{2}\) \((GEA_{T})\), according to Equation 1, must be:

\[
GEA_{T} = \frac{1}{8}A_{1}C_{1} + \frac{1}{8}A_{1}C_{2} + \frac{1}{8}A_{2}C_{1} + \frac{1}{8}A_{2}C_{2} + \frac{1}{8}B_{1}C_{1} + \frac{1}{8}B_{1}C_{2} + \frac{1}{8}B_{2}C_{1} + \frac{1}{8}B_{2}C_{2}
\]

(2)

The SynT is generated by the random mating of the \( mt \) representatives of the \( t \) three-way line crosses.
As a consequence, this type of mating also occurs among the $m$ representatives of each of these crosses. For example, the population derived from the three-way line cross of Equation 2 has the gametic array:


The population produced by the random mating of the \(GEA_t\) individuals (Equation 2) must include genotypes formed by two genes of two different parental lines, which do not contribute to inbreeding, and genotypes formed by genes from the same line, which do contribute. These last genotypes and their frequencies are:

\[(1/64) A_1A_1, (1/64) A_2A_2, (1/64) B_1B_1, (1/64) B_2B_2, (4/64) C_1C_1, (4/64) C_2C_2, (2/64) A_1A_2, (2/64) B_1B_2, \text{ and } (8/64) C_1C_2.\]

**Inbreeding Coefficient**

According to Expression (3), the IC of the offspring produced by the random mating of a three-way line cross \(F_r\) is:

\[F_r = \frac{1}{64} + \frac{1}{64} + \frac{1}{64} + \frac{1}{64} + \frac{4}{64} + \frac{4}{64} + \frac{2}{64} + \frac{2}{64} + \frac{8}{64} \frac{F}{14}.\]

\[= \frac{12 + 12}{64} F\]

\[= (3/8)(1 + F)/2.\] (4)

In addition, if the number of parents (three-way line crosses) is \(t\), the inbreeding coefficient of the synthetic produced by their random mating \(FSyn_t\) can be expressed in the form:

\[FSyn_t = 3(1 + F)/(16t).\] (5)

Below, an analysis is made to determine the genotypic structure of the \(Syn_t\) in order to know the level of accuracy of an inbreeding coefficient of a \(Syn_t\) developed with pure lines (Márquez-Sánchez, 2010).

The random mating of the 8 genotypes of the genotypic array of a three-way line cross (Equation 2) produces offspring that can be classified into: a) those produced by the union of two gametes from the same genotype, whether it is from the same individual (self-pollinations) or not (intraparental crosses), and b) those produced by crosses between individuals whose genotypes do not have genes in common. The inbreeding coefficient of the offspring produced by self-pollination is \(1/2\). The remaining intraparental crosses can be classified into 8 groups of 7 crosses, which have a parent in common. For example, the genotype \(A_1C_1\) is crossed with each of the 7 remaining genotypes of the \(GEA_t\) described in Equation 2 \((A_2C_1, A_2C_2, A_2C_1, B_1C_1, B_1C_2, B_1C_1, B_2C_1, B_2C_2)\). These 7 crosses produce the offspring whose genotypic array broken down by crosses is as follows:

\[
GA_{CA_1C_1} = \left\{ \frac{1}{4} [A_1A_1 + A_1C_2 + C_1A_1 + C_1C_2] + \frac{1}{4} [A_1A_2 + A_1C_1 + A_2C_1 + C_1C_2] + \frac{1}{4} [A_1A_2 + A_1C_2 + C_1A_2 + C_1C_2] + \frac{1}{4} [A_1B_1 + A_1C_1 + C_1B_1 + C_1C_1] + \frac{1}{4} [A_1B_1 + A_1C_2 + B_1C_1 + C_1C_2] + \frac{1}{4} [A_1B_1 + A_1C_2 + B_1C_2 + C_1C_1] + \frac{1}{4} [A_1B_2 + A_1C_2 + B_2C_1 + C_1C_2] \right\}/7
\]

