

## Inbreeding depression and genetic components for popping expansion and other traits in Brazilian populations of popcorn

Emmanuel Arnhold<sup>1</sup>, José Marcelo Soriano Viana<sup>2</sup>, Freddy Mora<sup>3</sup>, Glauco Vieira Miranda<sup>4</sup>, and Ricardo Gonçalves Silva<sup>5</sup>

<sup>1</sup>Escola de Veterinária, Departamento de Produção Animal, Campus II, Samambaia, Caixa Postal 131, CEP 74001-970, Universidade Federal de Goiás, Goiânia, GO, Brasil.

<sup>2</sup>Departamento de Biologia Geral, Universidade Federal de Viçosa, CEP 36570-000, Viçosa, MG, Brasil.

<sup>3</sup>Facultad de Ciencias Forestales, Universidad de Concepción. Victoria 631, Barrio Universitario, Concepción, Chile.

<sup>4</sup>Departamento de Fitotecnia, Universidade Federal de Viçosa, CEP 36570-000, Viçosa, MG, Brasil.

<sup>5</sup>Centro de Ciências Agrárias e Ambientais, Universidade Federal do Maranhão, CEP 65500-000, Chapadinha, MA, Brasil.

### Abstract

**E. Arnhold, J.M.S. Viana, F. Mora, G.V. Miranda, and R.G. Silva. 2010. Inbreeding depression and genetic components in Brazilian populations of popcorn. Cien. Inv. Agr. 37(3):125-132.** The aim of the study was to assess inbreeding depression and determine genetic components in landrace populations of popcorn. Six Brazilian popcorn landraces: Amarelo, Beija-Flor, Branco, Rosa-claro, Roxo and Viçosa, were subjected to self-pollination. Experiments with S0 populations and their selfing populations (S1) were conducted in a randomized complete block design. The estimates of inbreeding depression varied from 1.2% (popping expansion) to 79% (grain yield). The gene action was predominantly additive for plant height, ear height and hundred-grain-weight. The dominance genetic effects were important for index of prolificacy and grain yield. The genetic effect of popping expansion was bidirectional with null dominance and a predominance of additive gene effects. Based on these results, it was possible to identify popcorn populations suitable to extract inbred lines, develop hybrids and use in population improvement. The present study also confirmed that popping expansion is a trait that can be improved efficiently by recurrent selection programs of popcorn.

**Key words:** *Zea mays* L., improvement, popping expansion, popcorn, genetic variance.

### Introduction

The main objective in maize breeding programs is to obtain hybrids, and success depends on the

choice of parents (Miranda *et al.*, 2008; Santos *et al.*, 2008) and optimization of the genotypes by environmental interaction (Miranda *et al.*, 2009; Arnhold *et al.*, 2009a). The value of homozygous inbred lines depends on how much of the variance can be reduced by inbreeding, and on how much the environmental variance will be affected by inbreeding (Wiegertjes *et al.*, 1996). Inbreeding depression is higher in popcorn populations than in maize and it is difficult to obtain lines.

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Corresponding author: morapobelete@gmail.com,  
freddymora@udec.cl

In maize, several studies have found inbreeding depression for several traits in different populations (Hallauer and Sears, 1973; Good and Hallauer, 1977; Lima *et al.*, 1984; Nass and Miranda Filho, 1995). The difference between the panmitic population mean (S0) and the population mean after one generation of self-pollination (S1) is an estimate of inbreeding depression (Pacheco *et al.*, 2002; Berdahl and Ray, 2004). There are many studies related to the effects of inbreeding depression using S1 populations in several species of plants (Mena-Ali *et al.*, 2008; Zaffar *et al.*, 2001; Rojas *et al.*, 2009; Berdahl and Ray, 2004; Pacheco *et al.*, 2002). For instance, Rojas *et al.* (2009) quantified the inbreeding depression for different traits in eight S1 cassava families and analyzed the variation within these eight groups of S1 families. Berdahl and Ray (2004) determined the value of one generation of self-pollinating before selection for yield in crested wheatgrass, and yields were compared for synthetic populations derived from selection among and within S1 and open-pollinated progenies. In maize, Pacheco *et al.* (2002) studied the inbreeding depression using a diallel experiment of 28 maize elite open-pollinated varieties. In that study, yield reductions of the populations from S0 to S1 (mean of the 10 environments) varied from 34.6% to 59.2%, with an average of 49.1%. Inbreeding depression was greater in populations with a wider genetic base, which had never been exposed to inbreeding.

