Yield heterosis and average fruit weight as a function of inbreeding in *Cucurbita moschata* Duch. ex Poir.

Heterosis del rendimiento y peso promedio de fruto en función de la endogamia en *Cucurbita moschata* Duch. ex Poir.

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ABSTRACT

In order to estimate the mean heterosis, mid parent heterosis and heterobeltiosis (HB), three diallel crossings of *Cucurbita moschata* were evaluated, each formed by six parents with three levels of inbreeding (S_0, S_1, S_2). A randomized complete block experimental design was used with four replicates, arranged in split plots. The variables yield per plant (YPP) and average fruit weight (AFW) were analyzed. The hybrids between S_1 or S_2 inbred lines presented heterotic superiority regarding to those between S_0 parents for the variables YPP and AFW. Likewise, the hybrids between S_2 inbred lines reported heterotic superiority in comparison to those among S_1 inbred lines, for such variables. The hybrids between S_2 inbred lines that reported the highest expression levels of HB for YPP were P1xP3, P2xP6 and P1xP2, with values ranging between 131.42 and 98.24%; while the hybrids among S_1 inbred lines that recorded the highest values of HB, for this same variable, were P3xP5 and P1xP5 with values of 191.71 and 139.29%, respectively. Furthermore, the hybrids between S_2 and S_1 inbred lines that registered the highest level of HB for AFW were P1xP3 and P1xP5 with values of 108 and 83.7%, respectively.

Key words: butternut squash, selection, heterobeltiosis, diallel crossing, inbred lines, hybrids.

RESUMEN

Para estimar la heterosis promedia, heterosis relativa y heterobeltiosis (HB) se evaluaron tres cruzamientos dialélicos de *Cucurbita moschata*, conformados cada uno por seis progenitores con tres niveles de endogamia (S_0, S_1, S_2). Se utilizó el diseño experimental de bloques completos al azar con cuatro repeticiones y arreglo en parcelas divididas. Se analizaron las variables producción por planta (PFP) y peso promedio del fruto (PPF). Los híbridos producidos entre líneas endogámicas S_2 o S_1 presentaron superioridad heterótica en comparación a los híbridos formados entre padres S_0 para PFP y PPF. Igualmente, los híbridos entre líneas endogámicas S_2 reportaron para dichas variables superioridad heterótica con respecto a los híbridos entre líneas endogámicas S_1. Los híbridos entre líneas endogámicas S_2 que presentaron los mayores niveles de expresión de HB para PFP fueron P1xP3, P2xP6 y P1xP2 con valores entre 131.42 y 98.24%, respectivamente; mientras que los híbridos entre líneas endogámicas S_1 que registraron los niveles más altos de HB para dicha variable fueron P3xP5 y P1xP5 con 191.71 y 139.29%, respectivamente. Por otro lado, los híbridos entre líneas endogámicas S_2 y S_1 que registraron los niveles más altos de HB para PPF fueron P1xP3 y P1xP5, con valores de 108 y 83.7%, respectivamente.

Palabras clave: zapallo, selección, heterobeltiosis, cruzamientos dialélicos, líneas endogámicas, híbridos.

Introduction

The butternut squash *Cucurbita moschata* (Duch. ex Lam.) Duch. ex Poir. is grown and consumed in the tropical and subtropical regions of the American continent and other places in the world. In Colombia, this is the most cultivated and consumed species of the genus *Cucurbita*, with a planted area and an average production rate of 11,723 ha and 107,839 t, respectively (Minagricultura, 2016). It has a high genetic diversity and its center of domestication is located, possibly, around the northwest region of South America (Restrepo and Vallejo, 2008). It is characterized due to its nutritional, industrial and combustible properties (Restrepo, 2015). Among others, the butternut squash medicinal benefits include anti-carcinogenic (Zhang *et al.*, 2012), anti-diabetic (Chang *et al.*, 2014), anti-oxidant (Wu *et al.*, 2014) and hypolipidemic properties (Zhao *et al.*, 2014).

Heterosis is known as the hybrid vigor expressed in hybrids. It represents the superiority in performance of hybrid individuals compared with their parents (Hallauer *et al.*, 2010). According to the referent used to compare the behavior of the produced hybrid, heterosis can be expressed as three different terms: mid parent, standard variety and better

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parent heterosis. The standard variety is designated as standard heterosis and the better parent heterosis is better known as heterobeltiosis (Alam *et al.*, 2004).