Based on this equation, the inbreeding coefficient of is:

\[FGA_{CA_1C_1} = \left\{ \frac{1}{4} [1 + 0 + 0 + F] + \frac{1}{4} [F + 0 + 0 + 1] + \frac{1}{4} [F + 0 + 0 + F] + \frac{1}{4} [0 + 0 + 0 + 1] + \frac{1}{4} [0 + 0 + 0 + F] + \frac{1}{4} [0 + 0 + 0 + 1] + \frac{1}{4} [0 + 0 + 0 + F] \right\}/7\]

\[= \frac{1}{4} (4 + 6F)/7\]

\[= (2 + 3F)/14\]

The inbreeding coefficient of each of the 7 groups of remaining crosses is also \((2 + 3F)/14\). Therefore, the inbreeding coefficient of the population derived from the offspring of the 8 sets of crosses \(F_{78}\) is expressed as:

\[F_{78} = (2 + 3F)/14\] (6)
It is to be expected, particularly when \( m \) is large, that the sample of plants from each parent contains groups of the 8 genotypes that form the genotypic array of each three-way line cross (Equation 2). In these cases, \( F_{78} \) (Equation 6) is not the coancestry between the \( m \) individuals that represent a three-way line cross because it does not include the part due to mating between different plants that have the same genotype.

The intraparental coancestry \( r_{0,w} \) is formed with all contributions to the inbreeding coefficient of the offspring produced by the random mating between the \( m \) individuals representing the three-way line cross, except those produced by the \( m \) self-pollinations. According to these considerations and with Equation 4:

\[
 r_{0,w} = \frac{4m^2[3(1 + F)/16] - 4m(1/2)}{4m(m - 1)}
\]

Or, in simplified form:

\[
 r_{0,w} = \frac{3m(1 + F) - 8}{16(m - 1)} \quad (7)
\]

This coancestry of the intraparental crosses (Equation 7), reduced to the case \( F = 1 \), differs from that derived by Márquez-Sánchez (2010) for pure lines (3/8), and if \( m=8 \) reduces to (2+3F)/14

Based on Equation 7, the inbreeding coefficient of the offspring produced by the random mating between the \( m \) representatives of a three-way line cross is also expressible as:

\[
 F_T = \frac{4m(1/2) + 4m(m - 1)\left[\frac{3m(1 + F) - 8}{16(m - 1)}\right]}{(2m)^2} \quad (8)
\]

Equation 8 is reducible to the form \( F_T = 3(1 + F)/16 \). This result had already been generated based on the definition of the inbreeding coefficient of the offspring produced by the random mating of a three-way line cross (Equation 4).

Generalizing, since \( Syn_T \) is generated by the random mating of \( t \) three-way line hybrids, its inbreeding coefficient (\( FSyn_T \)) in terms of \( r_{0,w} \) (Equation 7) is:

\[
 FSyn_T = \frac{4m(1/2) + 4m(m - 1)\left[\frac{3m(1 + F) - 8}{16(m - 1)}\right]}{(2m)^2} \quad (9)
\]

Clearly, \( FSyn_T \) has an inverse relationship with \( t \) and, for a fixed value of \( t \), it reaches its maximum when the parental lines of the hybrids are pure (\( F = 1 \)).

If, on the other hand, the inbreeding coefficient of the \( 3t \) initial lines is \( F \) (0 \( \leq F \leq 1 \)) and these are subjected to random mating, a synthetic (\( Syn_L \)) is formed; its inbreeding coefficient (\( FSyn_L \)), according to Márquez-Sánchez (1993), is:

\[
 FSyn_L = (1 + F)/(6t) \quad (10)
\]

According to Equations 5 and 10, respectively, if \( F = 1 \) (pure lines):

\[
 FSyn_T = \frac{3}{8t} \quad (11)
\]

and

\[
 FSyn_L = \frac{1}{3t} \quad (12)
\]

Regarding the frequencies of genes contributed by the lines of \( Syn_L \) (Equations 10 and 12) and \( Syn_T \) (Equations 5 and 11), there are differences. While in \( Syn_L \) they are balanced, in \( Syn_T \) they are not. For this difference, Equations 5 and 10 do not coincide and, consequently, \( Syn_L \neq Syn_T \). In addition, \( FSyn_T > FSyn_L \).