Knowledge on the nature of genetic variation of different traits is also essential in breeding programs (Rodvalho *et al.*, 2008; Arnhold *et al.*, 2009b). The main feature of quality popcorn is its popping expansion volume (Mora and Scapim, 2007; Pereira *et al.*, 2008), and there is evidence of the predominance of additive genetic variation for this trait (Dofing *et al.*, 1991; Larish and Brewbaker, 1999; Miranda *et al.*, 2008). Four quantitative trait loci (QTLs) on chromosomes 1S, 3S, 5S and 5L were found to explain 45% of the phenotypic variation in popping expansion (Lu *et al.*, 2003).

Therefore, the aim of this study was to evaluate inbreeding depression and genetic components in six different Brazilian popcorn populations,

in order to identify those most suited to extract inbreds and generate hybrids, and for population improvement.

## Material and Methods

Self-pollination was performed in six Brazilian popcorn populations: Amarelo, Beija-Flor, Branco, Rosa-claro-Claro, Roxo and Viçosa. Amarelo, Viçosa and Beija-Flor have yellow and pearl grain, and Rosa-claro and Roxo have red and pearl grain. The Beija-Flor population exhibit grain segregation for red and white grain color and rice-type grains. All these populations are from the Germplasm Active Bank of the Maize Breeding Program, Department of General Biology, Federal University of Viçosa. The parents and inbred populations ( $F = 1/2$ ) were grown in Viçosa, state of Minas Gerais, Brazil.

The experiment was conducted in a randomized complete block design with two replicates. Each plot consisted of two 5-m long rows, spaced 0.9 m apart. After thinning, there were 5 plants  $m^{-2}$ , resulting in a density equivalent to 55,555 plants  $ha^{-1}$ .

Plant height (PH), ear height (EH), the prolificacy index (PI), hundred-grain-weight (P100), grain yield (GY) in  $kg ha^{-1}$ , and popping expansion (PE) in  $g ml^{-1}$  were evaluated.

The grain weight data were adjusted to standard moisture of 14.5% on a wet basis. Popping expansion was obtained from random grain samples with 12% moisture in the harvested plot. A sample of 30 g of kernels from each replication was weighed and then popped in a hot air electric popper at 237°C, and the volume of product measured in a graduated cylinder, producing the correspondent ratio (PE = volume after popping/ weight before popping).

Analysis of variance for each trait was applied to detect significant differences between S0 and S1 inbred lines. S0 and S1 lines consisted of 250 plants each. Fifty S0 plants (from each population) were self-pollinated to produce S1-generation plants. Inbreeding depression (ID) for each function was obtained by the difference

between the population average of each generation and their self-pollinated population (S1):

$$D = \bar{S}_0 - \bar{S}_1$$

and as a percentage:

$$D (\%) = \left[ \frac{\bar{S}_0 - \bar{S}_1}{\bar{S}_0} \right] 100$$

Therefore, the cumulative contribution of homozygous loci in the combined average of the population can be obtained by:

$$\mu + \alpha = 2\bar{S}_1 - \bar{S}_0$$

According to the additive-dominant model proposed by Gardner (1965),  $\mu$  is the general average,  $\alpha$  is the cumulative contribution of homozygous loci and  $\delta$  represents the contribution of loci heterozygosity.

The contribution of heterozygosity at the loci ( $\delta$ ) is estimated by:

$$\delta = 2(\bar{S}_0 - \bar{S}_1)$$

## Results and discussion

Inbreeding depression was significant for plant height in the Branco, Amarelo, Rosa-claro and Viçosa populations (Table 1) and for ear height in the Amarelo, Rosa-claro and Viçosa populations. The dominance effect was positive for plant height and ear height, where inbreeding depression was significant, explaining the decrease in the magnitude of these variables (Table 2). These results are in accordance with reports by Scapim *et al.* (2006). On the other hand, Simon *et al.* (2004) found some popcorn populations with a negative dominance effect for these traits, *i.e.* the S1 population average exceeded the S0 population average.

The average inbreeding depression was 18% for plant height and ear height with predominance of additive genetic effects ( $\mu + \alpha$ ) (Table 3). However, the Rosa-claro population (Table 2) showed greater genetic variation due to the

**Table 1.** Analysis of variance for agronomic traits (statistical significance between S0 and S1 plants) in Brazilian populations of popcorn evaluated at Minas Gerais, Brazil.

