Inbreeding depression and genetic variability of populations for green maize production[1]

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ABSTRACT

The production of green maize is considerable important for various regions of Brazil. It is vital that breeding programs of public institutions seek to meet the needs of this market sector, which has a relevant social role, mainly on small properties. The aim of this study was to estimate the inbreeding depression and the genetic components (m + a and d) of characters associated with green maize production and quality in three populations of different genetic basis: the variety UFG-Samambaia (P1), and two populations formed by crossing the commercial hybrids (P2 e P3). The S_1 progenies of each population, the three S_0 populations, and two checks were evaluated in a 14 × 14 triple lattice design. Agronomic and ear quality traits were evaluated. Genetic variability and greater inbreeding depression were observed for most of the traits among the P1 progenies. In P2 and P3, greater inbreeding depression was observed for male flowering, ear weight without straw, ear diameter, ear weight, female flowering, breakage and lodging, and grain color. The traits of ear quality, important for green maize production, had greater inbreeding depression than the agronomic traits, indicating that inbreeding depression and exploitation of heterosis should be considered in the selection process for these traits.

Keywords: *Zea mays*; line; hybrids; quality traits.

INTRODUCTION

Maize (*Zea mays* L.) is one of the most cultivated species in the world because of the breadth of its use as a raw material for industry and its use in the animal and human diet as a dry or unripe grain. Maize not grown for production of dry grain is called special maize, involving production of common unripe "green maize", sweet corn, popcorn, baby corn, degermed whole maize kernels (*canjica*), maize with high oil content, maize with high protein content, and others that serve market niches (Pereira Filho & Cruz, 2009).

Green maize is traditionally consumed, with constant demand, throughout Brazil *in natura* and in processed products such as *pamonha*, *curau* (corn pudding), juices, cakes and biscuits, ice cream, and other dishes (Magalhães *et al.*, 2002). Green maize is mainly grown by small and medium-sized growers near large consumer centers, facilitating placement of the product on the market. Its various uses add value to the product, ensuring the sustainability of the production system (Magalhães *et al.*, 2002; Lima *et al.*, 2019).

The options of cultivars for green maize production are limited; less than 2% of the maize cultivars available on the market are recommended for this purpose (Pereira Filho &

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Borghi, 2018). Growing demand for product quality has generated interest in some companies in serving the market through development of maize cultivars specifically for unripe/green consumption, as maize cultivars are generally developed for dry grain production (Pereira Filho, 2002). Thus, new cultivars are being developed, driven by high price on the market (Coan *et al.*, 2018). Paiva Junior *et al.* (2001) affirm that cultivars recommended for grain and silage production have wide variations regarding grain texture, which may make commercialization of the ear *in natura* unviable.

As the market is demanding, green maize cultivars should have particular characteristics, which are not always evaluated in genotypes grown for dry grain production. Among these characteristics are ear length and shape, ear straw production, commercial ear weight, cob and kernel color, kernel type and uniformity, soft pericarp texture, and shelf life (Magalhães *et al.*, 2002; Albuquerque *et al.*, 2008; Rodrigues *et al.*, 2018). Pereira Filho (2002) highlight other traits important for green maize cultivars, such as the possibility of planting throughout the entire year, ear yield greater than 12 t ha^{-1}, cycle ranging from 90 to 110 days, longevity in the harvest period, good straw production, and industrial grain yield greater than or equal to 30%.

Little information is available on obtaining cultivars for green maize production, and there are few genetic studies on the traits involved in this production (Kuki *et al.*, 2017; Somera *et al.*, 2018). Most studies are evaluation of the performance of existing cultivars (Cardoso *et al.*, 2004; Lima *et al.*, 2019; Couto *et al.*, 2017; Rodrigues *et al.*, 2018). As the aim of most maize breeding programs is obtaining hybrids from lines to exploit hybrid vigor, the estimate of inbreeding depression on the traits of interest in populations is essential to ensure success in breeding (Lima *et al.*, 1984).

Identification of populations promising for extracting lines in the initial phases of the program can be carried out from estimation of the mean components (‘m + a’ and ‘d’). The estimate of ‘m + a’ indicates the additive value and performance of the line *per se*; the estimate of ‘d’ indicates the deviation of the heterozygotes in relation to the mean and the divergence among lines, providing information on the existence of dominance in genetic control of the trait, an essential condition for there to be heterosis (Hallauer *et al.*, 2010). A potential population must not only have good performance *per se*, but must also have genetic variability. The aim of this study was to estimate inbreeding depression and the components of mean and variance of characters associated with green maize production and quality in three populations of different genetic basis, to evaluate the potential of these populations for breeding.

