ARTICLE

Effect of recurrent selection on the variability of the UENF-14 popcorn population

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Abstract: *This study aimed to evaluate the effect of recurrent selection on the genetic variability of UENF-14 population after six selections. Two hundred and ten half-sib families were evaluated in two environments in the state of Rio de Janeiro, using incomplete randomized blocks design with treatments arranged in replication within "Sets". There was significant effect for Families within the "Set" (F)/S, proving that there is enough genetic variability to be exploited in the popcorn breeding program of UENF. The significance for the source of variation Environment (E) shows that the environments were distinct enough to promote differences between the evaluated characteristics. It was found that for both characteristics of greatest interest, GY and PE, the magnitude of the additive variance remains with close values in advanced cycles of UENF-14 population, indicating that variability remains, with no evidence of decreases in advanced cycles. This is concluded by the longevity of UENF breeding program.*

Key words: Zea mays*, half-sib families, recurrent selection, genetic variability.*

INTRODUCTION

Popcorn (*Zea mays* L. ssp. *Mays*) is a special type of maize. It has hard and small grains, and its main characteristic is that when it is heated to approximately 180 °C, the grain internal moisture exerts pressure on the pericarp, until it breaks, forming the popcorn. This fact may multiply the grain volume up to 40 times, resulting in a tasty food (Zinsly and Machado 1987, Silva et al. 1993, Sawazaki 2001, Paes 2006). In Brazil, for popcorn culture, in 2013, it was cultivated 43,379 hectares, and it is expected to produce 171,111 tons of grains. Compared with the previous year, the planted area expanded 64.58%, and the harvested volume increased 67.39%. In 2012, 26,356, hectares were occupied with popcorn, and 102,221 million tons were harvested, according to GCEA/IBGE (2013).

Recurrent selection is an interesting strategy when the objective is to improve, in long-term, several characteristics of economic value in a base population. This improvement method consists of gradually increasing the frequency of favorable alleles in a population, with no genetic variability loss. Three steps make up the recurrent selection: progenies development; progenies evaluation; and progenies recombination. These steps are carried out cyclically until they reach satisfactory levels of frequency of favorable alleles in the population (Hull 1945, Hallauer and Miranda Filho 1988). Genetic variability in the population is one of the factors responsible for longevity of recurrent selection program, particularly

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recurrent selection program in 11th cycle with broad genotypic variation and with heritability estimates ranging from 33 to 73%, proving to be promising for the achievement of new selection cycles (Berilli et al. 2013). However, the success of any recurrent selection program necessarily depends on the genetic variability of the population. Genetic variability is the primary source of genetic studies and it is not possible to obtain adaptations and evolution in species without it, nor genetic improvement. Variability is generated by mutation, and it is enhanced by genetic recombination. In this context, there are several examples, which state the narrow genetic base of this special type of maize. According to Kantety et al. (1995), reduced genetic base of the culture is due to the flint form of common maize. Results obtained by Oliveira et al. (2010) corroborate this statement. The authors found narrow genetic base in this culture. In the evaluation of the genetic diversity of 34 popcorn accessions of UENF, they obtained the formation of five groups by the UPGMA method, using ISSR markers. It should be highlighted that five of seven genotypes recommended for different regions in Brazil were clustered in only one group. Thus, it is necessary to take care in order avoid genetic narrowing in breeding programs, especially in advanced generation of recurrent selection (Ribeiro et al. 2012).

In relation to recurrent selection, Vilela et al. (2008) evaluated the initial cycles (C_0, C_1 and C_2) of UNB-2U (currently UENF-14) and found that genetic gains in the different cycles did not interfere with the genetic narrowing of the studied population. In further studies, Oliveira et al. (2010) used ISSR markers to investigate the genetic variability among C_0, C_1, C_2, C_3 and C_4 cycles of UENF-14, and concluded that C_0 and C_1 were more genetically distant from C_2, C_3 and C_4, denoting that the distinction of cycles may be attributed to the fact that the advance of cycles (C_1 to C_2) through S_1 families provided the most significant predicted gains, favoring greater differentiation in genetic variability compared to the previous generation for the main evaluated characteristics.

