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SHORT REPORT

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ABSTRACT

A Bayesian analysis of genetic parameters for quantitative traits was carried out in full-sib families of popcorn through four cycles (C_5, C_6, C_7, and C_8) of recurrent selection. The parameters of Bayesian model were estimated using the independence chain algorithm. Grain yield and plant height were found to be moderately heritable ranging from 0.25 to 0.48 and 0.45 to 0.58, respectively. The highest heritability estimates were found for popping expansion volume at C_5 ($\hat{h}^2_{C_5} = 0.71$), and C_7 ($\hat{h}^2_{C_7} = 0.63$). The response of recurrent selection was 30.5 and 32.3% for grain yield and popping expansion volume, respectively. In C_8, predicted genetic advances (from the Bayesian prediction of genotypic values) were 4.8, 4.3, and 2.9% for plant height, grain yield, and popping expansion volume, respectively. The significant genetic variability among popcorn families in successive cycles of recurrent selection has sustained continued genetic progress in breeding for the traits of interest.

Among different types of maize, popcorn (*Zea mays* var. *everta* Sturt.) is an important commercial crop throughout the world (Sweley et al., 2013). Popping expansion volume is the most important quality trait in popcorn and the one that distinguishes it from all other types of maize (Babu et al., 2006; Lu et al., 2003). However, popcorn germplasm is generally inferior to normal maize in yield and other agronomic traits (Li et al., 2007). In that sense, the objective of popcorn breeding programs is to develop cultivars that unite good agronomic characteristics with a high popping expansion rate (Da Silva et al., 2015). To obtain popcorn cultivars, an appropriate level of parental divergence is required (Miranda et al., 2008). One approach is to adopt recurrent selection to gradually accumulate, by recombination cycles, the desirable, and available alleles in different parents (Bita & Gerats, 2013; Doná et al., 2012). This method increases the frequency of favorable alleles through repeated selection cycles of superior individuals and does not reduce the genetic variability of the population (Freitas et al., 2014; Zhang et al., 2014).

Recurrent selection is a key breeding procedure employed to improve the populations of crop plants particularly those of cross-pollinated species. In popcorn, recurrent selection has shown to be effective in providing genetic gains with respect to the commercial importance traits. The genetic gain is dependent on parental selection (Solalinde et al., 2014) and the heritability of the traits under selection (Zhang et al., 2014). Therefore, the knowledge of the aspects related to the inheritance of traits of interest in popcorn is of relevant importance and, in consequence, it should be calculated as accurately as possible (Mora & Scapim, 2007). The Bayesian approach, for instance, is a useful alternative for scientific inference in the genetic evaluation of popcorn (Rodovalho et al., 2014). Bayesian methods are increasingly being employed in plant breeding, enabled by Markov Chain Monte Carlo Methods (MCMC) methods. One advantage of the Bayesian procedures is the possibility of using the credibility regions as an alternative estimation of genetic parameters, which are obtained directly from posterior distribution (Mora & Serra, 2014). In the current study, a Bayesian analysis of genetic parameters for quantitative traits was carried out in full-sib families of popcorn through four cycles (C_5, C_6, C_7, and C_8) of recurrent selection, in the state of Rio de Janeiro, Brazil.

Materials and methods

The UENF-14 population, developed after five cycles of recurrent selection from UNB-2U (Amaral et al., 2013), was

used in this study. The UNB-2U population was derived from UNB-2 after two cycles of mass selection. To obtain the UNB-2 population, the UNB-1 variety, which came from an 'indigenous composite breed' selection, was crossed with the American popcorn, a high popping expansion volume variety. The selected progenies were crossed with yellow popcorn, a high-yielding and resistant to *Exserohilum turcicum* variety. After two cycles of mass selection, the population obtained was backcrossed three times with the American variety, resulting in the UNB-2 population (Pereira & Amaral, 2001).

The cycles were evaluated every two years, each consisting of 200 full-sib families. Thus, the populations corresponding to the cycles C_5, C_6, C_7, and C_8 were seeded in October 2007, 2009, 2011, and 2013, respectively, in two contrasting sites: Campos dos Goytacazes and Itaocara. Families were arranged in a randomized complete block design with two replications ($r = 2$) each consisting of 25 individual plants. Therefore, each family was represented by 50 plants per site and 100 plants over the two sites. The experimental plots consisted of single rows of 6 m long with a spacing of 0.9 m between rows and 0.2 m between plants (55,555 plants ha^{-1}). The populations evaluated in this study were UENF-14-C_5, UENF-14-C_6, UENF14-C_7, and UENF14-C_8 corresponding to the cycles 5, 6, 7, and 8, respectively. In each cycle, the selection intensity was 20% and the best families were selected by the index of Mulamba and Mock (1978) using random economic weights. Further information on the selection procedures can be obtained from Freitas et al. (2009), Rangel et al. (2011), Ribeiro et al. (2012) and Freitas et al. (2014). The following quantitative traits were assessed: plant height (PH; measured in m), grain yield (GY; in kg ha^{-1}), and popping expansion volume (PE; in mL g^{-1}).