Heterotic superiority has been demonstrated for the yield per plant (YPP) of *C. moschata* on F_1 hybrids produced from inbred lines with different degrees of inbreeding in contrast to the hybrids produced from the crosses between S_0 parents (Espitia *et al.*, 2006; Ortiz *et al.*, 2013). For the variables YPP and the average fruit weight (AFW), there was a greater magnitude and statistical significance in the estimates of mid parent heterosis (MPH), heterobeltiosis (HB) and standard variety heterosis (STH) in the hybrids between S_1 inbred lines compared to those from S_0 (Espitia *et al.*, 2006). In contrast, for these variables a significant decrease in the estimates of mid parent heterosis and heterobeltiosis was recorded in the hybrids between S_1 inbred lines related to the hybrids between S_0 parents (Vallejo and Gil, 1998).

The main objective of this research was to estimate the degree of MPH and HB of the resulting hybrids from three diallel crossings of *Cucurbita moschata*. Each crossing was composed by six progenitors with different degrees of inbreeding (S_0, S_1, and S_2) for the variables YPP and AFW. As a final product, the research results are intended to contribute significantly to the research program "Genetic Improvement, Agronomy and Production of Vegetables Seeds" of the Universidad Nacional de Colombia, Palmira Campus, committed to produce and release butternut squash hybrids to the market. Furthermore, the hypothesis of this study was that the level of inbreeding of parents can influence yield heterosis and average fruit weight in *C. moschata*.

Materials and methods

The research was carried out at the Experimental Center of the Universidad Nacional de Colombia, Palmira Campus (CEUNP, its Spanish acronym), located in Candelaria, department of Valle del Cauca, Colombia (3°25'34.42" N and 76°25'47.57" W, 980 m a.s.l., average annual temperature of 26°C, average annual precipitation of 1,100 mm and average relative humidity of 76%).

Three diallel crosses of pumpkin *C. moschata* were analyzed. Each cross was composed by six parents with varying levels of inbreeding (S_0 parents, S_1 and S_2 inbred lines). The following S_0 parents were selected considering their outstanding features such as size, external fruit color, pulp color and thickness and due to their diverse geographic origin: UNAPAL-Abanico-75-1 (P1), UNAPAL-Abanico-75-2 (P2), UNAPAL-Dorado (P3), an introduction from Costa Rica denominated IC3A (P4), UNAPAL-Llanogrande-1 (P5) and UNAPAL-Llanogrande-2 (P6). In the current research, the S_1 and S_2 inbred lines were produced from S_0 open-pollinated parents previously selected. A weighted selection index that included variables such as AFW (2.0-4.0 kg), pulp thickness (3.5-5.0 cm) and Salmon colored pulp was used to select the fruit. The selection ranges indicated for each variable correspond to optimum fruit values for fresh consumption market, where consumers prefer to buy small and whole fruits instead of sliced fruit. Twenty-one genotypes (six parents and fifteen direct crosses) were evaluated for each diallel cross.

The variables YPP (kg) and AFW (kg) were analyzed. The agronomic evaluation of 63 genotypes of three diallel crossings was carried out during the second semester of 2011. A randomized complete block experimental design with four replicates was used. Field treatments were arranged in split plots, with the main plot corresponding to the diallel cross (level of inbreeding) and the subplot corresponding to the evaluated genotypes (six parents and 15 F_1 hybrids, in each of the diallel crosses). Planting distance was 2.5 m between lines and 3.0 m between plants. Each experimental plot consisted on a furrow of five plants (37.5 m^2), with three central plants set as useful plot area. Genetic and statistical analysis were performed using the method proposed by Hallauer and Miranda in 1981 (Hallauer *et al.*, 2010). The statistical model associated with the experimental design for each diallel crossing was:

$$Y_{ijkl}= \mu+g_{ij}+b_k+D_l+(Db)_{lk}+(1/rn)\Sigma\Sigma e_{ijkl},$$

where:

i, j: 1, 2.......p parents; p = 6;

k: 1, 2…....r replicates; r = 4;

μ: population mean of all genotypes;

g_{ij}: effect of genotype ij – th;

b_k: effect of block k - th;

D_l: effect of inbreeding generation l;

$(Db)_{lk}$: effect of interaction of inbreeding generation by blocks;

$(1/rn)\ \Sigma\Sigma e_{ijkl}$: experimental error associated with the observation Yijkl;

Y_{ijkl}: phenotypic average value observed of the variable under study for the genotype (ij) in inbreeding generation l.