**Genotypic Mean**

The concept of genotypic array applied to a synthetic where the genotype of each plant from each parent is identified (Sahagún-Castellanos, 1998) will be applied to derive the genotypic mean of a \( Syn_T \).

Let \( A_{pik}A_{qjl} \) be the genotype of the individual whose parents are the individuals \( p \) and \( q \) (\( p, q = 1,2,\ldots,m \)) representing the three-way line hybrids \( i \) and \( j \), respectively \( (i, j = 1,2,\ldots,t) \), and \( k \) and \( l \) are the genes with which these parent individuals contribute \( (k, l = 1,2) \). According to this notation and Equation 1, the population that results from the random mating of the \( mt \) parent individuals must have a genotypic array (\( GEASyn_T \)) expressible as:
\[
GEASyn_T = \sum_{p=1}^{m} \sum_{q=1}^{m} \sum_{t=1}^{t} \sum_{i=1}^{2} \sum_{j=1}^{t} \sum_{k=1}^{2} [1/(2mt)^2] A_{pik} A_{qjl} 
\]

(13)

If in Equation 13 \(Y_{pik,qjl}\) and \(\bar{Y}_{Syn,T}\) are the genotypic value of \(A_{pik} A_{qjl}\) and the genotypic mean of \(Syn_T\), respectively:

\[
\bar{Y}_{Syn,T} = \sum_{p=1}^{m} \sum_{q=1}^{m} \sum_{t=1}^{t} \sum_{i=1}^{2} \sum_{j=1}^{t} \sum_{k=1}^{2} [1/(2mt)^2] Y_{pik,qjl}
\]

(14)

In addition, if: a) \(\bar{Y}_{RMT}\) is the genotypic mean of the \(t\) subpopulations generated by the random mating of the \(m\) individuals representing each TWLH, and b) \(\bar{Y}_{CP}\) is the mean of the \(t\) (\(t-1\)) subpopulations produced by the direct and reciprocal interparental crosses, according to Equation 14:

\[
\bar{Y}_{Syn,T} = \left[ \sum_{p=1}^{m} \sum_{q=1}^{m} \sum_{t=1}^{t} \sum_{i=1}^{2} \sum_{j=1}^{t} \sum_{k=1}^{2} Y_{pik,qjl} \right] / [2mt]^2
\]

\[
= [4m^2 t \bar{Y}_{RMT} + 4m^2 t (t-1) \bar{Y}_{CP}] / (2mt)^2
\]

\[
= (1/\bar{Y}_{RMT} + [(t-1)/t] \bar{Y}_{CP}
\]

\[
= \bar{Y}_{CP} - \frac{1}{t} (\bar{Y}_{CP} - \bar{Y}_{RMT})
\]

(15)

This specific result is consistent with that found in general terms by EUCARPIA-INRA (1981), presumably with a different methodology. Equation 15 is a prediction formula that deserves attention. While its application requires the experimental means of only two subpopulation groups, the one used by Márquez-Sánchez (2010) for \(Syn_T\) is based on the experimental means of each of three subpopulation groups generated by: 1) the interparental crosses (\(\bar{Y}_{CP}\)), 2) the self-pollinations of each parent (\(\bar{Y}_{CP}\)), and 3) the intraparental crosses of each parent (\(\bar{Y}_{CWP}\)). Regarding these three means from Equation 14, the following equation can also be arrived at:

\[
\bar{Y}_{Syn,T} = \bar{Y}_{CP} - \frac{1}{\bar{Y}_{CWP} - \bar{Y}_{CP}} (\bar{Y}_{CWP} - \bar{Y}_{ST})
\]

(16)

### Discussion

#### Inbreeding Coefficient

The inbreeding coefficient of \(Syn_T\) for \(F = 1\) (Equation 11) is lower than the one derived by Márquez-Sánchez (2010) for this case (\(F'Syn_T\)). The formula on which the derivation of \(F'Syn_T\) was based includes: a) \(r_{0,w}'\) = coancestry between the \(m\) individuals representing each parent, b) \(F_0 =\) inbreeding coefficient of the parents (three-way line hybrids), and c) \(r_{0,b}'\) = coancestry between individuals of different hybrids. The formula used by this author is:

\[
F'Syn_T = \left[ 1/(2mt) \right] [1 + 2m(t-1)r_{0,b}' + 2(m-1)r_{0,w}' + F_0]
\]