MATERIALS AND METHODS

Three populations of different genetic basis were used. The first was the synthetic variety UFG-Samambaia (P1), developed at UFG, adapted to the environmental conditions of the state of Goiás, Brazil. It was obtained through crossing of eight hybrids: C-901, C-701, G-85, AG-7391, P-3041, Z-8452, BR-201, and PL-30X12; only the last of these was an experimental hybrid. The hybrids were recombined by the Irish method for three generations in 1995 and 1996; after that they passed through a disruptive mass selection cycle for grain type. This process gave rise to two populations: UFG - Samambaia, with flint type kernels, and UFG - Samambaia “Dent”, with softer kernels (Reis, 2000).

The second population (P2) is formed from crossing of F_2 of two commercial hybrids, AG 8060 (single hybrid - flint kernel) and FORT (single hybrid - semi-flint kernel), considered hybrids of high yield potential, excellent grain quality, and adapted to altitudes above 700 m. This population was kindly granted by the Instituto Agronômico de Campinas (IAC).

The third population (P3) is formed from crossing two hybrids: DKB390 (single hybrid - flint kernel) and BM709 (single hybrid - semi-dent kernel) which were self-fertilized. These hybrids have high yield potential, wide adaptation to different types of soil, planting times, and management practices, good grain quality, and early maturity.

The S_1 progenies of the three populations were obtained in the first season of the 2018/2019 crop year. For that purpose, four 5-m rows were sown that after thinning had a total of 25 plants per row. The plants of the three base populations were self-fertilized to obtain the S_1 progenies. The number of plants that produced seeds coming from the self-fertilizations varied among the populations. Thus, the ears from the self-fertilized plants were harvested from each population, forming the S_1 progenies.

The experiment was conducted in Goiânia-GO (16°35’48”S; 49°16’39”W; altitude 730 m) in a conventional tillage system under center pivot irrigation.

Evaluations were performed of 75 S_1 progenies of the UFG-Samambaia population (P1), 45 S_1 progenies of the AG8060 F_2 × FORT F_2 population (P2), 71 S_1 progenies of the DKB390 × BM709 population (P3), two commercial check cultivars, AG 1051 and BM3061 (recommended for green maize), and three base populations in the S_0 generation. A 14 × 14 triple lattice experimental design was used, with plots consisting of one 4-m row. The between-row spacing was 0.80 m, and 15 plants per plot were left after thinning, to obtain a final stand of 46,875 plants ha^{-1}. The following variables were evaluated:

a) Agronomic: ear weight with straw (t ha^{-1}) and breakage and lodging (%) were performed for the total of plants per plot; female flowering (days), male flowering (days), plant height (cm), ear height (cm) and relative position of the ear were measured in five plants with five ears in each plot.

b) Ear quality: grain mass (kg ha^{-1}), ear weight without straw (kg ha^{-1}), ear length without straw (cm), ear diameter (cm), ear straw production (scoring scale), kernel alignment on the ear (scoring scale), and grain color (scoring scale). These traits were measured in five ears for plot. Green maize harvesting and the evaluation of the ears traits began at the R3 stage (kernel milk) when the moisture content was between 70 to 80%.

The grain mass was obtained cutting the grains at the base of ear and grating the corn kernels and subsequent weighing; for ear straw production, the mean score of five ears from the plot was considered, according to a scoring scale from 1 to 5: score 1 (excellent straw cover), score 2 (straw with incomplete closure), score 3 (exposed ear), score 4 (exposed kernels), and score 5 (many exposed kernels). For kernel alignment on the ear, a scoring scale from 1 to 4 was adopted, proposed by Santos *et al.* (2005), also considering the mean score of five ears from the plot, with score 1 (straight alignment), score 2 (slightly curved alignment), score 3 (spiral alignment), and score 4 (irregular alignment). Grain color also considered the mean score of five ears from the plot, according to a scoring scale from 1 to 5 proposed by Albuquerque *et al.* (2008), with score 1 (cream-colored kernels), score 2 (light yellow kernels), score 3 (yellow kernels), score 4 (dark yellow kernels), and score 5 (orange kernels).

Statistical analyses were carried out using the mixed model methodology via REML/BLUP (Restricted Maximum Likelihood / Best Linear Unbiased Predictor). The treatments were decomposed into effects of S_1 progenies, S_1 progenies within S_0, S_1 groups, S_0 populations, check cultivars, and the S_1 progeny × S_0 population × check cultivar interaction. Statistical model was used as $y = Xr + Zg + e$, which: y is the vector of observations of the trait evaluated; r is the vector of the fixed effect of replication and S₀ added to the overall mean; g is the vector of the random effects of check cultivars and blocks within replications; e is the error, or residual vector (random); X and Z represent the incidence matrices for the effects of r and g, respectively.

This same model was also used for combined analysis of all the S_1 progenies and for groups of S_1 progenies. For that purpose, the effects of S_0 populations (P1, P2, and P3, that is, the parents that gave rise to the S_1 progenies) were added to the fixed effects, and S_1 progenies were used instead of S_0 populations in the random effects.