Simultaneously, the source of genotypes variation (g_{ij}) was partitioned into three new sources of variation: parents, crosses and the contrast between crosses and parents following the methodology suggested by Hallauer *et al.* (2010). The mid parent heterosis (MPH) and heterobeltiosis (HB) were estimated as follows:

MPH: ratio between the mean value of the particular hybrid (F_1) and the mean value of the two parents for that hybrid (MP), expressed in percentage.

$$MPH = [(F_1 / MP) \times 100] - 100.$$

HB: ratio between the mean value of the particular hybrid (F_1) and the best parent mean value for that hybrid (BP), expressed as a percentage.

$$HB = [(F_1 / BP) \times 100] - 100$$

The two types of heterosis were statistically tested using the Student's T-test. The analysis of variance was performed using the SAS® software (SAS / STAT® package, version 9.4 of the SAS® system for Windows) from SAS Institute Inc. 2012 (Cary, North Carolina, USA). For the estimation of the different types of heterosis, the Excel® 2013 program version 15.0 of Microsoft® Office was used.

Results and discussion

Analysis of variance (ANOVA)

The Mean Squares from the ANOVA for the variables YPP and AFW in three generations of inbreeding of *C. moschata* are presented in Table 1. There were significant differences for YPP and AFW in the sources of variation genotypes and generations, indicating that at least one of the generations or one of the genotypes is different from the others. By partitioning the genotypes source of variation into their components in each generation of inbreeding, we observed for YPP and AFW the existence of significant differences in all sources of variation considered, except for the parental source in the S_0 generation of inbreeding. This exception was due, possibly, to the fact that in this work we used a selection index that included, among other variables, the AFW. Therefore, we selected the six S_0 parents, with similar values for this variable (2-4 kg). This range of selection corresponds to the optimal values of AFW for the fruits commercialization targeted to the fresh consumption market, mainly established by consumers who prefer buying the whole fruit.

Further analysis exposed a statistical significance in YPP and AFW for the parents vs. crosses contrast (P vs. C) in the three generations of inbreeding. This statistical difference showed that the mean performance of all F_1 crosses (between S_0 parents and between S_1 or S_2 inbred lines) was higher than the average performance of their parents as a whole, indicating significant heterotic effects in all three generations for these traits (Tab. 1).

The mean performances of the hybrids produced between six S_0 parents, between six S_1 inbred lines and between six S_2 inbred lines are presented in Table 2. It was observed that on average for YPP, the hybrids between S_2 inbred lines presented higher values compared to the hybrids between S_1 lines or between S_0 progenitors. For the AFW trait, it was found that hybrids between S_1 or S_2 lines presented higher means than those obtained between S_0 parents.

TABLE 1. Mean Squares (MS) from the ANOVA for the variables Yield per plant (YPP) and average fruit weight (AFW) in three generations of inbreeding of *C. moschata*, according to the method of Hallauer *et al.* (2010).

Sources of Variation	DF	Variables	
		YPP (kg)	AFW (kg)
		MS	MS
Replicates (R)	3	3.47	0.73
Generations (D)	2	34.60 *	7.56 **
R*D	6	10.18	1.02 *
Genotypes (G)	60	57.24 **	3.28 **
Genotypes (S_0 G)	20	26.59 **	1.51 **
Parents (P_0)	5	14.22	1.20
Crosses (C_0)	14	16.87 *	1.34 **
P_0 vs. C_0	1	224.54 **	5.55 **
Genotypes (S_1 G)	20	61.43 **	3.71 **
Parents (P_1)	5	31.62 **	1.81 **
Crosses (C_1)	14	44.23 **	2.85 **
P_1 vs. C_1	1	451.29 **	25.13 **
Genotypes (S_2 G)	20	83.70 **	4.62 **
Parents (P_2)	5	21.92	1.15 *
Crosses (C_2)	14	32.21 **	2.44 **
P_2 vs. C_2	1	1113.43 **	52.55 **
Error	180	9.63	0.40
Means		12.28	3.39
CV (%)		25.27	18.72

*, **: significant at 5% and 1% levels of probability, respectively, according to F-test.

In the S_0 generation, the hybrids P4xP5 (15.42 kg/plant) and P1xP3 (15.00 kg/plant) presented the highest mean values for YPP. In the S_1 inbreeding generation, the hybrids P1xP5 (20.50 kg/plant) and P3xP5 (19.08 kg/plant) had the best performances; while in the S_2 generation the hybrid P1xP3 (20.87 kg/plant) was highlighted. The hybrids P1xP5 (S_1

TABLE 2. Mean performance of fifteen hybrids from six S_0 parents, fifteen hybrids from six inbred lines S_1 and fifteen between six inbred lines S_2 of squash *C. moschata* for the variables Yield per plant (YPP) and average fruit weight (AFW).