A Bayesian variance component estimation model was assumed using the Independence Chain algorithm (Wolfinger & Kass, 2000), a variant of the MCMC methods. Phenotypic data were analyzed using the following general statistical model, which considered the four cycles simultaneously: $\mathbf{y} = \mathbf{X\beta} + \mathbf{Z\mu} + \mathbf{Wp} + \mathbf{\varepsilon}$, where $\mathbf{y}$ is a $3{,}200 \times 1$ column vector of a continuous random variable, normally distributed, and refers to the quantitative traits of interest (GY, PE, and PH). $\mathbf{\beta}$ is a 17×1 column vector with the effects due to environments, replicates and cycles. $\mathbf{\mu}$ is a 800×1 column vector of family effect nested within cycle. $\mathbf{p}$ is a $1{,}600 \times 1$ column vector of the family–environment interaction (F × E). $\mathbf{\varepsilon}$ is an unobserved $3{,}200 \times 1$ vector of residual errors. $\mathbf{X}$, $\mathbf{Z}$, and $\mathbf{W}$ are known incidence matrices. In this case, we consider families and environments nested within cycles, and the replicates nested within environments due to the field design. For single-cycle analysis, $\mathbf{y}$ is a 800×1 vector of observations; $\mathbf{\beta}$ is a 7×1 vector with the effects due to environments and replicates nested within

environments; $\mathbf{\mu}$ is a 200×1 vector of family effect; $\mathbf{p}$ is a 400×1 vector of the F × E interaction, and $\mathbf{\varepsilon}$ is a 800×1 vector of residual errors. In which, Variance $(\mathbf{\mu}) = \mathbf{G} = \mathbf{I}\sigma_F^2$, Variance $(\mathbf{p}) = \mathbf{P} = \mathbf{I}\sigma_{FE}^2$ and Variance $(\mathbf{\varepsilon}) = \mathbf{R} = \mathbf{I}\sigma_\varepsilon^2$, where $\mathbf{I}$ is an identity matrix with dimension equal to number of records, $\sigma_F^2, \sigma_{FE}^2$ and σ_ε^2 are the family, interaction, and residual variances, respectively. Heritability on a family-mean basis was estimated through the four cycles, as follows: $\hat{h}_{Cycles}^2 = \sigma_{F(C)}^2 \big/ (\sigma_{F(C)}^2 + \sigma_{F(C)E}^2/e + \sigma_\varepsilon^2/r \cdot e)$ where $\sigma_{F(C)}^2$ is the family variance (genotypic variance) nested within cycles of selection, e is the number of environments, and r is the number of replicates ($r = 2$). Heritability was estimated within each cycle as follows: $\hat{h}_{Ci}^2 = \sigma_F^2 \big/ (\sigma_F^2 + \sigma_{FE}^2/e + \sigma_\varepsilon^2/r \cdot e)$ with $i = 5, 6, 7$, and 8. The Bayesian information criterion (BIC) or Schwarz criterion was computed to check the significance of the family and interaction effects (Mora & Serra, 2014). In the case when the family–environment interaction was found to be statistically insignificant (according to BIC), the interaction variance was removed from the heritability equations. Response of recurrent selection (SR%) was calculated as: $\text{SR}\% = [(\hat{\mu}_{C_8} - \hat{\mu}_{C_5})/\hat{\mu}_{C_5}] * 100$, where $\hat{\mu}_{C_8}$ and $\hat{\mu}_{C_5}$ are the C_8 and C_5 population means, respectively. Predicted genetic gains (PG%) for selection of 20% of the best full-sib families were estimated in the cycle 8 as follows: $\text{PG}\% = [(\hat{\mu}_{s8} - \hat{\mu}_{g8})/y_p] * 100$, where, $\hat{\mu}_{s8}$ is the estimated posterior mean of the genotypic values of selected families, $\hat{\mu}_{g8}$ is the estimated posterior population mean of the genotypic values of all families; y_p is the mean of phenotypic value estimated in the cycle 8. Coefficients of genetic variation (CVG) were calculated from posterior samples as follows: $\text{CVG} = \sqrt{\hat{\sigma}_F^2/y}$, where y is the overall mean calculated across cycles of recurrent selection. Marginal posterior distributions of the variance components, genotypic values, CVG, and family-mean heritabilities, were obtained using the Independence Chain algorithm from the MIXED procedure of SAS, with the option PRIOR and posterior sample size of 5000. The prior densities of the variance components were obtained in the first run using Jeffreys' prior distribution; and subsequently, the second run was performed using these densities – DATA statement (Rodovalho et al., 2014).