Statistical analyses were carried out using the software of R Core Team (2020) and the agricolae, lme4, lsmean, and emmeans packages. The significance of the estimates of the random effects of all the models described above was tested through the LRT (Likelihood Ratio Test). Thus, two models were compared: a general model (M_g), with all the possible explicative variables, against a reduced model (M_r) identical to the first model without the parameter to be tested. The LRT tests the null hypothesis (H_0: $M_{G(\text{general model})} = M_{r(\text{restricted model})}$) against the alternative hypothesis ($H\alpha$: $Mg \neq Mr$), that is, if the reduction in the general model produces a high significance in deviance, which indicates that this reduction explains part of the total variation. The BLUP means were obtained for all the traits. Specifically for check cultivars, the mixed model was used only to obtain BLUE means.

The estimates of the variance components were made via REML/BLUP automatically by the lme4-R package for the random effects of each one of the mixed models described above. After that, these estimates were used to obtain the following genetic parameters: broad sense heritability, selective accuracy (SA), experimental coefficient of variation (CVe), and genotypic coefficient of variation (CVg).

From the BLUP means of the S_0 and S_1 progenies, the means components m + a' and 'd' were calculated, using a procedure similar to Vencovsky (1987), where $m + a = 2\bar{S}_1 - \bar{S}_0$ refers to the contribution of the loci in homozygosity, and $d = 2(\bar{S}_0 - \bar{S}_1)$ refers to the contribution of the loci in heterozygosity. Inbreeding depression was obtained by $ID(\%) = 100 \times \left(\frac{\bar{S}_0 - \bar{S}_1}{\bar{S}_0}\right)$.

RESULTS AND DISCUSSION

There was variability among the three S_0 populations only for ear weight with straw and ear weight without straw

(Table 1). The first is a trait of agronomic importance and the second is associated with ear quality aspects. Since these populations are quite distinct in terms of genetic basis, it is expected that, in spite of being divergent in only two traits, they may give rise to variability among the progenies after self-fertilization. For the S_1 progenies, only the breakage and lodging trait did not show significant difference. This shows the possibility of success with these populations.

The genetic parameters, such as genetic variance and heritability, allow the potential of success in selection of traits to be foreseen aiming at green maize production (Rodrigues *et al.*, 2011). High heritability estimates (greater than 0.50) were found for the traits of ear weight with straw, female and male flowering, ear weight without straw, and ear diameter (Table 1). This shows that, in general, these populations have potential for gain in these traits that are important in breeding of green maize.

Table 1: Estimates of deviance, mean (μ), genetic variance (σ_g^2), and heritability (h^2) for S_0 populations and S_1 progenies for agronomic traits and ear quality traits. Goiânia, GO, Brazil, 2019.

Trait^1	**Genotype**	**Deviance**	**μ**	σ_g^2	h^2
		Agronomic traits			
EW	S_0	41.60^{*}	12.37	6.25	0.82
	S_1	2675.20^{**}	7.10	1.70	0.56
PH	S_0	68.96	183.78	-	-
	S_1	4746.40^{**}	169.38	56.12	0.53
EH	S_0	66.38	95.11	-	-
	S_1	4482.10^{**}	92.62	59.16	0.71
RP	S_0	-37.23	0.52	-	-
	S_1	-1843.60^{**}	0.55	1.07	0.72
BL	S_0	58.47	5.14	-	-
	S_1	4362.70	7.83	-	-
FF	S_0	39.45	58.56	-	-
	S_1	2862.30^{**}	61.89	3.49	0.68
MF	S_0	37.02	60.44	-	-
	S_1	2972.60^{**}	63.60	3.22	0.58
		Ear quality traits			
GW	S_0	128.98	3837.43	-	-
	S_1	9135.70^{**}	1587.71	125700	0.48
EWW	S_0	130.11^{**}	5680.55	957340	0.84
	S_1	9512.1^{**}	3658.61	500633	0.73
EL	S_0	32.98	20.27	-	-
	S_1	2739.5^{**}	16.43	3.30	0.74
ED	S_0	4.90	4.28	-	-
	S_1	571.36^{**}	3.77	0.05	0.62
KA	S_0	6.39	1.73	-	-
	S_1	1328.60^{*}	2.59	0.05	0.24
HP	S_0	23.48	2.62	-	-
	S_1	1252.10^{**}	2.12	0.17	0.58
GC	S_0	25.10	2.91	-	-
	S_1	1095.00^{**}	1.88	0.06	0.36

$^{1/}$EW: ear weight (t ha^{-1}); PH: plant height (cm); EH: ear height (cm); RP: relative position of the ear; BL: breakage and lodging; FF: female flowering (days); MF: male flowering (days); GW: grain mass (kg ha^{-1}); EWW: ear weight without straw (kg ha^{-1}); EL: ear length without straw (cm); ED: ear diameter (cm); KA: kernel alignment on the ear (scoring scale); HP: ear straw production (scoring scale); GC: grain color (scoring scale). *,**: significant at 1% and 5% probability by the LRT.