Considering that the Popcorn Improvement Program of UENF started from different breeding strategies (Mass Selection for C_0 cycle; Selection of Full-sib families from C_0 cycle for C_1 cycle; Selection of S_1 families from C_1 cycle for C_2 cycle; Selection of half-sib families from C_2 cycle for C_3 cycle; and Selection of full-sib families for the other cycles), and considering the link between the different strategies, the varied responses of gain with selection - noted in the works of Oliveira et al. (2010) and Freitas et al. (2014), it is evident the doubt in relation to the genetic bottleneck in UENF-14 population after seven cycles (C_0 a C_6) of recurrent selection.

Thus, a condition for the longevity of the recurrent selection strategy is to combine genetic gains with the maintenance of variability in different cycles. In this context, this study aimed to investigate the effective gains and the impact on the genetic variability of UENF-14 population after seven cycles of recurrent selection of the Popcorn Breeding Program of UENF.

MATERIAL AND METHODS

Nevertheless, the different strategies adopted for selective gains made it impossible to reliably compare the genetic gains in successive cycles, generating an additional impediment to appropriate confronted analysis of the response to selection. This is because the components of dominance variance, which are intrinsic to genetic gains in structures of full-sib families, are not considered in the gains between half-sib families and S_1 families.

Thus, for the evaluation of the real variability and of the gains between UENF-14 cycles, it is necessary to have populations with the same genetic structure. An option is to constitute half-sib populations with a common male tester. In this case, desirable progeny tester is constituted by the less advanced cycle (C0), so that the actual differences between the cycles are evident.

Plant Material

To obtain the half-sib families, it was used ten lines of each cycle (C_0 to C_6), intercalated with 10 lines of the tester cycle (C_0), of UENF-14 population, so that the half-sib families were obtained from crosses of recurrent selection cycles with the tester (C_0). It was used spacing of 0.20 m between plants and 0.90 m between rows, and 5.0 m rows. Three seeds were planted per hole, at a depth of 0.05 m. At 21 days after emergence, thinning was carried out, leaving one plant per hole.

Thus, this procedure produced 210 half-sib families, and for each cycle, it was obtained 30 half-sib families. This is, from the C_0 x C_0 crosses, it was obtained 30 families; from the C_0 x C_1 crosses, 30 other families were obtained, and so on, until it reached 30 families of the C_0 x C_6 crosses. Afterwards, these 210 half-sib families were evaluated in trials, in Campos dos Goytacazes and in Itaocara, north and northwest regions of the state of Rio de Janeiro.

Experimental design

The design was a randomized block with replications within "Sets". It was used three "Sets" with three replications, and each "Set" contained 73 treatments, i.e., 70 half-sib families and three controls. For the composition of each "Set", families from each cycle were numbered from 1 to 30. In "Set" 1, families from 1 to 10 and one control were clustered and randomly selected; in "Set" two, families from 11 to 20 and one control were clustered and randomly selected; and "Set" 3, families from 21 to 30 and one control were clustered and randomly selected.

The design consisted of 2.40 m rows, spaced 0.90 m, with 13 plants spaced 0.20 m apart, with three seeds per hole, at a depth of 0.05 m. At 21 days after emergence, it was carried out thinning, leaving one plant per hole, totaling a population of 60,185 plants per hectare. Fertilization during the planting was carried out according to the soil analysis. Topdressing was carried out about 30 days after planting. Cultural treatments were carried out according to the crop's needs (Sawazaki 2001).

The off-season plantation was carried out on April 18th, 2013, in Campos dos Goytacazes (State College of Agriculture Anthony Sarlo), and on April 30th, 2013, in Itaocara (Experimental Station PESAGRO-RIO, in Ilha Barra do Pomba). The experiments were again repeated in the season, and planting was carried out in Campos dos Goytacazes (State College of Agriculture Anthony Sarlo), on September 4th, 2013, and in Itaocara (Experimental Station PESAGRO-RIO, in Ilha Barra do Pomba), on September 18th, 2013.

