

Estimation of Genetic Components in Popcorn Based on the Nested Design

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ABSTRACT

The quantification of genetic components in a base population is essential for the definition of the best breeding strategy to maximize the genetic gains. To evaluate several agronomic traits such as grain yield (GY) and popping expansion (PE) in half-sib and full-sib families derived from an open pollinated popcorn population, this study used a nested design, in two contrasting environments in the Northern Fluminense region of Rio de Janeiro, Brazil. Results showed: a) high significance of male and female within male sources of variation for most traits studied; b) absence of genotype by environmental interaction for PE; c) overdominance for GY and additivity for PE; d) low narrow sense of heritability for GY as opposed to PE; e) intermediate family heritability mean for GY and high for PE; and f) high genetic gain estimates for both GY and PE provided by the full-sib recurrent selection. These results indicate the perspective of success for intrapopulation breeding methods in popcorn for popping expansion allowing the prediction of satisfactory genetic gain for the Northern Fluminense.

KEY WORDS: Popcorn, *Zea mays*, Nested design, Design I, Genetic components, Genetic gain.

INTRODUCTION

The popcorn, despite being highly appreciated in the Brazilian market, is, in its majority, imported, mainly due to the low breeding efforts with this crop in the country (Linares, 1987; Zanette, 1989; Gama et al., 1990; Andrade, 1996). Thus, the development of genetic material with high agronomic potential and great consumer acceptance, especially for popping expansion, the main characteristic in defining popcorn quality, is highly desirable.

For the development of superior genotypes, the knowledge of the aspects related to the inheritance of key traits in popcorn is of relevant importance. The estimation of genetic components in a base population is fundamental for the definition of the best breeding procedure aiming at the maximization of genetic gains.

The design I or simply the nested design (Comstock and Robinson, 1948) is an appropriated alternative to study the genetic

structure of a population. Due to its random aspect, all the individuals contribute to the genetic information (Hallauer and Miranda Filho, 1988; Furtado, 1996). Yet, if the descendent are evaluated in different environments, the inferences become more efficient for the indication of the best breeding strategy to obtain higher genetic gains.

Despite being highly used in corn (Hallauer and Miranda Filho, 1988; Eyherabide and Hallauer, 1991; Furtado, 1996; Paterniani and Campos, 1999), the use of design I is rare in popcorn (Hallauer, 1985).

Thus, this investigation was planned with the main objective of estimating the genetic components in a base popcorn population in two contrasting environments to determine the best breeding procedure to reach satisfactory genetic gains, especially in relation to popping expansion and grain yield. The detailed knowledge of the genetic variability constitutes the first step to develop a breeding program for this crop in the Northern Fluminense region, of Rio de Janeiro, Brazil.

MATERIALS AND METHODS

A UNB-2U open pollinated variety, originated from UNB-2 variety, after two cycles of mass selection in Campos dos Goytacazes, Rio de Janeiro, Brazil, was used in this study. The UNB-2 originated from the UNB-1 variety which came from a 'Composto Indígena' selection donated to UNB (University of Brasília, Brazil) by ESALQ/USP, Piracicaba, São Paulo, Brazil. The UNB-1 was crossed with an American popcorn variety. Selected plants from that cross were crossed with yellow popcorn, a high yield and resistant to *Exserohilum turcicum* genotype. After the second crossing, mass selection was applied to form a population of resistant high yielding and with yellow kernels plants. Such population was than backcrossed three times to the American popcorn variety, eventually originating the UNB-2 open pollinated variety.