In general, the performance of the S_1 progenies was worse than that of S_0, except for the traits of ear straw production and grain color. This was already expected, since along with self-fertilization, inbreeding depression occurs, which causes reduction in plant performance.

The three populations have wide variations among the estimates of the parameters of their progenies, mainly due to the genetic variability resulting from their genetic formation (Table 2 and 3). The values of the coefficient of variation, in general, were similar to those found in the literature, indicating good experimental performance and, thus, estimation of more reliable parameters. According to Câmara *et al.* (2007), high magnitude estimates of heritability can be found when there is high genetic variability and low experimental error. Therefore, good experimental accuracy allows efficiency of selection.

Table 2: Estimates of deviance, genetic variance (σ_g^2), heritability (h^2), mean (μ), selective accuracy (SA), environmental coefficient of variation (CVe), and genetic coefficient of variation (CVg) of S_1 progenies of three green maize populations for agronomic traits. Goiânia, GO, Brazil, 2019.

Trait[1]	Pop.	Deviance	σ_g^2	h^2	μ	SA	CVe	CVg
EW	P1	955.66**	1.82	57.59	5.73	76.02	34.78	23.50
	P2	662.76	-	-	7.55	46.44	26.43	-
	P3	979.41	-	-	8.34	40.06	23.91	-
PH	P1	1881.2**	126.05	71.74	166.26	84.96	7.34	6.82
	P2	1111.2	-	-	169.09	0.00	7.22	-
	P3	1775.2	-	-	172.06	37.96	7.09	-
EH	P1	1745.2**	64.07	72.16	88.26	84.95	9.76	9.07
	P2	993.85**	25.77	51.04	89.09	71.45	9.67	5.73
	P3	1647.00	-	-	99.12	53.33	8.69	-
RP	P1	-742.06**	0.95	69.72	0.53	83.69	6.57	5.80
	P2	-481**	0.0004	0.10	0.52	3.11	6.87	3.81
	P3	-777.36*	0.0002	0.06	0.58	2.45	5.89	2.73
BL	P1	1745.3	-	-	9.23	0.50	94.17	-
	P2	1045.1	-	-	8.92	42.02	114.46	-
	P3	1561.30	-	-	5.23	0.08	195.20	-
MF	P1	1033.28**	2.57	61.47	60.31	78.4	2.88	2.66
	P2	637.58	-	-	61.79	40.79	3.55	-
	P3	1005.10	-	-	63.66	54.45	3.45	-
FF	P1	1179.8**	3.92	62.79	63.17	79.24	4.18	3.14
	P2	672.06*	1.98	99.88	62.78	99.94	4.21	2.24
	P3	1066.00	-	-	64.62	52.35	4.09	-

[1]EW: ear weight (t ha^{-1}); PH: plant height (cm); EH: ear height (cm); RP: relative position of the ear; BL: breakage and lodging; FF: female flowering (days); MF: male flowering (days).

*, **: significant at 1% and 5% probability by the LRT

The P1 population exhibited significant difference among S_1 progenies for nearly all the agronomic traits, except for plant breakage and lodging (Table 2). For that trait, no significant difference was found in any of the populations analyzed. The low genetic variation, together with the low mean, which is ideal for this trait, indicates that there is no need to include it in the process of selection of superior genotypes.

Among the three populations, P1 generally had the highest estimates of genetic variance and heritability for the agronomic traits, especially for plant height, ear height, relative position of the ear, and time to male and female flowering, with estimates higher than 60%, which favors selection during breeding (Rodrigues *et al.*, 2011; Crispim Filho *et al.*, 2020).

The progenies of the P2 population showed variability for few traits, such as ear height, relative position of the ear, and time to female flowering. However, the mean values were generally higher than those of P1, indicating that this population has greater frequency of favorable alleles for these traits. By the estimates of heritability, the traits that stood out were ear height and time to female flowering, with estimates of 51.04% and 99.88%, respectively.

The P3 population showed significant difference only for the relative position of the ear trait. Its estimates of genetic variability and heritability were the lowest among the three populations. Nevertheless, its high mean values, near the mean of the checks, indicate that this population has high potential for interpopulational breeding programs.

The P1 population, just as in the agronomic traits, showed significant difference among its progenies for all the ear quality traits, except for kernel alignment on the ear (Table 3). This response can be explained by the high genetic variability among the progenies, which also leads to a greater estimate of heritability, especially for grain mass, ear weight without straw, ear length without straw, and ear diameter. This indicates the presence of genetic variability to be exploited and gains in traits of interest, indicating that P1 has good potential to be included in green maize breeding programs.

Table 3: Estimates of deviance, genetic variance (σ^2_g), heritability (h^2), mean (μ), selective accuracy (SA), environmental coefficient of variation (CVe), and genetic coefficient of variation (CVg) of S_1 progenies from three green maize populations for ear quality traits. Goiânia, GO, Brazil, 2019.