(17)

In this equation, Márquez-Sánchez (2010) considered that since the parental lines of the TWLHs are not related, \(r_{0,b}' = 0\) and \(F_0 = 0\); also, according to the cited study, for \(F = 1\), \(r_{0,w}' = 3/8\). With this information, this author found that:

\[
F'Syn_T = \left[ 1/(2mt) \right] [1 + 2(m-1) \left( \frac{3}{8} \right)]
\]

\[
= \frac{3m+1}{8mt}
\]

(18)

Because the lines are unrelated, it must happen that \(r_{0,b}' = 0\) and \(F_0 = 0\). However, the intraparental coancestry between the \(m\) individuals representing each parent \((r_{0,w}')\) differs from 3/8 when \(F = 1\). In this case, according to Equation 7, \(r_{0,w}' = (3m - 4)/(8(m - 1))\). This implies that the inaccuracy of \(r_{0,w}'\) is 1/[8(\(m-1\)] and that with \(r_{0,b}'\) instead of \(r_{0,w}'\) in Equation 18, it turns out that instead of \(F'Syn_T\) we get \(F'Syn_T = 3/(8t)\); that is, \(F'Syn_T\) has a bias equal to \(1/(8mt)\).

On the other hand, if the inbreeding coefficient of the lines is \(F (0 \leq F \leq 1)\), \(r_{0,b}'\) and \(F_0\) are not affected, but \(r_{0,w}'\) is (Equation 7). This change, applied to Equation 17, produces the unbiased and general IC of \(Syn_T\) (Equation 5).

Regarding the synthetics derived from only the 3r lines (\(Syn_L\)) or only the 3r three-way line crosses (\(Syn_T\)), the \(Syn_T\) lines must be the parents that by self-pollination and intraparental crosses produce the highest proportion of genotypes derived from two identical genes by descent. This is because each
line only contains 1 \((F = 1)\) or 2 \((F < 1)\) genes non-identical by descent. On the other hand, the offspring of each three-way line cross may contain 3 (when \(F = 1\)) or more (when \(F < 1\)). These considerations suggest that Syn\(_L\) is the one that has the highest inbreeding coefficient; however, this is not the case (Equations 9 and 10); the smallest of the two inbreeding coefficients is \(FSyn_L\). Part of the explanation for this apparent contradiction lies in the fact that the synthetic that has the highest proportion of interparental crosses, which are not inbred, is the Syn\(_L\) (Table 1). This is because for a fixed number of initial lines the Syn\(_L\) has three-fold the number of parents (3\(t\)) of the \(t\) that Syn\(_L\) has, which means that the percentages of interparental crosses are always higher in Syn\(_L\) (Table 1). Another factor that makes \(FSyn_L\) greater than \(FSyn_T\) is the imbalance in the frequencies of the genes that contribute the lines that form each TWLH. With balanced gene frequencies (as in Syn\(_T\)) the formation of genotypes derived from non-identical-by-descent genes (which do not contribute to the inbreeding coefficient) is maximized (Sahagún-Castellanos et al., 2013).

Regarding the origin of the 2\(m\) genes that at a locus has the sample of \(m\) plants that represent a three-way line cross of the form (\(L_aXL_bXL_c\)), half (\(m\)) invariably contributes the \(L_c\) line, while the \(L_a\) and \(L_b\) lines contribute X (0,1,2,\ldots,\(m\)) and \(Y = m - X\) genes, respectively. By contrast, in a synthetic formed with only 3\(t\) lines (3\(/2\) single crosses) each line (single cross) invariably provides 2\(m\) (\(m\)) genes. This means that the genetically more stable synthetics are those derived from only one type of parent (lines or single crosses).