Population	Generation	Mean values and statistical significance					
		PH	EH	PI	P100	GY	PE
Branco	S0	1.07*	0.50 ns	0.79 ns	11.76*	326.8*	16.12 ns
	S1	0.97	0.46	0.68	15.02	54.1	16.39
Roxo	S0	1.61 ns	0.74 ns	0.67*	14.11 ns	1597.0*	19.43*
	S1	1.24	0.58	0.43	12.77	354.8	16.94
Beija-flor	S0	1.59 ns	0.67 ns	0.83*	15.30*	1571.4*	14.66*
	S1	1.53	0.69	0.48	12.15	281.7	19.6
Amarelo	S0	1.55*	0.74*	0.60*	16.38*	1100.6*	24.39*
	S1	1.39	0.68	0.65	13.12	458.7	18.34
Viçosa	S0	1.58*	0.74*	0.87*	19.59*	1729.0*	20.53*
	S1	1.46	0.68	0.78	13.55	430.5	24.44
Rosa-claro	S0	1.72*	0.72*	1.20*	19.78*	3516.8*	23.86*
	S1	0.95	0.45	0.66	15.59	189.3	18.77

\*there was statistically significant difference between S0 and S1 generations, which was calculated by F Test (5% of probability); ns non-significant. PH: plant height (m); EH: ear height (m); PI: prolificacy index; P100: hundred-kernel-weight (g); GY: grain yield (kg ha<sup>-1</sup>); PE: popping expansion (mL g<sup>-1</sup>).

effects of dominance ( $\delta$ ), increased inbreeding and increased dominance effect for plant height and ear height compared to other populations. Scapim *et al.* (2006) also found a predominance of additive effects and 10% of inbreeding depression for plant height and ear height. In maize, the dominance effects of plant height and ear height were higher than those in popcorn (Hallauer and Miranda Filho, 1981). Therefore, selection for plant height and ear height can be exploited differently in different populations. The exploitation of heterosis in crosses and recurrent selection are efficient for these characteristics in popcorn populations.

With regard to the prolificacy index, there were significant differences between populations S0 and S1 in all populations except in Branco population (Table 1), probably due to the effects of dominance for the character in this population. Dominance was generally positive, with the exception of the Amarelo population. The average inbreeding depression was 25% and it was mostly influenced by the effects of dominance (Tables 2 and 3). Thus, depending on population, it is possible to explore a different selection for index of prolificacy. The intercrossing between Roxo, Beija-Flor and, Rosa-claro due to increased dominance effects, as well as methods of recurrent selection on Amarelo, Branco and Viçosa populations due to increased additive effects can be explored (Table 2).

The Roxo population showed no differences between the S0 and S1 population in terms of hundred-grain-weight (Table 1); probably as a result of the low variation due to the dominance effect (d). This dominance effect was generally positive, the exception being the Branco population (Table 2). The average inbreeding depression was 12.95%. The Viçosa population was greatly influenced by additive genetic effects (Tables 2 and 3). So, with the exception of the Viçosa population, which can be used in crosses, all other populations should be improved by recurrent selection methods.

With regards to grain yield, inbreeding depression was important, positive and very high in all populations (Table 2). On average, inbreeding depression was 78.56%. Simon *et al.* (2004)

found less inbreeding depression for this variable, but they used popcorn populations that had undergone more cycles of selection, in contrast to the less improved popcorn population used in this study. Although, in general, we found a predominance of dominance effects, there were some exceptions in which additive effects were more important.

The Amarelo, Roxo and Viçosa populations had the lowest inbreeding depression for grain yield (Table 2). Therefore, they are the most appropriate as sources from which to extract inbred lines. Matta and Viana (2003) found the highest general combining ability for grain yield in these three populations, supporting our results. Rosa-Claro showed the highest (94.60%) inbreeding depression and is therefore the least suitable for extracting inbred lines.

Regarding grain yield in maize, Pacheco *et al.* (2002) observed a small degree of inbreeding depression, ranging from 34.6% to 59.2%, with an average of 49.1%, but they evaluated elite open pollinated varieties of maize. A lower value of inbreeding depression is expected to improve a population, because there is a lower frequency of deleterious alleles due to the selection process (Pacheco *et al.*, 2002).

The Branco population was the only one that showed no significant differences between the S0 and S1 population in terms of popping expansion (Table 1). In this case, no effects were dominant. For the other populations, the inbreeding depression was significant and the dominance was bidirectional. Larish and Brewbaker (1999) observed negative heterosis in popping expansion, and in some crosses, this trait was less than half of that of the parents. Scapim *et al.* (2002) also found bi-directional dominance. Simon *et al.* (2004) only found positive and zero dominance.