Trait	Prog.	Deviance	σ^2_g	h^2	μ	SA	CVe	CVg
GW	P1	3537.2**	233768	94.53	1413.52	97.22	45.05	34.20
	P2	2132.6	-	-	1679.23	0	37.77	-
	P3	3452.4	-	-	1716.94	34.21	34.73	-
EWW	P1	3574.5**	274163	60.19	2844.72	77.58	25.93	18.41
	P2	2245.5	-	-	4057.75	53.61	18.18	-
	P3	3478.7	-	-	4258.50	0.04	17.32	-
EL	P1	1019.2**	2.75	70.71	14.95	84.09	12.37	24.71
	P2	610.17	-	-	16.81	51.77	2.94	-
	P3	929.21	-	-	17.86	26.58	11.72	-
ED	P1	252.99**	0.09	74.32	3.62	86.21	8.53	8.38
	P2	117.39	-	-	3.86	0	8.01	-
	P3	142.26	-	-	3.87	43.56	7.97	-
KA	P1	507.63	-	-	2.75	43.72	26.26	-
	P2	286.89	-	-	2.66	0.16	27.11	-
	P3	495.88	-	-	2.38	22.05	30.40	-
HP	P1	428.5*	0.08	38.40	1.84	61.96	32.89	14.99
	P2	278.9**	0.13	99.91	2.16	99.95	28.08	16.66
	P3	446.98*	0.08	39.72	2.41	63.02	25.17	11.79
GC	P1	454.49**	0.14	56.22	2.03	74.98	28.30	18.51
	P2	266.35	-	-	1.79	50.63	32.17	-
	P3	351.79	-	-	1.78	1.14	32.34	-

GW: grain mass (kg ha^{-1}); EWW: ear weight without straw (kg ha^{-1}); EL: ear length without straw (cm); ED: ear diameter (cm); KA: kernel alignment on the ear (scoring scale); HP: ear straw production (scoring scale); GC: grain color (scoring scale).

*, **: significant at 1% and 5% probability by the LRT.

For the progenies of the P2 and P3 populations, there was a significant difference only for ear straw production among the ear quality traits. However, only the P3 had a high heritability estimate for that trait. The two populations would not have potential for intrapopulational breeding, but due to the high mean values, they can be used in interpopulational breeding. P3 had the best mean values for the traits in general, indicating that this population has potential to be used in breeding programs.

Rodrigues *et al.* (2011) evaluated lines and hybrids regarding ear diameter and grain color using the same scoring scale as in this study, founding high heritability for these traits. The population that most approximated of their estimates was P1, with 74.32% and 56.22% heritability. This shows that although it does not have the best mean values, P1 has potential for inclusion in breeding programs.

The populations did not show genetic variance for kernel alignment on the ear; however, they had mean values suitable for the market (score 2: slightly curved) and values similar to those found in hybrids (Santos *et al.*, 2005). For these populations, it is not necessary to expend effort to select ears with better kernel alignment.

The traits related to ear quality, especially ear length and diameter and grain color, merit more attention during the breeding program because green maize is directed to human consumption, and acceptance by consumers is decisive for the cultivar to remain on the market. Thus, the ears must be longer than 15 cm and diameter greater than 3 cm, with grain color ranging from cream-colored (score 1) to light yellow (score 2) (Pereira Filho, 2002).

Doná (2010) evaluated the F_2 generation of the hybrids AG8060 and Fort, parents of P2 in this study, and found ear lengths of 15.77 and 15.17 cm, plant height of 218.67 and 220.33 cm, and ear height of 121.67 and 141.33 cm, respectively. In the present study, the mean values of the P2 population were more suitable than the results found by Doná (2010), with mean values of 16.81 cm ear length, 169.09 cm plant height, and 89.09 cm ear height. The formation of a population from crossing the genotypes used (AG8060 and FORT) showed improvements in these traits, though they were discrete.

Kernel alignment on the ear, ear straw production, and grain color were evaluated by scoring scales, as already mentioned, with lower mean scores being desirable. For ear straw production in the P1 population, a mean score of 1.84 was observed, with better performance than the check cultivars (mean score of 2.13). For the other two traits, the P3 population had better performance, with a mean score of 2.38 for kernel alignment on the ear and 1.78 for grain color. P2 had the worst performance, with mean scores of 2.66 and 1.79 for kernel alignment and grain color, respectively. Even so, the estimates are within the values desired by the market.

Albuquerque *et al.* (2008) evaluated commercial and experimental hybrids using the same scoring scale and found values of 2.75 for grain color. These data indicate that the populations in this study already have ideal grain color for the green maize market, and selection for this trait is not necessary.