Genotypic Mean

According to the magnitudes of the inbreeding coefficients and the consideration that there is an inverse linear relationship between them and the genotypic means of the synthetics (Busbice, 1970), the genotypic mean of the Syn\(_L\) of a variable such as grain yield must be greater than Syn\(_L\)'s. On the other hand, Equation 16 differs from the one derived by Márquez-Sánchez (2010) for the genotypic mean of Syn\(_T\). The difference is the sign of the term \((1/t)(\overline{Y}_{CP} - \overline{Y}_{CWP})\), which in this work is negative and in that of the cited author is positive. Regarding this difference, the details of the derivation of are shown below. From an equation analogous to that of Equation 14, Sahagún-Castellanos (1998) arrived at an expression that, adapted for \(\overline{Y}_{Syn_T}\) is:

\[
\overline{Y}_{Syn_T} = \left[\sum_{p=1}^{m} \sum_{t=1}^{m} \sum_{k=1}^{2} \sum_{l=1}^{2} Y_{pik,pl} + \sum_{p=1}^{m} \sum_{q=1}^{m} \sum_{t=1}^{2} \sum_{k=1}^{2} Y_{pik,qil} + \sum_{p=1}^{m} \sum_{q=1}^{m} \sum_{t=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} Y_{pik,qjl} \right] / (2mt)^2
\]

From the genotypic means of all the offspring of each of the three terms of the Equation 19 numerator \([self-pollinations (\overline{Y}_{S1}),\text{ intraparental crosses (} \overline{Y}_{CWP} \text{) and interparental crosses (} \overline{Y}_{CP}\text{)}], it turns out that:

\[
\overline{Y}_{Syn_T} = [4mt\overline{Y}_{S1} + 4m(m - 1)t\overline{Y}_{CWP} + 4m^2t(t - 1)\overline{Y}_{CP}] / (2mt)^2
\]

\[
= [1/(mt)][4m(t - 1)\overline{Y}_{CWP} + [m - 1]/mt]\overline{Y}_{CP} + [t - 1]t\overline{Y}_{CP}
\]

\[
= \overline{Y}_{CP} - (\overline{Y}_{CP} - \overline{Y}_{CWP}) / (t - \overline{Y}_{CWP} - \overline{Y}_{S1}) / (mt)
\]

According to Sahagún-Castellanos (1998), the prediction based on Equation 20 would be more accurate than that of Equation 15 due to having a phenotypic mean with a lower variance (Wricke and

<table>
<thead>
<tr>
<th>Synthetic variety</th>
<th>Number of initial lines (3(t))</th>
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<tbody>
<tr>
<td>SynL</td>
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</tr>
<tr>
<td></td>
<td>66.67</td>
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<tr>
<td>SynT</td>
<td>0.00</td>
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Weber, 1986). However, its strict application is not realistic because, strictly speaking, it requires: forming and evaluating in field experiments with replicates: a) \( tm \) offspring derived from self-pollination, b) \( t(t-1) \) interparental crosses and c) \( tm(m-1) \) intraparental crosses. Applying Equation 15, on the other hand, only requires forming and evaluating the \( t \) populations produced by the random mating of each three-way line cross and the \( t(t-1) \) direct and reciprocal crosses of the \( t \) three-way line hybrids.

**CONCLUSIONS**

In this study a formula was derived for predicting the genotypic mean and another for the unbiased inbreeding coefficient (IC) of the synthetic variety whose parents are \( t \) three-way line crosses generated with 3 unrelated and not necessarily pure lines (\( FSyn_T \)). With \( FSyn_T \), the problem of having only an IC that is overvalued and restricted to the use of pure lines is solved. However, \( FSyn_L \) is greater than the IC of the synthetic whose parents are the \( 3t \) lines (\( Syn_L \)). This is because: 1) the frequencies of the genes in the 3 parental lines of the \( Syn_L \) are balanced and the frequencies of these in the \( t \) three-line parental crosses of the \( Syn_T \) are not; and 2) with \( 3t \) parents in the \( Syn_T \) and \( t \) in the \( Syn_L \) the percentages of interparental crosses, which do not contribute to inbreeding, are always higher in the \( Syn_L \). Regarding the genotypic means, the inverse relationship between them and the ICs implies that \( Syn_T \)'s exceeds that of \( Syn_L \) in a variable such as grain yield.

**REFERENCES**