The average inbreeding depression for popping expansion was 1.23%. The additive gene effects were higher than the dominant effects (Tables 2 and 3) in several studies that have shown the predominance of additive genetic effects in the control of popping expansion (Dofing *et al.*, 1991; Larish and Brewbaker, 1999). Therefore, pop-

**Table 2.** Inbreeding depression and genetic components in Brazilian populations of popcorn evaluated at Minas Gerais, Brazil.

Population	Parameter	Parameter estimates					
		PH	EH	PI	P100	GY	PE
Branco	ID	0.1	--	--	-3.26	272.7	--
	ID %	9.3	--	--	-27.73	83.44	--
	$\mu + \alpha$	0.88	--	--	18.29	-437.01	--
	$\delta$	0.2	--	--	-6.52	1090.4	--
Roxo	ID	--	--	0.24	--	1 242.2	2.49
	ID %	--	--	36.14	--	77.78	12.8
	$\mu + \alpha$	--	--	0.19	--	-1774.7	14.45
	$\delta$	--	--	0.49	--	4968.7	4.97
Beija-flor	ID	--	--	0.35	3.15	1289.7	-4.94
	ID %	--	--	42.24	20.6	82.1	-33.76
	$\mu + \alpha$	--	--	0.13	9	-2016.0	25.55
	$\delta$	--	--	0.71	6.30	5158.8	-9.9
Amarelo	ID	0.16	0.06	-0.05	3.26	642	6.05
	ID %	10.29	8.05	-8.37	19.89	58.3	24.79
	$\mu + \alpha$	1.24	0.63	0.70	9.86	-366.6	12.29
	$\delta$	0.32	0.12	-0.10	6.52	2567.9	12.1
Viçosa	ID	0.12	0.06	0.09	6.05	1299	-3.91
	ID %	7.88	8.72	10.22	30.87	75.1	-19.04
	$\mu + \alpha$	1.34	0.62	0.69	7.50	-1736.5	28.35
	$\delta$	0.25	0.13	0.18	12.10	5194.5	-7.82
Rosa-claro	ID	0.77	0.26	0.54	4.18	3327.5	5.09
	ID %	44.64	36.80	45.04	21.14	94.6	21.35
	$\mu + \alpha$	0.19	0.18	0.12	11.41	-6276.3	13.67
	$\delta$	1.54	0.54	1.09	8.36	13309.9	10.19

ID: inbreeding depression; %ID: inbreeding depression in percentage;  $\mu + \alpha$ : additive effects;  $\delta$ : dominance effect; PH: plant height (m); EH: ear height (m); PI: prolificacy index; P100: hundred-kernel-weight (g); GY: grain yield (kg ha<sup>-1</sup>); PE: popping expansion (mL g<sup>-1</sup>).

**Table 3.** Overall mean values calculated considering the popcorn populations in which inbreeding depression was significant. Populations were evaluated in Minas Gerais, Brazil.

Trait	Generation		Inbreeding depression		Genetic components	
	S <sub>0</sub>	S <sub>1</sub>	ID	ID%	$\mu + \alpha$	$\delta$
PH (m)	1.49	1.20	0.29	18.03	0.91	0.58
EH (m)	0.74	0.61	0.13	18.09	0.47	0.26
PI	0.84	0.60	0.24	25.05	0.37	0.47
P100 (g)	16.56	13.89	2.68	12.95	11.21	5.35
GY (kg ha <sup>-1</sup> )	3280.55	589.69	2690.86	78.56	-2101.16	5381.71
PE (mL g <sup>-1</sup> )	20.57	19.62	0.96	1.23	18.66	1.91

ID: inbreeding depression; %ID: inbreeding depression in percentage;  $\mu + \alpha$ : additive effects;  $\delta$ : dominance effect; PH: plant height (m); EH: ear height (m); PI: prolificacy index; P100: hundred-kernel-weight (g); GY: grain yield (kg ha<sup>-1</sup>); PE: popping expansion (mL g<sup>-1</sup>).

ping expansion is a character that can be exploited efficiently in recurrent selection programs. For the production of hybrids, selection based on popping expansion is also recommended during development of lines because, in general, heterosis is null or bidirectional with a low magnitude (Scapim *et al.*, 2002). Following the same idea, selecting for popping expansion is also recommended to be applied in the base population.