Evaluated characteristics

The following characteristics were evaluated: mean plant height (PH) in cm; first ear mean height (EH) in cm; grain yield (GY), in kg ha^{-1}; mean number of days to flowering (DF); and popping expansion (PE), in mL g^{-1}.

For mean plant height, it was measured (in cm) the distance from the ground level to the insertion of the flag leaf, just after tasseling, of six competitive plants. For the first ear mean height, it was carried out the quantification of the distance, in cm, from the ground level to the base of insertions of first ear of six competitive plants. Grain yield was determined by weighing the grain after eliminating the cob, and it was expressed in kg ha^{-1}. The mean number of days to flowering was measured by quantifying the period between the planting and the release of silks of 50% of plants in the rows. Popping expansion was determined in the laboratory using a 31 L, 1000W microwave oven, with 2.5 minutes popping for each plot.

Genetic x Statistical analysis

Analysis of variance of the data of the characteristics was carried out according to the statistical model $Y_{ijkl} = \mu + A_i + S_j + AS_{ij} + R/AS_{ijk} + F/S_{jl} + AF/S_{ijl} + e_{ijkl}$, in which μ is the mean; A_i is the fixed effect of the ith environment; S_j is the effect of the jth "Set"; AS_{ij} is the effect of the interaction between environments and "Sets"; R/AS_{ijk} is the effect of the kth replication within the interaction between the ith environment and the jth "Set"; F/S_{jl} is the random effect of the ith family within the j-th "Set" (NID, 0, $\sigma^2_{F/S}$; AF/S_{ijl} is the effect of the interaction between environments x families within the j-th "Set"; and e_{ijkl} is the experimental error (NID, 0, σ^2). Based on the proposed model, data of the characteristics were used for analysis of variance, using the SAS software (SAS 1985).

It was obtained the genetic, phenotypic and environmental components, where: $\hat{\sigma}^2_G = \frac{QMF/S - QMR}{ar}$ is the estimator of the genotypic variance among families; $\hat{\sigma}^2_F = \frac{QMF/S}{ar}$ is the estimator of the phenotypic variance among families; $\hat{\sigma}^2_R = \frac{QMR}{ar}$ is the estimator of the mean residual variance; $\hat{\sigma}^2_{GA} = \frac{QM(AxF)/S - QMR}{r}$, $\frac{a-1}{a}$ is the estimator of the variance of genotype x environment interaction; $\hat{h}^2_x = \frac{\hat{\sigma}^2_G}{\hat{\sigma}^2_F} = \frac{QMF/S - QMR}{QMF/S}$. 100 is the percentage heritability based on the family means; $\hat{I}_v = \frac{C\hat{V}g}{C\hat{V}e}$ is the estimator of the variation index, in which $C\hat{V}g$ is the coefficient of genetic variation; and $C\hat{V}e$ is the coefficient of experimental variation.

Genetic gain was obtained through the expression $\Delta_g = \frac{DSxh^2}{\bar{X}_0}$, in which Δ_g = genetic gain; *DS* = selection differential; h^2 = narrow sense heritability; and $\bar{X}_0$ = mean of the original population.

In order to evaluate the evolution of mean popping expansion and grain yield over the cycle, it was carried out regression analysis using a linear regression equation between dependent variable (X) cycles, ranging C_0 x C_0 to C_0 x C_6, popping expansion and grain yield, mean of progenies in each selection cycle, dependent variable (Y).

RESULTS AND DISCUSSION

Impact on variability

By the analysis of variance, significant differences were observed for the source of variation Environment in all the evaluated characteristics (Table 1). The significance for this source of variation shows that the environments were distinct enough to promote differences between the evaluated characteristics. In relation to the source of variation "Set", mean squares were significant at 1% probability level for popping expansion (PE) and mean number of days to flowering (DF). Grain yield (GY), first ear mean height (EH), and mean plant height (PH) were not significant at 5% probability level. According to Rangel et al. (2011), the significance for characteristics of economic value is strong indicator of the need for using a randomized block design with arrangement of treatments within "Sets", and the absence of such source of variation would produce changes that could result in the loss of experimental accuracy.