Hybrids	YPP (kg)			AFW (kg)		
	S_0	S_1	S_2	S_0	S_1	S_2
P1xP2	10.27 bcd	12.08 cde	17.88 abc	2.62 ef	4.19 cdef	4.84 abc
P1xP3	15.00 a	12.32 cde	20.87 a	4.02 ab	3.64 fgh	4.98 a
P1xP4	13.89 ab	14.75 bc	15.33 bcd	3.90 ab	4.15 def	4.53 abc
P1xP5	13.05 abc	20.50 a	15.00 bcd	3.16 cde	5.73 a	3.50 def
P1xP6	10.71 bcd	10.33 def	14.00 de	2.60 ef	3.20 hi	2.89 efg
P2xP3	12.46 abc	17.19 ab	16.00 bcd	3.36 bcd	5.16 ab	4.79 abc
P2xP4	12.04 abcd	13.67 bcde	16.73 bcd	3.21 cde	3.82 fgh	4.22 bcd
P2xP5	12.04 abc	15.38 bc	15.56 bcd	2.69 def	4.86 bcd	4.15 cd
P2xP6	12.25 abcd	14.88 bc	18.47 ab	3.00 cde	4.56 bcde	4.89 ab
P3xP4	14.95 a	10.13 ef	13.73 de	4.28 a	3.32 gh	3.76 d
P3xP5	14.45 a	19.08 a	14.98 bcd	3.53 bc	4.01 efg	3.84 d
P3xP6	13.38 ab	13.08 cde	14.81 cd	3.37 bcd	3.41 gh	3.73 d
P4xP5	15.42 a	13.83 bcd	14.30 cd	3.40 bcd	3.49 fgh	4.17 cd
P4xP6	8.63 d	12.54 cde	10.46 ef	2.95 cde	3.49 fgh	2.91 fg
P5xP6	9.71 cd	8.03 f	9.47 f	2.17 f	2.47 i	2.49 g
Means	12.55	13.85	15.17	3.22	3.97	3.98
CV (%)	16.36	24.01	18.73	17.91	21.18	19.62
LSD (5%)		3.63			0.74	

P1 = Unapal-Abanico-75-1; P2 = Unapal-Abanico-75-2; P3 = Unapal-Dorado; P4: IC3A Central American introduction; P5 = Unapal-Llanogrande-1; P6 = Unapal-Llanogrande-2. Means within a column followed by the same letter are not significantly different, according to least significant differences multiple range test.

generation) and P1xP3 (S_2 generation) were the genotypes that registered the highest AFW mean values (5.73 and 4.98 kg, respectively); thus, they are considered as the most indicated genotypes to enhance the features required by the industry and fresh market consumers (big and whole fruit with no weight limit). Furthermore, regarding the market of fresh consumption conformed by consumers who prefer to purchase small and whole fruits instead of sliced fruit, the most indicated hybrid is P1xP6 (S_2 generation), since this genotype presented the highest mean value of YPP of all those genotypes that registered an optimal AFW value for this market.

Estimates of heterosis

The expression of the mid parent heterosis (MPH) and heterobeltiosis (HB) for YPP showed a greater magnitude and statistical significance in the hybrids of S_2 inbred lines than those obtained from the S_1 inbred lines (Tab. 3). Similar results were reported by Ortiz *et al*. (2013) in *C. moschata*, who found higher values of MPH for YPP in the hybrids of S_2 inbred lines. In turn, the MPH and HB were of greater magnitude and significance in the hybrids of S_1 inbred lines than in those produced from the S_0 parents (Tab. 3). Likewise, Ortiz *et al*. (2013) recorded higher estimates of MPH for YPP in the hybrids of S_1 inbred lines than those of S_0 lines. Furthermore, and regarding *C. moschata*, Espitia *et al*. (2006) found a greater magnitude and statistical significance after calculating the MPH and HB values in the hybrids from S_1 inbred lines compared to those from S_0 parental lines.

In the diallel crossings between S_2 inbred lines for YPP, the MPH varied from 69.35 to 229.02%, thus the statics value varied from zero across the 100% of hybrid lines. In the diallel crosses among S_1 inbred lines, the MPH ranged between 9.31 and 209.25% showing in the 60.00% of the hybrids statics values different from zero. In contrast, for diallel crossings between S_0 parents the MPH only fluctuated from 2.02 to 81.90%, recording 60.00% of the hybrids with statics values different from zero. Regarding the mean heterosis (MH), the estimations in the diallel crosses among S_1 and S_2 inbred lines represented the 46.79 and 182.29%, a higher value, compared to the estimation made in the diallel crossings between S_0 parents, indicating that as the inbreeding progresses, the MH also goes forward gradually (Tab. 3).