The Amarelo and Rosa-claro populations showed the highest capacity for popping expansion, and they are recommended to obtain inbred lines (Table 1). The Beija-Flor and Viçosa populations had the largest additive effects, and positive inbreeding depression. Therefore, these two populations are excellent sources of lines in terms of popping expansion and are recommended for recurrent selection methods.

Matta and Viana (2003) recommended the Beija-Flor and Viçosa populations for the extraction of lines and production of hybrids and for reciprocal recurrent selection. In fact, the re-

sults on production and capacity of expansion (Table 1) suggest that these two populations are best suited for extracting lines and population improvement.

In the present study, it was possible to identify popcorn populations suitable for use in inbred lines, hybrids and population breeding; these populations are Beija-Flor and Viçosa, which evidenced large additive effects and had a positive value of inbreeding depression. It was also confirmed that popping expansion is a trait that can be exploited efficiently in recurrent selection programs of popcorn.

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### Resumen

**E. Arnhold, J.M.S. Viana, F. Mora, G.V. Miranda y R.G. Silva. 2010. Depresión endogámica y componentes genéticos en poblaciones Brasileñas de maíz-roseta. Cien. Inv. Agr. X(X):125-132.** Los objetivos del estudio fueron evaluar la depresión endogámica y determinar los componentes genéticos en poblaciones de maíz-roseta. Se realizaron autopolinizaciones en seis poblaciones Brasileñas: Amarelo, Beija-Flor, Branco, Rosa-claro, Roxo and Viçosa. Las poblaciones S0 y las poblaciones de autopolinización S1 se evaluaron en un diseño de bloques completos al azar. Las estimaciones de depresión endogámica variaron de 1,2% (capacidad de expansión) a 79% (productividad de granos). Los efectos genéticos fueron predominantemente aditivos para altura de planta, altura de mazorca y peso de cien granos. Los efectos genéticos de dominancia fueron importantes para índice de prolificidad y rendimiento de grano. El efecto genético de la capacidad de expansión fue bidireccional, con nulo efecto de dominancia y predominancia de efectos genéticos aditivos. Basado en los resultados, fue posible identificar poblaciones de maíz-roseta para la obtención de líneas puras, híbridos y mejoramiento poblacional. El presente estudio confirmó, además, que la capacidad de expansión es una característica que puede ser mejorada eficientemente en los programas de selección recurrente de maíz.