Regarding the Environment x "Set" interaction, there was lack of significance only for the first ear mean height (HE) (Table 1). The other characteristics were significant at 1% probability, confirming that families were randomly distributed

***Table 1**.* Estimates of mean squares, means and percentages coefficients of experimental variation of five characteristics evaluated in 210 half-sib families of UENF-14 popcorn population

Source of variation	df	Mean Squares[1]				
		GY	PE	PH	HE	DF
Environment (E)	3	324446393.5**	2698.36**	36.62**	11.76**	418.85**
Set (S)	2	143478.7	115.49**	0.006	0.002	83.7**
E x S	6	2542754.5**	50.98*	0.1**	0.016	36.09**
Replication (R)/ExS	24	3609424.1**	92.77**	0.29**	0.25**	92.0**
Families (F)/ S	207	16745569.6**	102.47**	0.07**	0.05**	27.95**
C_0	27	731223.13	135.82**	0.07**	0.04**	24.52**
C_1	27	1169927.3*	91.4**	0.08**	0.05**	41.2**
C_2	27	955266.5	40.26**	0.08**	0.05**	21.48**
C_3	27	1730843.8**	88.07**	0.04*	0.03*	21.49**
C_4	27	1136925.1**	95.57**	0.07**	0.06**	20.52**
C_5	27	1087569.5**	95.31**	0.09**	0.06**	20.01**
C_6	27	1201874.02*	83.87**	0.08**	0.05**	17.0**
(E x F)/ S	621	865190.0**	22.44*	0.03**	0.02*	6.31
C_0	81	559266.12	18.03	0.02	0.01	7.08
C_1	81	652629.8	23.41	0.05**	0.02*	6.89
C_2	81	1042610.3*	18.88	0.04	0.02	4.8
C_3	81	605095.2	17.78	0.03	0.01	4.09
C_4	81	855634.9*	19.28	0.03	0.01	5.87
C_5	81	737565.3*	27.13	0.04	0.01	6.51
C_6	81	508647.23	24.18	0.03	0.01	4.27
Errors	1618	615876.0	19.78	0.02	0.01	5.79
Mean		3070.05	26.43	1.75	0.99	63.1
CVe (%)		25.56	16.82	9.58	12.25	3.81

[1] GY = grain yield, in kg ha^{-1}; PE = popping expansion, in mL g^{-1}; PH = mean plant height, in cm; and EH = first ear mean height, in cm.
** = Significant at 1% probability level by the F test;
* = Significant 5% probability level by the F test; and

in the "Sets" and that they presented phenotypic changes caused by environmental soil and climatic changes. Regarding the source of variation Families within the "Set" (F/S), it was found that all of the evaluated characteristics presented significance ($p < 0.01$), proving that there is enough genetic variability to be exploited in the popcorn breeding program of UENF in the next cycles. The same is observed in the unfolding of the half-sib families within the "Set", whose most characteristics presented significance at 1% probability, except for GY in the C_1 and C_6 cycles, which were significant at 5% probability, and the same occurred for PH and EH in the C_3 cycle.

For the source of variation Environment x Families within the "Set" (EXF)/S, there was significance at 1% probability for grain yield (GY) and mean plant height (PH). Significance at 5% probability was obtained for popping expansion (PE) and first ear mean height (EH). There was lack of significance at 5% probability only for mean number of days to flowering (DF). Significance regarding (ExF)/S indicates that the evaluated families behaved distinctly in all the four evaluated environments. However, being the significance a probability question, with greater degree of freedom, there is also more sensitivity, which allows detecting significant differences. Regarding the unfolding per cycle, the "Set" of treatments in each cycle is much smaller, which reduces the ability of detecting differences, since it would require greater interaction values to detect significance. Thus, greater attention should be given to unfoldings, since they allow verifying whether it occurred or not significance of the main effects and of the interactions within each level. Thus, it was not observed significances for most characteristics in the unfoldings.