In general, the three populations showed good results for breeding with the aim of green maize production. The P1 population had the lowest mean values for some traits, although it had high genetic variability. The P2 and P3 populations had higher mean values and lower genetic variability. Thus, it is possible to obtain consistent gains from the use of a specific selection strategy for each one of the populations.

According to Vencovsky & Barriga (1992), selection of vigorous lines presupposes the existence of genetic dispersion or variation among them. Such diversity is caused by different types of genetic components of the total genotypic variation present in the base population. Cockerham (1983) affirms that it is not an easy task to describe the complete profile of a population regarding the nature of genetic variability that it has so as to assess its potential as a source of lines. One way of doing this is to know the inbreeding depression of the populations under self-fertilization.

Reduction in the phenotypic value of allogamous plants that pass through the self-fertilization process is brought about by inbreeding depression, increase of the loci in homozygosity, and reduction in the loci in heterozygosity. This phenomenon occurs due to the increase in genetic load, which is the expression of the deleterious recessive alleles in homozygosity and reduction of loci in heterozygosity (Hallauer *et al.*, 2010). Therefore, to study this effect on the populations, it is also important to estimate the contribution of the loci in homozygosity (m + a) and in heterozygosity (d).

It can be inferred that the estimate of inbreeding depression comes from the contribution of loci in heterozygosity (d) in the population. Thus, in comparison of two populations to obtain lines, the population with a greater estimate of ‘d’ will have greater inbreeding depression. However, in evaluation of the genotypes, it is important to consider both the additive effect and the dominance effect, related to the level of inbreeding (Botelho *et al.*, 2016).

The estimates of the contributions of loci in homozygosity (m + a) were greater than the contributions of loci in heterozygosity (d) in most of the traits in the three populations, except for ear weight with straw, grain mass, ear weight without straw, and grain color, which had greater contribution from loci in heterozygosity (Table 4 and 5). For the traits with greater estimates of ‘m + a’ and the mean values desired, in the event of lower inbreeding depression, the population will be considered a good source of lines (Vencovsky & Barriga, 1992).

Table 4: Estimates of components of mean ‘m + a’ and ‘d’ and inbreeding depression (ID%) with their respective confidence intervals (95%, between parentheses) of agronomic traits evaluated in S_1 progenies of three green maize populations. Goiânia, GO, Brazil, 2019.

Trait[1]	**POP**	**m + a**	**d**	**ID%**
EW	P1	1.75 (1.23; 2.28)	8.27 (7.75; 8.79)	41.26 (30.11; 52.40)
	P2	2.82 (2.70; 2.96)	9.45 (9.32; 9.58)	38.48 (24.26; 52.70)
	P3	1.84 (1.75; 1.93)	12.96 (12.87; 13.04)	43.78 (32.15; 55.40)
PH	P1	149.01 (144.50; 153.52)	37.24 (32.80; 41.68)	10.00 (3.21; 16.79)
	P2	158.95 (158.95; 158.95)	20.29 (20.29; 20.29)	5.66 (1.09; 12.41)
	P3	158.19 (1.57.74; 158.63)	27.67 (27.23; 28.11)	7.44 (1.29; 13.59)
EH	P1	84.81 (81.75; 87.86)	8.42 (5.41; 11.43)	4.52 (0.18; 9.22)
	P2	87.53 (85.30; 89.77)	3.13 (0.93; 5.33)	1.73 (-2.08; 5.53)
	P3	96.57 (95.89; 97.24)	4.88 (4.21; 5.54)	2.40 (-1.18; 5.99)
RP	P1	0.57 (0.56; 0.58)	-0.08 (-0.09; -0.06)	-7.64 (-13.65; -1.63)
	P2	0.54 (0.53; 0.55)	-0.03 (-0.04; -0.03)	-3.26 (-8.45; 1.93)
	P3	0.60 (0.60; 0.61)	-0.06 (-0.06; -0.05)	-5.10 (-10.25; 0.05)
BL	P1	10.87 (10.87; 10.87)	-3.29 (-3.29; -3.29)	-21.73 (-31.06; 12.40)
	P2	12.45 (11.83; 13.08)	-7.03 (-7.65; -6.42)	-64.93 (-78.87; -50.99)
	P3	8.03 (8.03; 8.03)	-5.60 (-5.60; -5.60)	-115.15 (-115.15; -115.15)
MF	P1	63.72 (63.16; 64.28)	-6.79 (-7.34; -6.23)	-5.96 (-11.32; -0.60)
	P2	65.48 (65.33; 65.63)	-7.40 (-7.55; -7.25)	-6.37 (-13.51; 0.76)
	P3	66.67 (66.47; 66.87)	-6.02 (-6.22; -5.82)	-4.96 (-10.05; 0.12)
FF	P1	66.04 (65.32; 66.75)	-5.60 (-6.3; -4.89)	-4.63 (-9.39; 0.13)
	P2	65.09 (64.51; 65.67)	-4.67 (-5.24; -4.11)	-3.87 (-9.50; 1.77)
	P3	68.67 (68.45; 68.90)	-8.20 (-8.42; -7.98)	-6.78 (-12.67; -0.89)

[1] EW: ear weight (t ha^{-1}); PH: plant height (cm); EH: ear height (cm); RP: relative position of the ear; BL: breakage and lodging; FF: female flowering (days); MF: male flowering (days).