**Palabras clave:** *Zea mays* L, mejoramiento, capacidad de expansión, maíz roseta, varianza genética.

## References

- Arnhold, E., F. Mora, R.G. Silva, P.I.V. Good-God, and M.A. Rodovalho. 2009a. Evaluation of top-cross popcorn hybrids using mixed linear model methodology. *Chilean J. Agric. Res.* 69:46-53.
- Arnhold, E., J.M.S. Viana, R.G. Silva, and F. Mora. 2009b. Relative efficiencies of selection methods of inbred families in popcorn. *Acta Scientiarum Agronomy* 31(2):203-207.
- Berdahl, J.D., and I.M. Ray. 2004. Comparison of S1 with open-pollination progenies in selection for yield in crested wheatgrass. *Crop Science* 44:768-771.
- Dofing, S. M., N. D'Croz-Mason, and M.A. Thomas-Compton. 1991. Inheritance of expansion volume and yield in two popcorn x dent corn crosses. *Crop Science* 31(3):715-718.
- Gardner, C.O. 1965. Teoría de genética estadística aplicable a las medias de variedades, sus cruces y poblaciones afines. *Fitotecnia Latinoamericana* 2:11-22.
- Good, R.L., and A.R. Hallauer. 1977. Inbreeding depression in maize by selfing and full-sibbing. *Crop Science* 17:935-940.
- Hallauer, A.R., and J.H. Sears. 1973. Changes in quantitative traits associated with inbreeding in a synthetic variety of maize. *Crop Science* 13:327-330.
- Hallauer, A.R., and J.B. Miranda-Filho. 1981. Quantitative genetics in maize breeding. Iowa State University. Ames, USA. 468 pp.
- Larish, L.L.B., and J.L. Brewbaker. 1999. Diallel analyses of temperate and tropical popcorns. *Maydica* 44:279-384.
- Lima, M., J.B. Miranda-Filho, and P.B. Gallo. 1984. Inbreeding depression in Brazilian populations of maize (*Zea mays* L.). *Maydica* 29:203-215.
- Lu, H.J., R. Bernardo, and H.W. Ohm. 2003. Mapping QTL for popping expansion volume in popcorn with simple sequence repeat markers. *Theoretical and Applied Genetics* 106:423-427.
- Matta, F.P., and M.S. Viana. 2003. Eficiências relativas dos processos de seleção entre e dentro de famílias de meios-irmãos em população de milho-pipoca. *Ciência e Agrotecnologia* 27:548-556.
- Mena-Ali, J.I., L.H. Keser, and A.G. Stephenson. 2008. Inbreeding depression in *Solanum carolinense* (Solanaceae), a species with a plastic self-incompatibility response. *BMC Evolutionary Biology* 8:10.
- Miranda, G.V., L.V. Souza, J.C.C. Galvão, L.J.M. Guimarães, A.V. Melo, and I.C. Santos. 2008. Genetic variability and heterotic groups of Brazilian popcorn populations. *Euphytica* 162:431-440.
- Miranda, G.V., L.V. Souza, L.J.M. Guimarães, H. Namorato, L.R. Oliveira, and M.O. Soares. 2009. Multivariate analyses of genotype x environment interaction of popcorn. *Pesquisa Agropecuária Brasileira* 44:45-50.
- Mora, F., and C.A. Scapim. 2007. Predicting breeding values of population effect of maize evaluated in Brazil and Paraguay. *Agricultura Técnica* 67:139-146.
- Nass, L.L., and J.B. Miranda-Filho. 1995. Inbreeding depression rates of semi-exotic maize (*Zea mays* L.) populations. *Revista Brasileira de Genética* 18:585-592.
- Pacheco, C.A.P., M.X. Santos, C.D. Cruz, S.N. Parentori, P.E.D. Guimarehs, and P.A. Vieira. 2002. Inbreeding depression of 28 maize elite open pollinated varieties. *Genetics and Molecular Biology* 25:441-448.
- Pereira, L.K., C.A. Scapim, C. Mangolim, M.F.P. Machado, C.A.P. Pacheco, and F. Mora. 2008. Heterozygosity following half-sib recurrent selection in popcorn using isoenzyme markers. *Electronic Journal of Biotechnology* 11(1):107-115.
- Rodvalho, M.A., F. Mora, E.M. Santos, C.A. Scapim, and E. Arnhold. 2008. Survival heritability in 169 families of white grain popcorn: a Bayesian approach. *Cien. Inv. Agr.* 35(3):255-260.
- Rojas, M.C., J.C. Pérez, H. Ceballos, D. Baena, N. Morante, and F. Calle. 2009. Analysis of inbreeding depression in eight S1 cassava families. *Crop Science* 49:543-548.
- Santos, F.S., A.T. Amaral, S.P. Freitas Jr, R.M. Rangel, C.A. Scapim, and F. Mora. 2008. Genetic gain prediction of the third recurrent selection cycle in a popcorn population. *Acta Scientiarum Agronomy* 30:651-655.
- Scapim, C.A., A.L. Braccini, R.J. B. Pinto, A.T. Amaral Júnior, M.A. Rodvalho, R.M. Silva, and L.M. Mortele. 2006. Componentes genéticos de médias e depressão por endogamia em populações de milho-pipoca. *Ciência Rural* 36(1):63-69.
- Scapim, C.A., C.A.P. Pacheco, A. Tonet, A.L. Braccini, and R.J.B. Pinto. 2002. Análise dialélica e

- heterose de populações de milho-pipoca. *Bragantia* 61:219-230.
- Simon, G.A., C.A. Scapim, C.A.P. Pacheco, R.J.B. Pinto, A.L. Braccini, and A. Tonet. 2004. Depressão por endogamia em populações de milho-pipoca. *Bragantia* 63(1):55-62.
- Viana, J.M.S., and F.P. Matta. 2003. Analysis of general and specific combining abilities of popcorn populations, including selfed parents. *Genetics and Molecular Biology* 26(4):465-471.
- Wiegertjes, G.F., Stet, R.J.M., Parmentier, K.K., and W.V. Van Muiswinkel. 1996. Immunogenetics of disease resistance in fish: A comparative approach. *Developmental and Comparative Immunology* 20(6):365-381.
- Zaffar, G., G.H. Zargar, W.A. Shafiq. 2001. Estimation of genetic variances in a maize composite. *The Indian Journal of Genetics and Plant Breeding* 61:111-114.