TABLE 3. Mid parent heterosis (MPH), heterobeltiosis (HB) and mean heterosis (MH) of F_1 hybrids from diallel crossings between S_0 parents and between S_1 and S_2 inbred lines, in squash *C. moschata* for the variable yield per plant (YPP).

	YPP (kg)					
Generation	**S_0**		**S_1**		**S_2**	
F_1 Hybrids	**MPH**	**HB**	**MPH**	**HB**	**MPH**	**HB**
P1xP2	14.16	-7.77	9.31	-10.76	104.38**	98.24**
P1xP3	33.33*	32.06*	63.04*	43.77*	147.43**	131.42**
P1xP4	37.03*	24.68	57.12**	44.48*	76.40**	69.96**
P1xP5	37.67	17.12	185.38**	139.29**	96.50**	66.35**
P1xP6	13.21	-3.88	27.31	20.62	137.96**	55.26*
P2xP3	36.77	9.68	71.20**	26.95*	96.01**	88.79**
P2xP4	50.59*	31.84	15.08	0.92	98.71**	97.34**
P2xP5	80.01**	68.97**	58.98**	13.53	111.31**	83.57**
P2xP6	67.42*	57.55*	40.35*	9.90	229.02**	117.89**
P3xP4	45.91*	31.62	20.99	-0.73	69.35**	64.20**
P3xP5	50.71*	27.21	209.25**	191.71**	112.52**	90.87**
P3xP6	39.80*	17.75	84.16**	70.65**	179.40**	88.64**
P4xP5	81.90**	68.79**	72.82**	35.51	95.77**	71.08**
P4xP6	2.02	-5.56	40.32	22.85	88.29*	25.12
P5xP6	24.53	24.20	19.18	4.67	110.40 *	51.46
MH (%)	40.09		58.85		113.17	

* and **: significant at 5% and 1% levels of probability, respectively, according to the Student's T-test. P1: UNAPAL-Abanico-75-1; P2: UNAPAL-Abanico-75-2; P3: UNAPAL-Dorado; P4: IC3A Central American introduction; P5: UNAPAL-Llanogrande-1; and P6: UNAPAL-Llanogrande-2.

At an individual level, the hybrids among S_2 inbred lines for YPP that registered the highest levels of HB were: P1xP3, P2xP6, P1xP2, P2xP4 and P3xP5, with values of 131.42, 117.89, 98.24, 97.34 and 90.87%, respectively. On the other hand, hybrids between S_1 inbred lines that recorded the highest expression levels of HB for YPP were the P3xP5, P1xP5 and P3xP6 with values of 191.71, 139.29 and 70.65%, respectively; the hybrids among S_0 parents that presented the highest values of HB were P2xP5 and P4xP5 (68.97 and 68.79%, respectively) (Tab. 3). Most of these hybrids were produced by crossings among parents that were developed from accessions collected in distant geographical regions (departments of Cauca and Magdalena in Colombia and Costa Rica). A high genetic differentiation (Fst = 0.17) between the Colombian accessions collected in the departments of Cauca and Magdalena had been reported in a previous study by Restrepo and Vallejo (2008), indicating a high possibility to find important levels of genetic divergence among several parents selected to produce the hybrids of this study. The other factor that must have occurred in hybrids expressing heterosis or hybrid vigor was the existence of unidirectional dominance levels in most of loci that controlled the trait YPP.

Regarding the variable AFW, the expression of the MPH and HB also registered a higher magnitude and significance in the hybrids of S_2 inbred lines than those of the S_1 inbred lines (Tab. 4). Similarly, the hybrids of S_1 inbred lines presented a greater heterotic superiority compared with those of the S_0 parents. According to Espitia *et al.* (2006) in *C. moschata*, AFW values presented a higher magnitude and statics significance in the MPH and HB estimations in the S_1 inbred lines compared to the S_0 parents as well.

In the diallel crosses among S_1 inbred lines for AFW the MPH fluctuated between 10.84 and 122.54%, presenting statics values different from cero in the 73.33% of the hybrids. In the diallel crossings between S_2 inbred lines the MPH varied between 49.96 and 147.00%, showing statics values different from zero in the 100.00% of the hybrids. In contrast, the diallel crosses between S_0 parents the MPH ranged between -8.01 and 35.54%, and only the 46.67% of the hybrids registered values different from zero. The MH value showed a gradual increase in its estimation as long as the inbreeding process continued, in such way that the diallel crosses among S_1 or S_2 inbred lines represented 105.73 and 265.24% more, compared to the estimation made in the diallel crosses between S_0 parents (Tab. 4). Furthermore, the HB in the diallel crossings between S_1 inbred lines ranged between 2.51 and 83.70%, showing static values different from zero in the 46.67% of the hybrids' lines. In the diallel crosses among S_2 inbred lines the HB fluctuated between

TABLE 4. Mid parent heterosis (MPH), heterobeltiosis (HB) and mean heterosis (MH) of F_1 hybrids from diallel crossings between S_0 parents and between S_1 and S_2 inbred lines, in squash *C. moschata* for the variable average fruit weight (AFW).