Half-sib and full-sib progenies in UNB-2U were developed by using random S_0 plants as parents with an inbreeding coefficient of $F = 0$ followed by the nested (design I) mating design (Comstock and Robinson, 1948). Design I progenies were obtained from random S_0 plants using one plant as male crossed with four random plants as females. The 20 full-sib progenies developed from five males constituted one set. One hundred design I full-sib progenies or five sets were programmed. As eight full-sib progenies failed, they were replaced on the fifth set by controlling genotypes: a) Braskalb (B); b) UNB-2U (U); c) Viçosa (V); d) UNB-2S1; e) UNB-2S2; f) B x U; g) B x V; and h) U x V. Braskalb and Viçosa genotypes are commercial varieties, UNB-2S1 and UNB-2S2 are different selections from UNB-2U, while B x U, B x V and U x V are their respective hybrids. Both Braskalb and Viçosa are American popcorn type varieties.

The 92 full-sib progenies plus the eight controlling genotypes were grown during the traditional corn planting season (October, 1997 to March, 1998), in a randomized complete block experimental design with two replications within sets, in two distinct environments: Experimental Station at

PESAGRO-RIO in Campos dos Goytacazes and in Itaocara, Rio de Janeiro, Brazil. Each progeny was evaluated in a five meter long, two-row plot spaced one meter among rows and 0.20 meter among plants within row.

Data were collected in both environments for sixteen agronomic traits. For simplicity, only six traits were analyzed and discussed: a) days from planting to 50 % silk emergence (FLO); b) plant height in m (PH); c) grain yield in Kg/ha (GY) – about 12 % grain moisture; d) one hundred seed weight in g (SW); e) one hundred seed volume in cm^3 (SV); and f) popping expansion (PE).

The PE was obtained from random samples from the harvested plot. The volume in cm^3 of 40 g of grain with about 12 % of moisture was measured before and after popping, producing the correspondent ratio (PE = volume after popping/volume before popping). The PE evaluation was conducted after the corn seeds were submitted to a microwave at maximum power (900 W) for three minutes for each sample. The data were the mean of two samples for each plot.

The genetic-statistic model and its assumptions, the analysis of variance (Table 1) as well as the translation of the covariances of relatives into genetic variances for the nested mating design were those based on Comstock and Robinson (1948) and Hallauer and Miranda Filho (1988). Each set was analyzed separately and then pooled for each environment, over the five sets and finally pooled over the two environment, over the five sets and finally pooled over the two environments. All sources of variation, except environments were considered to be random effects. The SAS (1985) program was used to analyze the data.

The design I (Comstock and Robinson, 1948) provided the estimation of the variance components: male variance (\mathbf{S}_M^2); female within male variance ($\mathbf{S}_{F/M}^2$); environment and male interaction variance (\mathbf{S}_{EM}^2); environment and female/male interaction variance ($\mathbf{S}_{EF/M}^2$); and the residual (plot) variance (\mathbf{S}^2). The within plot

variance (\mathbf{s}_w^2) was considered to be $10 \mathbf{s}^2$ as indicated by Hallauer and Miranda Filho (1988). The variance components were translated into covariances which allowed the estimation of the genetic components of the variances: additive genetic (\mathbf{s}_A^2); deviation due to dominance (\mathbf{s}_D^2); interaction of the additive genetic and environment (\mathbf{s}_{AE}^2); interaction of the deviation due to dominance and environment (\mathbf{s}_{DE}^2).

With the genetic components of variance the following genetic parameters were obtained (Hallauer and Miranda Filho, 1988; Falconer, 1989): narrow sense heritability (h^2); broad sense heritability (h_b^2); heritability on the family mean base (h_u^2); and the average degree of dominance (K), where:

$$h^2 = \frac{\mathbf{s}_A^2}{\mathbf{s}_A^2 + \mathbf{s}_D^2 + \mathbf{s}_{AE}^2 + \mathbf{s}_{DE}^2 + \mathbf{s}^2};$$

$$h_b^2 = \frac{\mathbf{s}_A^2 + \mathbf{s}_D^2}{\mathbf{s}_A^2 + \mathbf{s}_D^2 + \mathbf{s}_{AE}^2 + \mathbf{s}_{DE}^2 + \mathbf{s}^2};$$