For the agronomic traits, the P2 and P3 populations exhibited these desired conditions for plant height, ear height, and relative position of the ear. The P1 and P2 populations stood out through earlier female flowering and lower inbreeding depression for that trait, and P1 stood out for earlier male flowering and lower inbreeding depression for that trait (Table 4).

For the ear quality traits, the aforementioned conditions were observed for ear diameter in the three populations, for ear length in the P2 and P3 populations, and for ear straw production in P3. Thus, the populations cited are good sources of lines for these traits (Table 4).

Negative ‘m + a’ values indicate restrained estimation errors, as well as the fact that the genetic model adopted is an approximation of reality. Negative ‘d’ values indicate that dominance occurs in the sense of decreasing the mean value of the trait. This was observed in some traits, as breakage and lodging, female flowering, male flowering and kernel alignment, which is the aim in breeding programs (Table 4 and 5).

The estimates of inbreeding depression varied a great deal among the agronomic traits. The highest estimates were for ear weight with straw, and breakage and lodging. High values of inbreeding depression (greater than 30%) were found in the traits associated with production, similar to that reported in the literature (Farias Neto & Miranda Filho, 2000; Viana *et al.*, 2009; Kuki *et al.*, 2017). From various studies on inbreeding depression and observation of similar results, the authors concluded that the gene effects of dominance in traits related to production are more complex and important than other traits, such as plant height (Botelho *et al.*, 2016).

Inbreeding depression was observed in the agronomic traits in the three populations (Table 4). Lima *et al.* (1984) reported inbreeding depression in 32 Brazilian maize populations, varying from 27.0 to 59.9% for grain yield, 6.6

to 20.3% for plant height and 6.9 to 27.4% for ear height.

High estimates of inbreeding depression were also observed for the ear quality traits, ranging from 11.33% to 63.01% (Table 5). P1 had the highest estimates, especially for the grain mass, ear length without straw, kernel alignment on the ear, and ear straw production traits. They are traits that are little studied in maize breeding, yet fundamental for the green maize crop. Therefore, identifying populations that allow advancement in specific traits can contribute to the development of more promising genotypes.

Botelho *et al.* (2016) evaluated inbreeding depression in the F_1 and S_0 generations and found reduction of up to 83.24% for ear weight without straw after self-fertilization. Somera *et al.* (2018) also observed reduction of up to 79.45% in grain weight of S_1 progenies. In general, high rates of inbreeding depression can compromise hybrid production, confirming once more that for the ear weight without straw trait, the P3 population is the most promising to obtain lines of high standard, due to the lower inbreeding depression observed, which makes it feasible to develop promising hybrids through interpopulational breeding.

The results of this study for estimates of inbreeding depression were similar to the reported by Viana *et al* (2009) and Kuki *et al.* (2017) for grain yield and grain mass of green maize. This shows that the high estimates of inbreeding depression in some traits do not impede these populations from being used in breeding programs.

In general, P1 stood out as the source of lines for the time to female and male flowering and ear diameter traits. They are traits that exhibited suitable variability and mean values. Therefore, during the intrapopulational breeding, new combinations can be obtained, as well as improvement in the traits related to agronomic production and quality. However, the time dedicated to P1 in relation to the other populations is greater, due to the lower frequency of alleles favorable for important traits.

Table 5: Estimates of components of means 'm + a' and 'd' and inbreeding depression (ID%) with their respective confidence intervals (95%, between parentheses) of ear quality traits evaluated in S_1 progenies from three green maize populations. Goiânia, GO, Brazil, 2019