Of the evaluated characteristics, popping expansion (PE) and grain yield (GY) are of greatest concern in a popcorn breeding program, and this is the reason for further study on interactions. When observing the unfoldings for these two characteristics, it is noted that for PE there was no significance at 5% probability, and for GY, only three of the seven cycles expressed significance of 5% probability. Similar results were obtained on the seventh recurrent selection cycle with full-sib families, in which Freitas et al. (2014) identified significance of 1% probability for GY and no significance for PE.

Genetic parameters

Table 2 shows that popping expansion expressed high values for heritability and for variation index. These results are in accordance with those obtained by Pereira and Amaral Júnior (2001), who employed the Design I (Comstock and Robinson 1948) in the initial studies of UENF-14. The high heritability estimates favors the hypothesis that the characteristic is oligogenic (Alexander and Creech 1977, Zanette 1989, Pacheco et al. 1998, Coimbra et al. 2001, Pereira and Amaral Júnior 2001, Miranda et al. 2008). Except for the second cycle, in which there was reduction in the heritability estimate, there is a balance regarding the magnitude of values, confirming the predominance of additive genetic effects on the expression of the popping expansion (Scapim et al. 2002, Simon et al. 2004, Freitas Júnior et al. 2009).

In relation to yield, it is observed something similar to that observed for popping expansion. In C_3 cycle, there was a recovery in heritability magnitude (65.11%) after the narrowing of C_2 cycle, whose magnitude was 27.10%. In cycles C_4, C_5 and C_6, heritability remained the same (45.97%, 51.94% and 45.04%, respectively). C_0 cycle had the lowest heritability value, 18.59%, although it was a high value. However, the stability of magnitudes of heritability in the superior cycles corroborate the findings of Pereira and Amaral Júnior (2001), who estimated magnitude of 44.88% for heritability in full-sib families.

Higher magnitude of heritability for PE in relation to GY was expected in the UENF-14 popcorn population, as demonstrated by Pereira and Amaral Júnior (2001). Results like these, in which estimates of heritability for popping expansion are higher when compared to yield, are confirmed by other authors in studies with other populations (Pacheco et al. 1998).

In relation to DF, PH and HE, since they present high magnitudes of heritability, genetic progress is very promising, even by means of simple breeding methods. Family means in the cycles varied for DF, from the lowest to the highest value, between 62.56 and 64.43 days. In relation to PH, family means ranged from 1.71 to 1.80 m. In relation to EH, family means ranged between 0.96 and 1.03 m. These results reaffirm the importance of the use of recurrent selection and breeding methods to obtain desirable gains in UENF-14 population.

By analyzing the additive variances for PE (Table 2), it is clearly noted when it was used S_1 inbred families as a breeding strategy in UENF-14 population. This is because σ_a^2 for C2 was 6.60, and its estimate presented the lowest magnitude

Table 2. Estimates of phenotypic variance ($\hat{\sigma}^2_F$), genotypic variance ($\hat{\sigma}^2_G$); residual variance ($\hat{\sigma}^2_r$); variance of genotype x environment interaction ($\hat{\sigma}^2_{GA}$); heritability based on the families means ($\hat{h}^2_X$), coefficient of genetic variation ($C\hat{V}g$), variation index ($\hat{I}_v$), and of additive variance ($\hat{\sigma}^2_a$) for five characteristics evaluated in 210 families of UENF-14 popcorn population