$h_u^2 = \frac{\mathbf{s}_M^2}{MSM / efr}$, where **MSM** is the mean square for male and **e**, **f** and **r** are the number of environments, female within male and replications, respectively (Table 1); and

$$K = \sqrt{\frac{2\mathbf{s}_D^2}{\mathbf{s}_A^2}}; \text{ and}$$

Also, besides the genetic parameters, the genetic components of variance allowed the estimation of the genetic gain according to different intrapopulation recurrent selection methods (Hallauer and Miranda Filho, 1988) using the general formulae (Eberhart, 1970) as indicated:

$$\Delta G = \frac{ck\mathbf{s}_g^2}{y\mathbf{s}_p},$$

where:

ΔG = estimated genetic gain per year;

c = parental control;

k = standard selection intensity assuming the value of 1.4 when 20 % of the superior genotypes are selected;

\mathbf{s}_g^2 = proportion of additive genetic variation of the respective progenies;

y = number of years per cycle of selection; and

\mathbf{s}_p = standard deviation of the phenotypic variation.

Table 1 - Analyses of variance table for the evaluated agronomic traits.

| SV | DF | MS | E(MS) ^{1/} | F |
|--------------------------|---------------------|------|--|-------------|
| Environments (E) | e - 1 | MSE | $\mathbf{s}^2 + r\mathbf{q}\mathbf{s}_{EF/M}^2 + fr\mathbf{s}_{EM}^2 + fm\mathbf{s}_R^2 + fmr\mathbf{q}\mathbf{s}_{ES}^2 + fmrs\Phi_E$ | |
| Sets (S) | s - 1 | MSS | $\mathbf{s}^2 + er\mathbf{s}_{F/M}^2 + efr\mathbf{s}_M^2 + efmr\mathbf{s}_S^2$ | |
| E x S | (e - 1) (s - 1) | MSES | $\mathbf{s}^2 + r\mathbf{q}\mathbf{s}_{EF/M}^2 + fr\mathbf{q}\mathbf{s}_{EM}^2 + fm\mathbf{s}_R^2 + fmr\mathbf{q}\mathbf{s}_{ES}^2$ | |
| Replications (R) / E x S | es (r - 1) | MSR | $\mathbf{s}^2 + fm\mathbf{s}_R^2$ | |
| Males (M) / S | s (m - 1) | MSM | $\mathbf{s}^2 + er\mathbf{s}_{F/M}^2 + efr\mathbf{s}_M^2$ | MSM / MSF |
| Females (F) / M / S | ms (f - 1) | MSF | $\mathbf{s}^2 + er\mathbf{s}_{F/M}^2$ | MSF / MSER |
| E x M / S | s (e - 1) (m - 1) | MSEM | $\mathbf{s}^2 + r\mathbf{q}\mathbf{s}_{EF/M}^2 + fr\mathbf{q}\mathbf{s}_{EM}^2$ | MSEM / MSEF |
| E x F / M / S | ms (e - 1) (f - 1) | MSEF | $\mathbf{s}^2 + r\mathbf{q}\mathbf{s}_{EF/M}^2$ | MSEF / MSER |
| Error | es (r - 1) (fm - 1) | MSER | \mathbf{s}^2 | |
| Total | emrs - 1 | | | |

$$1/ \mathbf{q} = \frac{e}{e-1}; \quad \Phi_E = \frac{\sum E_i^2}{e-1}.$$

RESULTS AND DISCUSSION

Table 2 shows the estimated means for the highest and lowest family values and for the eight controlling genotypes and the LSD (0.05) for the evaluated traits. For all the traits there is at least one family superior to all the controlling genotypes, indicating high agronomic potential of the UNB-2U population as the source of superior genotypes. Comparing the variation amplitude and the LSD for all the traits, it is possible to infer the existence of high variability in the population.

For GY, there is no significant difference between the high family and the high controlling genotype, the UNB-2U itself. On the other hand, the high family for PE was statistically superior to the high controlling genotype, the hybrid between the UNB-2U and the Braskalb. This denotes more accentuated variability for PE, indicating that this trait can be easier improved than GY in the present population.