Trait[1]	**POP**	**m + a**	**d**	**ID%**
GW	P1	-998.30 (-1176.89; -819.72)	4835.74 (4659.85; 5011.63)	63.01 (52. 08; 73.93)
	P2	-479.97 (-479.97; -479.97)	4316.40(4316.40; 4316.40)	56.24 (41.75; 71.74)
	P3	397.76 (-416.5; -379.02)	4235.19 (4216.73; 4253.65)	55.18 (43.53; 66.83)
EWW	P1	1130.16 (936.07; 1324.25)	3448.49 (3257.83; 3640.15)	37.66 (26.69; 48.63)
	P2	-118.43 (-412.57; 175.70)	6175.24 (5885.54; 6464.95)	50.98 (36.37; 65.58)
	P3	2111.28 (1735.15; 2487.41)	4294.42 (3926.96; 4664.88)	33.52 (22.46; 44.56)
EL	P1	10.65 (10.00; 11.29)	9.08 (8.44; 9.71)	23.01 (13.49; 32.53)
	P2	13.46 (13.28; 13.63)	6.70 (6.54; 6.88)	16.63 (5.75; 27.51)
	P3	14.81 (14.78; 14.85)	6.10 (6.07; 6.13)	14.59 (6.32; 22.85)
ED	P1	4.56 (4.50; 4.62)	0.93 (0.81; 1.05)	11.33 (4.16; 18.51)
	P2	4.85 (4.85; 4.85)	1.00 (1.00; 1.00)	11.44 (2.14; 20.74)
	P3	4.88 (4.87; 4.88)	1.00 (0.98; 1.02)	11.41 (3.96; 18.85)
KA	P1	3.77 (3.73; 3.81)	-2.04 (-2.08; -2.00)	-58.82 (-69.96; -47.68)
	P2	3.44 (3.44; 3.44)	-1.57 (-1.57; -1.57)	-41.69 (-56.09; -27.28)
	P3	3.16 (3.15; 3.17)	-1.58 (-1.58; -1.57)	-49.58 (-61.29; -37.86)
HP	P1	3.04 (3.00; 3.08)	1.25 (1.18; 1.33)	25.95 (16.03; 35.87)
	P2	3.39 (3.32; 3.47)	1.24 (1.08; 1.39)	-22.30 (10.14; 34.46)
	P3	3.13 (3.09; 3.18)	0.72 (0.64; 0.80)	12.97 (5.10; 20.84)
GC	P1	1.21 (1.08; 1.34)	1.70 (1.58;1.83)	29.27 (18.97; 39.57)
	P2	0.68 (0.63; 0.72)	2.23 (2.19; 2.28)	38.38 (24.17; 52.60)
	P3	0.65 (0.65; 0.65)	2.26 (2.26; 2.26)	38.9 (27.48; 50.32)

GW: grain mass (kg ha^{-1}); EWW: ear weight without straw (kg ha^{-1}); EL: ear length without straw (cm); ED: ear diameter (cm); KA: kernel alignment on the ear (scoring scale); HP: ear straw production (scoring scale); GC: grain color (scoring scale).

In this same direction, P2 seems to be a possible source of lines for plant height, ear height, relative position of the ear, time to female flowering, ear diameter, and ear length. P3 stood out for the same traits as P2, except for time to female flowering; however, P3 drew attention to the ear straw production trait.

It is important to highlight that the traits related to height and flowering are important in the process of hybrid seed production. The P1 progenies had higher contributions of the loci in heterozygosity in the traits of plant height, ear height, grain mass, ear length without straw, kernel alignment on the ear, and ear straw production, for which there was greater genetic variability and, consequently, greater inbreeding depression (Tables 2 and 3). The greater the frequency of loci in heterozygosity, the greater the possibility of obtaining different combinations of genes when total homozygosity in attained. Inbreeding depression is foreseen if there is heterozygosity, among other factors (Botelho *et al.*, 2016). Farias Neto & Miranda Filho (2000) obtained estimates of ‘m + a’ similar of the ones in this study for plant height and ear height.

Although the P2 and P3 populations come from crosses of more modern hybrids, inbreeding depression is still high for the traits associated with production in these populations. The P3 population had higher estimates of ‘m + a’ for most of the traits evaluated. This can be explained by the fact that their mean values are higher than those of the other populations (Tables 2 and 3), raising their ‘m + a’ estimate.

The progenies of the P3 population had lower rates of inbreeding depression compared to the two other populations for the traits of ear straw production, grain mass, ear length without straw, and ear weight without straw (Table 5). For this last trait, the S_1 progenies of P3 had a 33.52% reduction in their yield compared to S_0, which is a low value compared to the other populations. As already mentioned, for the ear weight without straw trait, P3 not only had a lower rate of inbreeding depression, but also had greater contribution of loci in homozygosity than the other populations for most of the traits, showing its high potential, both *per se* and for hybrid production.

In general, the ear quality traits, important for green maize production, had greater inbreeding depression than the agronomic traits. This shows that inbreeding depression should be considered in the selection process, and it is necessary to increase the frequency of favorable alleles throughout the breeding process.

CONCLUSIONS

All the populations showed potential for extraction of lines for some trait, with high estimates of ‘m + a’, high mean values, and lower inbreeding depression.

The P1 population stood out for the time to female and male flowering and ear diameter traits; the P2 population stood out for plant height and ear height, relative position of the ear, time to female flowering, ear diameter, and ear length traits; and the P3 population stood out for plant height and ear height, relative position of the ear, and diameter, length, and straw production of the ear traits.

Both the agronomic traits and the ear quality traits have inbreeding depression, which should thus be considered by green maize breeding program. The P1 population showed inbreeding depression for most of the traits, P2 for male flowering, ear weight without straw and ear diameter and P3 for ear weight, female flowering, breakage and lodging and grain color.

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