GY[1]	$\hat{\sigma}^2_F$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_r$	$\hat{\sigma}^2_{GA}$	$\hat{h}^2_X$	$C\hat{V}g$	$\hat{I}_v$	$\hat{\sigma}^2_a$
C_0	60935.26	11325.24	49610.03	0.00	18.59	4.10	0.14	45300.94
C_1	97493.94	38619.63	58874.31	0.00	39.61	6.83	0.23	154478.53
C_2	79605.54	21575.30	58030.24	86561.85	27.10	4.70	0.18	86301.20
C_3	144236.98	93919.78	50317.20	322.20	65.11	9.63	0.39	375679.13
C_4	94743.76	43550.01	51193.75	60327.48	45.97	6.53	0.27	174200.03
C_5	90630.79	47073.37	43557.43	53719.05	51.94	6.68	0.30	188293.47
C_6	100156.17	45111.04	55045.13	0.00	45.04	6.48	0.26	180444.14
PE[1]	$\hat{\sigma}^2_F$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_r$	$\hat{\sigma}^2_{GA}$	$\hat{h}^2_X$	$C\hat{V}g$	$\hat{I}_v$	$\hat{\sigma}^2_a$
C_0	11.3183	9.5900	1.7283	0.0000	84.73	12.3525	0.6798	38.36
C_1	7.6167	5.7208	1.8958	0.1650	75.11	9.0360	0.5017	22.88
C_2	3.3550	1.6508	1.7042	0.0000	49.21	5.1394	0.2843	6.60
C_3	7.3392	6.0008	1.3383	0.4300	81.76	9.4145	0.6113	24.00
C_4	7.9642	6.4483	1.5158	0.2725	80.97	9.6224	0.5954	25.79
C_5	7.9425	6.1792	1.7633	1.4925	77.80	9.0590	0.5402	24.72
C_6	6.9892	5.2508	1.7383	0.8300	75.13	8.0065	0.5017	21.00
PH[1]	$\hat{\sigma}^2_F$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_r$	$\hat{\sigma}^2_{GA}$	$\hat{h}^2_X$	$C\hat{V}g$	$\hat{I}_v$	$\hat{\sigma}^2_a$
C_0	0.0058	0.0042	0.0017	0.0000	71.43	3.6676	0.4098	0.0167
C_1	0.0067	0.0042	0.0025	0.0050	62.50	3.7098	0.3728	0.0167
C_2	0.0067	0.0042	0.0025	0.0025	62.50	3.7748	0.3790	0.0167
C_3	0.0033	0.0017	0.0017	0.0025	50.00	2.2807	0.2574	0.0067
C_4	0.0058	0.0033	0.0025	0.0000	57.14	3.2075	0.3490	0.0133
C_5	0.0075	0.0050	0.0025	0.0025	66.67	4.0873	0.4075	0.0200
C_6	0.0067	0.0042	0.0025	0.0000	62.50	3.7312	0.3788	0.0167
HE[1]	$\hat{\sigma}^2_F$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_r$	$\hat{\sigma}^2_{GA}$	$\hat{h}^2_X$	$C\hat{V}g$	$\hat{I}_v$	$\hat{\sigma}^2_a$
C_0	0.0033	0.0025	0.0008	0.000	75.00	5.2083	0.4541	0.0100
C_1	0.0042	0.0025	0.0017	0.000	60.00	5.0505	0.3832	0.0100
C_2	0.0042	0.0025	0.0017	0.000	60.00	5.0505	0.3812	0.0100
C_3	0.0025	0.0008	0.0017	0.000	33.33	2.8582	0.2238	0.0033
C_4	0.0050	0.0042	0.0008	0.000	83.33	6.2670	0.5929	0.0167
C_5	0.0050	0.0042	0.0008	0.000	83.33	6.5867	0.5373	0.0167
C_6	0.0042	0.0033	0.0008	0.000	80.00	5.9521	0.4716	0.0133
DF[1]	$\hat{\sigma}^2_F$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_r$	$\hat{\sigma}^2_{GA}$	$\hat{h}^2_X$	$C\hat{V}g$	$\hat{I}_v$	$\hat{\sigma}^2_a$
C_0	2.04	1.53	0.51	0.23	74.88	1.96	0.50	6.12
C_1	3.43	2.87	0.57	0.02	83.50	2.63	0.65	11.47
C_2	1.79	1.36	0.43	0.00	75.74	1.84	0.51	5.42
C_3	1.79	1.41	0.38	0.00	78.87	1.90	0.56	5.65
C_4	1.71	1.29	0.42	0.21	75.39	1.82	0.51	5.16
C_5	1.67	1.08	0.59	0.00	64.82	1.66	0.39	4.32
C_6	1.42	0.97	0.45	0.00	68.35	1.56	0.42	3.87