In fact, investigations have demonstrated some difficulty to combining high yield and good PE. Such difficulty has been attributed to the existence of negative correlations among PE of popcorn and other important agronomic traits (Brunson, 1937; Lima *et al.*, 1971; Verma and Singh, 1979; Lira, 1983; Andrade, 1996). However, Pacheco *et al.* (1998) based on estimated genetic parameters of the second cycle half-sib progenies derived from the populations CMS-42 e CMS-43, reported that it is possible to select genotypes combining high yield and good popping expansion. But, they considered easier the selection for PE than for GY, which is in agreement with results obtained by Lira (1983) and with the present results.

The analysis of variance results (Table 3), including only the 92 design I families indicated significant differences for all traits, for the male and female within male sources of variation. The significance for male is an evidence for the presence of genetic variability in the UNB-2U, indicating possibility of genetic gains with selection.

Table 2 - Mean estimates of the highest and lowest family values among the 92 design I progenies for the six evaluated traits and the correspondent mean values of the eight controlling genotypes and the LSD (0.05).

| Traits ^{1/} | FLO | PH | GY | SW | SV | PE |
|----------------------|-------|------|------|-------|-------|-------|
| Highest value | 65.00 | 2.10 | 1.51 | 17.88 | 24.00 | 13.82 |
| Lowest value | 57.00 | 1.44 | 0.31 | 10.63 | 14.00 | 6.11 |
| LSD (0.05) | 2.55 | 0.16 | 0.33 | 1.17 | 1.55 | 1.61 |
| Controlling | | | | | | |
| Braskalb (B) | 59.50 | 1.87 | 1.00 | 12.91 | 17.00 | 9.13 |
| UNB-2U (U) | 59.75 | 1.83 | 1.31 | 13.13 | 17.50 | 10.01 |
| Viçosa (V) | 62.25 | 1.76 | 0.86 | 12.95 | 17.12 | 10.01 |
| UNB2-S1 | 59.00 | 1.66 | 0.88 | 13.73 | 18.50 | 8.00 |
| UNB-2S2 | 62.25 | 1.74 | 0.81 | 12.49 | 16.37 | 8.77 |
| V x B | 61.75 | 1.74 | 0.57 | 11.94 | 16.25 | 8.25 |
| U x B | 61.00 | 1.84 | 0.95 | 13.69 | 18.25 | 10.73 |
| V x U | 58.25 | 1.72 | 1.25 | 12.91 | 17.37 | 9.23 |

^{1/} FLO = days from planting to 50 % silk emergence; PH = plant height; GY = grains yield; SW = one hundred seed weight; SV = one hundred seed volume; and PE = popping expansion.

Table 3 - Mean squares for the six evaluated traits for the 92 design I progenies of popcorn.

| Source | df | Mean Squares ^{1/} | | | | | |
|---------------------|-----|----------------------------|---------------------|---------------------|----------|----------|---------------------|
| | | FLO | PH | GY | SW | SV | PE |
| E | 1 | 7.347 | 8.050 | 31.989 | 2610.208 | 4363.575 | 15.256 |
| S | 4 | 78.686 | 0.549 | 0.301 | 22.175 | 34.866 | 25.596 |
| ES | 4 | 38.502 | 0.117 | 0.466 | 14.336 | 15.098 | 9.458 |
| R/ES | 10 | 8.816 | 0.138 | 0.094 | 2.631 | 4.564 | 1.581 |
| M/S | 18 | 24.943** | 0.151** | 0.228* | 12.439** | 26.325** | 36.117** |
| F/M/S | 69 | 7.333** | 0.036** | 0.125** | 3.405** | 7.377** | 5.573** |
| EM/S | 18 | 6.674* | 0.024 ^{ns} | 0.140* | 4.047** | 6.210* | 2.617 ^{ns} |
| EF/M/S | 69 | 3.601 ^{ns} | 0.018* | 0.066 ^{ns} | 1.275** | 2.268** | 1.477 ^{ns} |
| Error | 174 | 3.361 | 0.013 | 0.061 | 0.729 | 1.230 | 1.309 |
| CV _e (%) | | 3.011 | 6.441 | 26.737 | 6.272 | 6.135 | 11.874 |

^{1/} FLO = days from planting to 50 % silk emergence; PH = plant height; GY = grains yield; SW = one hundred seed weight; SV = one hundred seed volume; and PE = popping expansion.