AFW (kg)						
Generation	**S_0**		**S_1**		**S_2**	
F_1 Hybrids	**MPH**	**HB**	**MPH**	**HB**	**MPH**	**HB**
P1xP2	6.97	-12.40	22.49*	12.47	88.30**	76.06**
P1xP3	29.54*	24.88*	34.37*	16.69	110.90**	108.00**
P1xP4	28.21*	26.11*	31.92*	30.86*	86.35**	83.32**
P1xP5	22.93	5.72	122.54**	83.70**	49.96**	46.45**
P1xP6	-6.34	-13.10	20.12	2.51	60.47**	20.89
P2xP3	31.01*	4.22	71.12**	38.30**	88.73**	74.19**
P2xP4	28.59	3.91	10.84	2.53	61.41**	53.28**
P2xP5	32.80	25.13	68.62**	30.22**	64.94**	50.87**
P2xP6	34.59*	17.33	53.63**	22.23*	147.00**	77.93**
P3xP4	35.54**	32.80**	21.49	4.79	56.83**	52.18**
P3xP5	31.53*	9.71	85.11**	74.32**	66.48**	64.84**
P3xP6	16.74	4.78	51.48**	48.39**	111.00**	60.44**
P4xP5	29.75*	10.06	34.38*	10.23	75.49**	68.66**
P4xP6	4.35	-4.58	29.71*	9.96	75.49**	17.82
P5xP6	-8.01	-15.40	16.80	12.18	75.49*	9.34
MH (%)	21.29		43.80		77.76	

* and **: significant at 5% and 1% levels of probability, respectively, according to the Student's T-test. P1: UNAPAL-Abanico-75-1; P2: UNAPAL-Abanico-75-2; P3: UNAPAL-Dorado; P4: IC3A Central American introduction; P5: UNAPAL-Llanogrande-1; and P6: UNAPAL-Llanogrande-2.

9.34 and 108.00%, showing values significantly different from zero in the 80.00% of the hybrids. Finally, the HB value varied from -15.40 to 32.80% in the diallel crosses between S_0 parents, registering only the 20.00% of the hybrids with statics values different from zero.

The hybrids produced between S_2 inbred lines for AFW that presented the highest levels of HB were: P1xP3, P1xP4, P2xP6, P1xP2 and P2xP3, with values of 108.00, 83.32, 77.93, 76.06 and 74.19%, respectively. On the other hand, hybrids between S_1 inbred lines that registered the highest values of HB for AFW were P1xP5, P3xP5 and P3xP6 with values of 83.70, 74.32 and 48.39%, respectively. The hybrid among S_0 parents that showed the highest expression of HB was P3xP4 with a value of 32.80% (Tab. 4). Most of these hybrids were also formed by crossings between parents that were developed from accessions collected in distant geographic regions (departments of Cauca and Magdalena in Colombia and Costa Rica), indicating that it was very probable to find important levels of genetic divergence as it was mentioned before.

The greater expression of the types of heterosis previously mentioned in the hybrids of S_2 or S_1 inbred lines compared to those produced from the S_0 parental lines found in this research for YPP and AFW, confirmed the hypothesis proposed in this study. Furthermore, the results obtained concur with those reported by Hallauer *et al*. (2010) and Falconer and Mackay (1996), who stated that the progenies of inbred lines express a higher heterosis compared with those expressed by the progenies with a broad genetic base. This higher heterosis condition is only possible if important levels of genetic divergence are present among the parents and there is an existence of unidirectional dominance levels in most of loci that control the trait in the parental lines.

Most of the hybrids produced in this study by crossings among S_0 parents and between S_1 or S_2 inbred lines, presented positive MPH for the variables YPP and AFW. Similar results were obtained in hybrids of *C. moschata* produced from lines with different level of inbreeding for both of the variables by Vallejo and Gil (1998), Espitia *et al*. (2006), Jahan *et al*. (2012), Ortiz *et al*. (2013), El-Tahawey *et al*. (2015), Begun *et al*. (2016), Ahmed *et al*. (2017), and Darrudi *et al*. (2018). In contrast, Du *et al*. (2011) in *C. moschata* for AFW found negative estimations for MPH in most of the hybrids produced among S_8 inbred lines. On the other hand, Li *et al*. (2013) reported hybrids of *C. moschata* produced from inbred lines for AFW, positive and negative MPH values. Pandey *et al*. (2010) in *C. moschata* for AFW registered similar results in the hybrids formed from S_1 inbred lines.