Results and discussion

The family effect was significant for all the traits studied (Table 1). According to the BIC, there was a very strong evidence against the reduced models in which the family effects are assumed to be zero. This result confirmed a significant amount of genetic variation among full-sib families for the traits studied, indicating a significant contribution of additive genes in the expression of these traits (Bhandari et al., 2010). This result is also in accordance with other studies in which the family effect was significant

Table 1. Bayesian information criterion of Schwarz (BIC; smaller is better) for model selection (family and family–environment interaction) in popcorn full-sib families evaluated through four cycles of recurrent selection.

	Plant height		Grain yield		Popping expansion volume	
Model	−2LLR	BIC	−2LLR	BIC	−2LLR	BIC
$\mathbf{y = X\beta + Z\mu + \varepsilon}$	−2,169	−2,155	51,266	51,279	19,599	19,612
$\mathbf{y = X\beta + \varepsilon}$	−2019	−2011	51,361	51,369	19,678	19,686
$\mathbf{y = X\beta + Z\mu + Wp + \varepsilon}$	−2,169	−2,155	51,264	51,284	19,598	19,618
$\mathbf{y = X\beta + Z\mu + \varepsilon}$	−2,169	−2,155	51,266	51,279	19,599	19,612

−2LLR: −2 multiplied by log likelihood (restricted). $\mathbf{y = X\beta + Z\mu + Wp + \varepsilon}$ is the full model, which include genotypic effect of families and family–environment interaction; $\mathbf{y = X\beta + Z\mu + \varepsilon}$ is a model without family–environment interaction; $\mathbf{y = X\beta + \varepsilon}$ is a null model, without family and family–environment interaction effects.

using the recurrent selection scheme (Daros et al., 2002; Freitas et al., 2009; Rangel et al., 2011).

Table 2 presents the Bayesian point estimates and high posterior density interval (at 90%) for the heritability values calculated through four cycles of recurrent selection. Grain yield and plant height were found to be moderately heritable ranging from 0.25 (C_5 and C_8) to 0.48 (C_6) and 0.45 (C_6) to 0.58 (C_5), respectively. The highest heritability estimates were found for popping expansion volume at C_5 and C_7; posterior mode $\hat{h}^2_{C_5} = 0.71$ (90% credible interval: 0.63–0.77) and $\hat{h}^2_{C_7} = 0.63$ (90% credible interval: 0.56–0.70), respectively. One possible explanation for this result may be because the recurrent selection method led to a higher concentration of alleles with additive effects for popping expansion volume. Moreover, Lu et al. (2003) indicated that popping expansion is less influenced by the environment and dominance deviations than yield, and that three to four genes may be involved in the

inheritance of popping expansion. In contrast, many genes control grain yield and plant height (Flint-Garcia et al., 2005; Yan et al., 2006). In the present study, the heritability calculated on a family-mean basis through the four cycles was 0.49, 0.37, and 0.36 for plant height, grain yield, and popping expansion, respectively. These results are in agreement with those found by Rodovalho et al. (2014) in a trial of half-sib families of popcorn evaluated using a Bayesian approach; family-mean heritability estimates ranged from 0.22 to 0.44, and from 0.28 and 0.49, for popping expansion volume and grain yield, respectively. On the other hand, Arnhold et al. (2009) found larger estimates of heritability in Brazil suggesting good potential for improving popping expansion volume by selection and breeding; single-site heritability for popping expansion in S3 families ranged from 0.58 to 0.85 with a mean of 0.7. Similarly, Lu et al. (2003) found a heritability of 0.73 on an S1 family mean.

Table 2. Family-mean heritability estimates for plant height, grain yield and popping expansion volume calculated through four cycles of recurrent selection (C_5, C_6, C_7, and C_8).