[1] GY = grain yield, in kg ha^{-1}; PE = popping expansion, in mL g^{-1}; PH = mean plant height, in cm; EH = first ear mean height, in cm; and DF = mean number of days to flowering.

among the cycles, with sharp increase in the subsequent cycle, with σ^2_a value equal to 24.00, keeping the value in subsequent cycles, 25.79, 24.72 and 21.00, for the cycles C4, C5 and C6, respectively. With these results, it is confirmed that if there had been continuity in the use of selection strategy through inbred families (S_1) for more generations, the genetic progress of UENF-14 population would have been compromised, due to the maintenance of additive variance at low levels. This is a concern for the success of a recurrent selection program, whose intention is to obtain long-term gains.

For GY, it is observed that C_2 also had the lowest σ^2_a magnitude, corroborating other results. The strategy used in C_2 (S_1 families) resulted in the reduction of additive variance in both characteristics of greatest interest in popcorn culture (GY and PE). However, σ^2_a was recovered with the recombination of families for the formation of the next cycle. This is a fact that proved to be essential for further results in UENF-14.

According to the results obtained in this study, it appears that for the two characteristics of greatest interest, GY and PE, the magnitude of additive variance is maintained with close values in the advanced cycles of UENF-14 population, indicating that variability is maintained without evidence of decreases in advanced cycles. This is concluded by the longevity of UENF breeding program.

Genetic gain

The genetic gain for a certain characteristic expresses the advance of the next generation in relation to the original population due to selection. Thus, it is clear that the greatest gains for GY were observed in the first cycles (17.11% gain in C_1, and 10.19% gain in the C_2) (Table 3). Similar results were obtained by Ribeiro et al. (2012), who found percentage gain per cycle of 37.58 for C_1 and of 6.03% for C_2. In further cycles, genetic gains were significant for GY, except for the C_4, in which the gain was only 0.93%. The lowest gains found in more advanced cycles are expected in a population under selection, given the accumulation of favorable alleles in these generations.

***Table 3**.* Strategies used in the experiment and means of popping expansion (mL g^{-1}) and of grain yield (kg ha^{-1}) obtained for the cycles C_0, C_1, C_2, C_3, C_4, C_5 and C_6, of UENF-14 population subjected to intrapopulation recurrent selection

Cycle	Selection Strategy	GY (kg ha^{-1})	Δg* (%)	PE (mL g^{-1})	Δg* (%)
C_0	Mass	2597.52		25.07	
C_1	Full-sib	2878.03	17.11	26.47	16.78
C_2	S_1	3122.07	10.19	25.00	0.00
C_3	Half-sib	3182.98	6.11	26.02	13.31
C_4	Full-sib	3196.14	0.93	26.39	4.78
C_5	Full-sib	3246.21	4.00	27.44	13.03
C_6	Full-sib	3278.65	2.25	28.62	14.14

PE = popping expansion and GY = grain yield.
* Percentage genetic gains per cycle

For PE, it was observed genetic gain equal to zero for C_2. This result was due to the high magnitude of C_1 mean, even surpassing C_4 mean. Similar result was obtained by Daros et al. (2004), who studied the genetic progress in the first recurrent selection cycle with full-sib families, and in the second cycle, with S_1 families, using UENF 14 population. The authors affirm that, although genetic gains in C_1 and C_2 have been reported for popping expansion and grain yield, C_2 presented decrease in means of the selected families, when compared with C_1. According to Vilela et al. (2008), this reduction is probably due to inbreeding depression (S_1 families).

However, in the remaining cycles, gains were promising and high, with values of 13.31%, 4.78%, 13.03% and 14.14%, for the cycles C_3, C_4, C_5, and C_6, respectively, reaffirming that PE is strong and closely influenced by additive variance. By comparing the evolution of the means obtained for PE and GY in cycles C_0, C_1, C_2, C_3, C_4, C_5, and C_6, it is observed that there was gradual increase for both PE and GY (Table 3). This gradual increase was also found in C_4 (Freitas Júnior et al. 2009), in which even with the change in the strategy of C_3 with half-sib families by full-sib families in C_4, gains for grain yield and popping expansion continued increasing. Similar results were observed by Santos et al. (2007), who found that with the change of the strategy of inbred families selection, carried out by Daros et al. (2002) for selection between half-sib families (Santos et al. 2007), gains for popping expansion were satisfactory, as well as the increase in grain yield.