Regarding HB, most of hybrids formed between S_0 parents and among S_1 or S_2 inbred lines, reported also positive values for the variables YPP and AFW. These results concur to those reported in hybrids of *C. moschata* produced between lines with different levels of inbreeding for both of the variables by Mohanty and Mishra (1999), Espitia *et al.* (2006), Jha *et al.* (2009), Ortiz *et al.* (2013), El-Tahawey *et al.* (2015), Begun *et al.* (2016), Ahmed *et al.* (2017), and Darrudi *et al.* (2018). In contrast, Vallejo and Gil (1998) and Jahan *et al.* (2012) obtained negative estimations of the HB for the same variables in the same species. Furthermore, Sirohi *et al.* (2002) reported positive and negative estimations for both variables in the HB value for *C. moschata*. Pandey *et al.* (2010), also found positive and negative values of HB in *C. moschata* for the variable YPP.

Conclusions

A direct relationship between levels of inbreeding and heterotic superiority of hybrids for the variables yield per plant and average fruit weight was established.

The hybrids from S_2 inbred lines that reported the highest expression levels of HB for YPP were P1xP3, P2xP6 and P1xP2, while the hybrids among S_1 inbred lines that recorded the highest values of HB, for this same variable, were P3xP5 and P1xP5.

The hybrids among S_2 inbred lines that registered the highest levels of HB for AFW were P1xP3, P1xP4, P2xP6 and P1xP2, while the hybrids from S_1 inbred lines that showed the highest values of HB for this same variable were P1xP5 and P3xP5.

The genetic materials selected in this study are experimental hybrids with a high potential to be used in the Research Program "Genetic Improvement, Agronomy and Production of Vegetables Seeds" of the Universidad Nacional de Colombia, Palmira campus.

Literature cited

Ahmed, B., M.A.T. Masud, M. Zakaira, M.M. Hossain, and M.A.K. Mian. 2017. Heterosis and combining ability of pumpkin (*Cucurbita moschata* Duch. Ex Poir.). J. Agric. Stud. 5(3), 132-139. Doi: 10.5296/jas.v5i3.11920

Alam, M.F., M.R. Khan, M. Nuruzzaman, S. Parvez, A.M. Swaraz, I. Alam, and N. Ahsan. 2004. Genetic basis of heterosis and inbreeding depression in rice (*Oryza sativa* l). J. Zhejiang Univ. Sci. 5(4), 406-411. Doi: 10.1631/jzus.2004.0406

Begum, F., A.M. Akanda, M.A.T. Masud, M.G. Rasul, and M.A. Islam. 2016. Combining ability and heterosis for PRSV-W resistance in pumpkin (*Cucurbita moschata*). J. Int. Acad. Res. Multidiscip. 4(1), 92-102.

Chang, C.I., C.M. Hsu, T.S. Li, S.D. Huang, C.C. Lin, C.H. Yen, C.H. Chou, and H.L. Cheng. 2014. Constituents of the stem of *Cucurbita moschata* exhibit antidiabetic activities through multiple mechanisms. J. Funct. Foods 10, 260-273. Doi: 10.1016/j.jff.2014.06.017

Darrudi, R., V. Nazeri, F. Soltani, M. Shokrpour, and M.R. Ercolano. 2018. Evaluation of combining ability in *Cucurbita pepo* L. and *Cucurbita moschata* Duchesne accessions for fruit and seed quantitative traits. J. Appl. Res. Med. Aromat. Plants 9, 70-77. Doi: 10.1016/j.jarmap.2018.02.006

Du, X., Y. Sun, X. Li, J. Zhou, and X. Li. 2011. Genetic divergence among inbred lines in *Cucurbita moschata* from China. Sci. Hortic. 127, 207-213. Doi: 10.1016/j.scienta.2010.10.018

El-Tahawey, M.A.F.A., A.M. Kandeel, S.M.S. Youssef, and M.M.M. Abd El-Salam. 2015. Heterosis, potence ratio, combining ability and correlation of some economic traits in diallel crosses of pumpkins. Egypt. J. Plant Breed. 19(2), 419-439. Doi: 10.12816/0011721

Espitia, C.M.M., C.F.A. Vallejo, and G.D. Baena. 2006. Depresión en vigor por endogamia y heterosis para el rendimiento y sus componentes en zapallo *Cucurbita moschata* Duch. Ex Poir. Rev. Fac. Nal. Agron. Medellín 59(1), 3089-3103.