	Bayesian estimates					
Trait /parameter	Mean	Median	Mode	SD	LL	UL
Plant height						
$\hat{h}^2_{C_5}$	0.580	0.581	0.580	0.049	0.495	0.657
$\hat{h}^2_{C_6}$	0.454	0.455	0.449	0.066	0.334	0.557
$\hat{h}^2_{C_7}$	0.523	0.527	0.532	0.054	0.426	0.605
$\hat{h}^2_{C_8}$	0.548	0.551	0.558	0.054	0.455	0.629
$\hat{h}^2_{Cycles}$	0.487	0.487	0.486	0.0289	0.438	0.533
CVG%	4.0	4.0	4.0	0.2085	3.7	4.4
Grain yield						
$\hat{h}^2_{C_5}$	0.245	0.248	0.252	0.102	0.070	0.410
$\hat{h}^2_{C_6}$	0.482	0.489	0.498	0.070	0.357	0.583
$\hat{h}^2_{C_7}$	0.405	0.409	0.413	0.069	0.285	0.511
$\hat{h}^2_{C_8}$	0.247	0.247	0.233	0.097	0.076	0.400
$\hat{h}^2_{Cycles}$	0.374	0.377	0.384	0.044	0.302	0.444
CVG%	10.3	10.4	10.6	0.815	9.0	11.6
Popping expansion						
$\hat{h}^2_{C_5}$	0.705	0.708	0.711	0.043	0.631	0.768
$\hat{h}^2_{C_6}$	0.078	0.064	0.030	0.061	0.004	0.201
$\hat{h}^2_{C_7}$	0.632	0.633	0.633	0.042	0.556	0.699
$\hat{h}^2_{C_8}$	0.270	0.274	0.277	0.086	0.116	0.397
$\hat{h}^2_{Cycles}$	0.361	0.364	0.365	0.043	0.283	0.429
CVG%	6.4	6.4	6.4	0.525	5.5	7.2

*SD: standard deviation; $\hat{h}^2_{Ci}$: heritability on a family-mean basis for each cycle; $\hat{h}^2_{Cycles}$: heritability calculated through cycles; CVG%: coefficient of genetic variation; LL and UL: lower and upper limits of the Bayesian credible intervals ($p = 90\%$).

Table 3. Response of recurrent selection measured in full-sib families of popcorn, in the state of Rio de Janeiro, Brazil.

	Grain yield (kg ha^{-1})	Popping expansion volume (mL g^{-1})
Cycle 5		
Phenotypic mean	2,394	25.1
Cycle 8		
Phenotypic mean	3,124	33.2
PG%	4.3	2.9
SR%	30.5	32.3

PG%: predicted genetic advance (in percentage), estimated in the cycle 8; SR%: selection response (in percentage), calculated through the four cycles of recurrent selection.

The response of recurrent selection, through the four cycles under study, was 30.5 and 32.3 for grain yield and popping expansion volume, respectively (Table 3). In C_8, predicted genetic advances were 4.8%, 4.3%, and 2.9% for plant height, grain yield, and popping expansion volume, respectively. Numerous studies using recurrent selection have been conducted to evaluate the improvement of traits of interest (Daros et al., 2002; Freitas et al., 2009, 2014; Rangel et al., 2011). Results of this study are consistent with those found by Freitas et al. (2014) that found a gradual increase in genetic progress of popping expansion volume and grain yield (gains of 5.1 and 7.8%, respectively) using the Mulamba and Mock index and random economic weights in the selection of superior progenies. In this study, the predicted genetic advances obtained for full-sib families are in concordance with previous reports, which observed that there were more accentuated discrepancies between C_0 and C_1 (mass selection vs. full-sib families), C_1 and C_2 (full-sib families vs. inbred S1 families), and C_3 and C_4 (half-sib vs. full-sib families). This corroborates the higher predicted gains found for full-sib families and S1, as opposed to possible gains with the selection among half-sib families, mass, and stratified mass. The genetic gains observed across the cycles of recurrent selection have been extensively documented. For instance, in the first cycle of recurrent selection of full-sib families, conducted in a popcorn base population, Daros et al. (2002) found genetic gains of 10.39 and 4.69% for popping expansion and grain yield, respectively, concluding that this method of population improvement enables to increase the frequencies of favorable alleles and allelic combinations conditioning quantitative trait variation.

In summary, the significant genetic variability among popcorn families of the UENF-14 population in successive cycles of recurrent selection has sustained continued genetic progress in breeding for the traits of interest.

Disclosure statement

No potential conflict of interest was reported by the authors.

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