^{ns} = Nonsignificant at the 0.05 level;

* = Significant at the 0.05 level; and

** = Significant at the 0.01 level.

The absence of significance for the interactions environment by male and environment by female within male for PE indicates a similar behavior of the design I progenies in the two distinct environments. Such behavior suggests the possibility of simultaneous recommendation of superior segregants in advanced generations for the evaluated locals in the North Fluminense region.

The estimates for genetic components (Table 4) show a greater importance of the dominance deviation (\mathbf{S}_D^2) in relation to additivity (\mathbf{S}_A^2) for GY only. Actually, for some traits (FLO, PH and PE) the \mathbf{S}_D^2 assumed negative values, considered nulls in this study. According to Hallauer and Miranda Filho (1988), since different females are crossed with the same male, these females within male may be similar in flowering to the male. So the component due to the $\mathbf{S}_{F/M}^2$ may be reduced, naturally underestimating the dominance deviation. Also, the design I system of mating tends to favor the homozygosity, resulting in a superestimation of the additive variance at the expense of the dominance deviation, as discussed by Gouesnard and Gallais (1992).

The average degree of dominance (Table 4) indicated the presence of overdominance for GY, partial dominance for SW and SV and additivity for the other traits (FLO, PH and PE). These results reflect the magnitude and the importance of the knowledge of the genetic component of variance (\mathbf{S}_A^2 and \mathbf{S}_D^2).

The narrow sense heritability estimates were high (82.72 %) for PE and low (17.85 %) for GY (Table 4). These values permit to infer that expressive genetic gain in selection programs are expected for popping expansion.

Furtado (1996) points out that despite the predictive nature of the narrow sense heritability, such high estimates don't necessarily indicate expressive genetic gains by selection, once the high values may occur for traits with low additive variance, since the environmental effect on such trait may be small.

In the present investigation there was a large difference between additive variance component (\mathbf{S}_A^2) and the residual component (\mathbf{S}_D^2) for PE

Table 4 - Genetic component estimates for the six evaluated traits for the 92 design I progenies of popcorn.

| Traits ^{1/} | Genetic Components ^{2/} | | | | | | | | |
|----------------------|----------------------------------|--------------|--------------|-----------------|-----------------|--------|---------|---------|---------|
| | σ^2 | σ_A^2 | σ_D^2 | σ_{AE}^2 | σ_{DE}^2 | K | h^2 | h_b^2 | h_u^2 |
| FLO | 3.3611 | 4.4027 | 0.0000 | 0.7684 | 0.0000 | 0.0000 | 51.6010 | 51.6010 | 70.6030 |
| PH | 0.0134 | 0.0242 | 0.0000 | 0.0008 | 0.0000 | 0.0000 | 63.0208 | 63.0208 | 75.7900 |
| GY | 0.0610 | 0.0257 | 0.0388 | 0.0184 | 0.0000 | 1.7377 | 17.8596 | 44.7800 | 44.8864 |
| SW | 0.7296 | 2.2584 | 0.4180 | 0.6932 | 0.0000 | 0.6084 | 55.0937 | 65.2908 | 72.6274 |
| SV | 1.2309 | 4.7369 | 1.4100 | 0.9856 | 0.0516 | 0.7716 | 56.2911 | 73.0469 | 71.9747 |
| PE | 1.3093 | 7.6360 | 0.0000 | 0.2848 | 0.0000 | 0.0000 | 82.7293 | 82.7293 | 84.5663 |

^{1/} FLO = days from planting to 50 % silk emergence; PH = plant height; GY = grains yield; SW = one hundred seed weight; SV = one hundred seed volume; and PE = popping expansion.