Figure 1A represents the regression line of the evolution of UENF-14 popcorn population in relation to grain yield in seven recurrent selection cycles. It was also verified that R^2 estimate was high (0.89), which implies good adjustment of the regression model. C_0 cycle of the population expressed mean yield of 2,597.52 kg ha^{-1}. On the other hand, C_6

presented yield of 3,278.65 kg ha^{-1}, which represents an increment of 26.22% in the mean grain yield in seven cycles, confirming that the breeding methods used were efficient in selection responses. Also, Figure 1A shows outstanding yield increment in the first three cycles, followed by a moderate increment from C_3 cycle.

Figure 1B presents the excessive gains in UENF-14 popcorn population in relation to popping expansion (PE). It is noted that R^2 was high (0.84), indicating that the equation model for PE was also well adjusted. The same figure shows the progress in intrapopulation recurrent selection cycles, in which the base population (C_0) presented popping expansion of 25.07 mL g^{-1}. When comparing C_0 with C_6, it appears that the latter expressed PE of 28.62 mL g^{-1}, i.e., there was increment of 14.16% in popping expansion in seven recurrent selection cycles, confirming the premise of the gradual increase in the frequency of favorable alleles in the base population.

C_1 cycle proved to be atypical (Figure 1B), as previously discussed, and it did not correspond to what was expected. However, cycles C_2, C_3, C_4, C_5 and C_6 presented increment expected in a population subjected to recurrent selection, in which with the advancement of generations over the years, there is the accumulation of favorable alleles in the population under selection, resulting in considerable gains in the advanced cycle, when compared to the previous cycle.

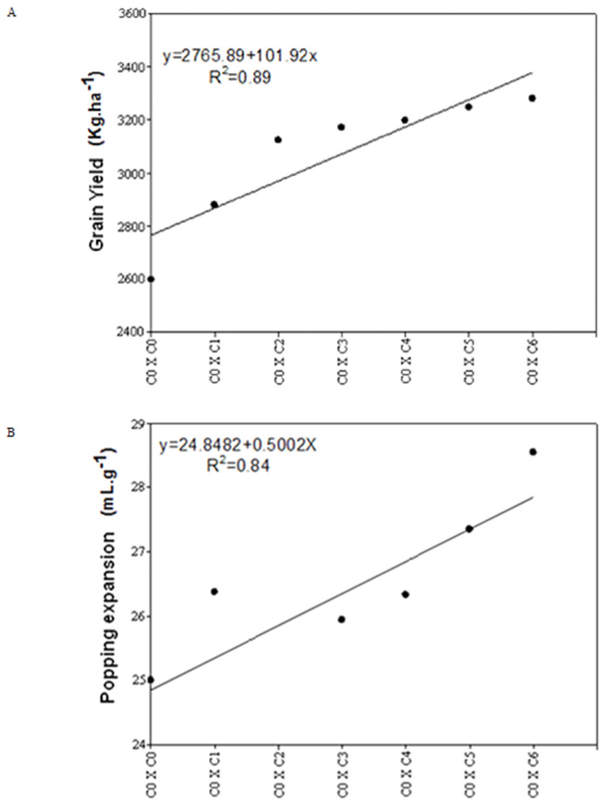

Figure 1. Evolution of the means obtained in cycles C0, C1, C2, C3, C4, C5 and C6 for the characteristic (A) grain yield (kg ha^{-1}) and (B) popping expansion (mL g^{-1}).

Thus, it can be concluded that in relation to the characteristics of greatest economic value (GY and PE), good results have been achieved, given the good performance of the population in successive cycles of intrapopulation recurrent selection. The maintenance of the additive variance at high magnitudes in the superior cycles in UENF-14 provides reliable information that the use of inbred S_1 families in C_2 as a breeding strategy did not cause genetic narrowing in the studied population, evidencing even more the promising future of the program.

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