Falconer, D.S. and T. Mackay. 1996. Introduction to Quantitative Genetics. Fourth edition. Longmans Green, Harlow, Essex, UK.

Hallauer, A.R., M.J. Carena, and J.B. Miranda. 2010. Quantitative genetics in maize breeding. Springer, New York, Dordrecht, Heidelberg, London. Doi: 10.1007/978-1-4419-0766-0

Jahan, T.A., A. Islam, M.G. Rasul, M. Mian, and M.M. Haquez. 2012. Heterosis of qualitative and quantitative characters in sweet gourd (*Cucurbita moschata* Duch. ex Poir.). Afr. J. Food Agric. Nutr. Dev. 12(3), 6186-6199.

Jha, A., S. Pandey, M. Rai, D.S. Yadav, and T.B. Singh. 2009. Heterosis in relation to combining ability for flowering behaviors and yield parameters in pumpkin. Veg. Sci. 36 (3 Suppl.), 332-335.

Li, X.Z., Z.W. Liu, L. Sun, X.H. Du, and J.G. Zhou. 2013. The Combining ability analysis and the heterosis performance of pumpkin. Acta Agric. Boreali Sinica. 28(S1), 61-68. Doi: 10.7668/hbnxb.2013.S1.013

Minagricultura. 2016. Red de Información y comunicación del sector agropecuario colombiano. URL: http://www.agronet.gov.co/Documents/AHUYAMA2016.pdf; (accessed 10 May 2018).

Mohanty, B.K. and R.S. Mishra. 1999. Heterosis for yield and yield components in pumpkin (*Cucurbita moschata* Duch. ex. Poir.). Indian J. Genet. Pl. Br. 59(4), 505-510.

Ortiz, S., F.A. Vallejo, G.D. Baena, E.I. Estrada, and M.P. Valdes. 2013. Zapallo para consumo en fresco y fines agroindustriales investigación y desarrollo. Universidad Nacional de Colombia-Sede Palmira-Facultad de Ciencias Agropecuarias. Palmira, Colombia.

Pandey, S., A. Jha, S. Kumar, and M. Rai. 2010. Genetics and heterosis of quality and yield of pumpkin. Indian J. Hort. 67(3), 333-338.

Restrepo, J.A. 2015. Heterosis y habilidad combinatoria en función de la endogamia para el rendimiento y características del fruto de zapallo *Cucurbita moschata* Duch. ex Poir. Tesis Doctoral en Ciencias Agrarias-Mejoramiento Genético Vegetal. Universidad Nacional de Colombia-Sede Palmira-Facultad de Ciencias Agropecuarias. Palmira, Colombia.

Restrepo-Salazar, J.A. and F.A. Vallejo-Cabrera. 2008. Caracterización molecular de introducciones Colombianas de Zapallo *Cucurbita moschata*. Acta Agron. 57(1), 9-17.

Sirohi, P.S., Y.S. Reddy, and T.K. Behera. 2002. Heterosis for yield and its attributing traits in pumpkin (*Cucurbita moschata* Duch. ex Poir.). Veg. Sci. 29(2), 178-179.

Vallejo, C.F.A. and M.O.V. Gil. 1998. Efecto de la endocría sobre algunos caracteres agronómicos del zapallo, *Cucurbita moschata* Poir. Acta Agron. 48(1/2), 46-50.

Wu, H., J. Zhu, W. Diao, and C. Wang. 2014. Ultrasound-assisted enzymatic extraction and antioxidant activity of polysaccharides from pumpkin (*Cucurbita moschata*). Carb. Pol. 113, 314-324. Doi: 10.1016/j.carbpol.2014.07.025

Zhang, B., H. Huang, J. Xie, C. Xu, M. Chen, C. Wang, A. Yang, and Q. Yin. 2012. Cucurmosin induces apoptosis of BxPC-3 human pancreatic cancer cells via inactivation of the EGFR signaling pathway. Oncol. Rep. 27, 891-897. Doi: 10.3892/or.2011.1573

Zhao, X.H., L. Qian, D.L. Yin, and Y. Zhou. 2014. Hypolipidemic effect of the polysaccharides extracted from pumpkin by cellulase-assisted method on mice. Int. J. Biol. Macromol. 64, 137-138. Doi: 10.1016/j.ijbiomac.2013.12.001