^{2/} σ^2 = residual variance; σ_A^2 = additive variance; σ_D^2 = dominance variance; σ_{AE}^2 = interaction of the additive genetic and environment; σ_{DE}^2 = interaction of the dominance and environment; K = average degree of dominance; h^2 = narrow sense heritability; h_b^2 = broad sense heritability; and h_u^2 = heritability on the family mean base.

(Table 4) showing that the additivity was the most important source of variation. This indicated that the narrow sense heritability is a good predictor of genetic gains for selection for popping expansion.

Considering that for PE, the most important trait for popcorn, the inheritance was typically additive (Table 4), interpopulational breeding methods, emphasizing the exploitation of heterosis are not applicable to this population. Thus, in this investigation, only the intrapopulation recurrent selection methods were considered for the

estimation of genetic gains (Table 5).

Referring to the intrapopulation breeding strategies, Borém (1997) points out that the estimated genetic gain per year is the best way to evaluate the efficiency of the different methods. The main reason for that is that each breeding recurrent selection procedure takes a specific number of year per cycle and, consequently the only valid comparison is the genetic gain on a year basis.

The estimated values on Table 5 indicates that the full-sib recurrent selection method may provide the

Table 5 - Estimated genetic gain in the UNB-2U popcorn for grain yield (GY) and for popping expansion (PE), considering a selection intensity of 20 % of the genotypes, based on the intrapopulacional recurrent selection methods.

| Recurrent Selection Methods | Genetic Gains (% , per year) | |
|---------------------------------|------------------------------|-------|
| | GY | PE |
| Mass Selection | 2.23 | 11.77 |
| Stratified Mass Selection | 2.33 | 12.13 |
| Half-sib Family Selection | 6.26 | 18.45 |
| Full-sib Family Selection | 9.42 | 27.09 |
| S ₁ Family Selection | 7.93 | 19.54 |

largest annual genetic gain, reaching 9.42 % for GY and 27.09 % for PE. This demonstrates the perspective of success for intrapopulation methods for popping expansion and grain yield. The expectation is that, after a few cycles of full-sib

recurrent selection, the UNB-2U population will present a very high potential to be released as a new popcorn variety for the Northern Fluminense region of Rio de Janeiro, Brazil.

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RESUMO

Estimativas de Componentes Genéticos em Milho Pipoca com Base no Delineamento I de Comstock e Robinson

A quantificação de componentes genéticos em uma população-base é essencial para se definir a estratégia de melhoramento que maximize os ganhos desejados. Para tanto, foi utilizado o Delineamento I, de Comstock e Robinson (1948), na avaliação de noventa e duas famílias de irmãos completos de milho pipoca, em dois ambientes contrastantes da Região Norte do Estado do Rio de Janeiro. Foram avaliadas diversas características, dentre as quais, produtividade de grãos (GY) e capacidade de expansão (PE). Os principais resultados obtidos foram: a) elevada significância das fontes de variação ‘macho’ e ‘fêmea/macho’ ocorreu para a maioria das características; b) houve ausência de interação dos genótipos por ambientes para PE; c) a sobredominância destacou-se para GY e a aditividade para PE; d) ao contrário de PE, GY exibiu baixa herdabilidade no sentido restrito; e) as magnitudes da herdabilidade com base na média de famílias foram média para GY e elevada para PE; e f) tanto para GY quanto para PE, os maiores ganhos são possíveis com a seleção recorrente entre famílias de irmãos completos. Tais resultados indicam a perspectiva de sucesso no melhoramento intrapopulacional para capacidade de expansão em milho pipoca, antevendo-se

ganhos genéticos satisfatórios para o Norte Fluminense.

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