Revista Facultad Nacional de Agronomía

Combining ability as a function of inbreeding for fruit traits in *Cucurbita moschata* Duch. ex Poir.

UNIVERSIDAD NACIONAL DE COLOMBIA

Habilidad combinatoria en función de la endogamia para caracteres del fruto en *Cucurbita moschata* Duch. ex Poir.

Javier Alonso Restrepo-Salazar[1*], Franco Alirio Vallejo-Cabrera[1] and Edwin Fernando Restrepo-Salazar[2]

ABSTRACT

Keywords:
Agroindustry
Consumers
Diallel analysis
Hybrids
Inbred lines
Squash

Three diallel crosses of butternut squash (*Cucurbita moschata*), each consisting of six parents with S_0, S_1, and S_2 levels of inbreeding, were evaluated to estimate the effect of inbreeding on both general (GCA) and specific combining abilities (SCA) for the following traits: fruit pulp thickness, number of seeds per fruit, fruit pulp color, dry matter, 100-seed weight, diameter of placental cavity, polar diameter of fruits, and equatorial diameter of fruits. A randomized complete block experimental design was used with four replicates, arranged in split plots, with the main plot corresponding to the diallel cross (level of inbreeding) and the subplot for the evaluated genotypes (six parents and 15 F_1 hybrids, in each of the diallel crosses). Additive effects (GCA) were responsible for the genetic control of most of the traits in the three diallel crosses, whereas non-additive effects (SCA) were also responsible for the genetic expression of most of the traits, but almost exclusively in crosses between S_1 and S_2 inbred lines. Recommended genotypes for the simultaneous genetic improvement of fruit pulp thickness and color for the fresh consumption market, which is formed by consumers who prefer whole, non-sliced fruit, were the S_0 parents (P3 and P4) as well as the between S_2 lines hybrid (P1×P6). On the other hand, a genotype recommended for the improvement of the same traits but intended either for agro-industrial use or for the fresh consumption market formed by consumers for whom fruit weight is not a limiting characteristic for purchase (large fruits), was the S_2 parent (P2).

RESUMEN

Palabras clave:
Agroindustria
Consumidores
Análisis dialélico
Híbridos
Líneas endogámicas
Ahuyama

Se evaluaron tres cruzamientos dialélicos de zapallo *Cucurbita moschata*, conformados cada uno por seis progenitores con niveles de endogamia S_0, S_1 y S_2, para estimar el efecto de la endogamia en la habilidad combinatoria general (HCG) y específica (HCE) para las siguientes variables: grosor de la pulpa del fruto, número de semillas por fruto, color de la pulpa del fruto, materia seca, peso de cien semillas, diámetro de la cavidad placentaria, diámetro polar del fruto y diámetro ecuatorial del fruto. Se utilizó un diseño experimental de bloques completos al azar con cuatro repeticiones y arreglo en parcelas divididas, donde la parcela principal estuvo conformada por los cruzamientos dialélicos (tres niveles de endogamia) y la subparcela por los genotipos analizados en cada uno de los cruzamientos dialélicos (seis padres y 15 híbridos F_1). Los efectos aditivos (HCG) fueron los responsables del control genético de la mayoría de las variables en los tres cruzamientos dialélicos, mientras que los efectos no aditivos (HCE) fueron también los responsables de la expresión genética de la mayoría de las variables, pero casi exclusivamente en los cruzamientos realizados entre líneas endogámicas S_1 y S_2. Los genotipos recomendados para el mejoramiento genético simultáneo del grosor y color de la pulpa del fruto, con destino al mercado de consumo en fresco, constituido por consumidores que prefieren frutos enteros y no en rodajas, fueron los progenitores S_0 (P3 y P4) y el híbrido entre líneas S_2 (P1×P6). Por otro lado, el genotipo recomendado para el mejoramiento de las mismas variables mencionadas previamente, pero dirigido al uso agroindustrial o al mercado de consumo en fresco conformado por consumidores en los cuales el peso del fruto no es una característica limitante para su adquisición (frutos grandes), fue el progenitor S_2 (P2).

[1] Facultad de Ciencias Agropecuarias. Universidad Nacional de Colombia. AA 237 Palmira, Colombia.
[2] Escuela de Ingeniería. Universidad Pontificia Bolivariana. km 1 vía Tienda Nueva, Palmira, Colombia.
* Corresponding author: <jarestrepos@unal.edu.co>

The butternut squash *Cucurbita moschata* (Duch. ex Lam.) Duch ex Poir. is an important species for food safety in the world due to its high nutritional value (Restrepo-Salazar *et al.*, 2018a) or for providing medicinal benefits such as improved immune response through β-carotene (Kim *et al.*, 2016). It also presents other medical benefits, such as anti-inflammatory, antioxidant, antidiabetic, antimicrobial, hypotensive, hepatoprotective, antiparasitic, and anticancer properties (Yadav *et al.*, 2010). In addition, this species is used for agro-industrial purposes as food production for humans and animals, and biodiesel production from seed oil (Restrepo *et al.*, 2018b).

Very few studies have been published about the effect of inbreeding on the genetic expression and control of different plant traits in *Cucurbita moschata*. Espitia (2004) evaluated two diallel crosses of *C. moschata* (between S_0 varieties and between S_1 inbred lines) and reported that additive effects played an important role in the expression of the following traits in the two generations evaluated: fruit production per plant, average fruit weight, number of fruits per plant, and 100-seed weight. Non-additive effects were only important in diallel crosses between S_1 inbred lines. Similar results were obtained by Ortiz *et al.* (2013) when evaluating the fruit production per plant in Candelaria (Valle del Cauca, Colombia) and by Restrepo-Salazar *et al.* (2018a), when evaluating the fruit production per plant and the average fruit weight in the same area. The above-mentioned researchers found, after evaluating three diallel crosses of *C. moschata* (between S_0 parents, between S_1 inbred lines, and between S_2 lines), that additive effects played an important role in the genetic control of the traits in all inbreeding generations, whereas non-additive effects were only important in crosses between S_1 and S_2 inbred lines (Ortiz *et al.*, 2013; Restrepo-Salazar *et al.*, 2018a). In other crops, such as maize, records also indicate that non-additive effects are more important in diallel crosses between inbred lines than in crosses between S_0 parents (Crossa *et al.*, 1990; Rezende and Souza-Junior, 2000).

According to published literature on diallel crosses of *C. moschata,* there is no consensus about the type of gene action that predominates in the expression and genetic control of the traits: fruit pulp thickness, number of seeds per fruit, and 100-seed weight. In the case of diallel crosses between S_0 parents of *C. moschata*, some authors reported that both additive and non-additive effects was important in the genetic expression of the fruit pulp thickness (Espitia, 2004; Nisha and Veeraragavathatham, 2014; Abdein *et al.*, 2017), the number of seeds per fruit (Marxmathi *et al.*, 2018; Darrudi *et al.*, 2018), and 100-seed weight (Nisha and Veeraragavathatham, 2014). Other authors like Espitia (2004) and Valdés *et al.* (2014) found that only additive gene effect was important for 100-seed weight, while Darrudi *et al.* (2018) reported that only non-additive gene effect was important for the same trait. Espitia (2004), for the number of seeds per fruit, and Marxmathi *et al.* (2018), for the fruit pulp thickness, found that neither of those effects was important in the expression and genetic control. On the other hand, in the specific case of diallel crosses between S_1 inbred lines of *C. moschata*, studies conducted by Mohanty (2000), Pandey *et al.* (2010), El-Tahawey *et al.* (2015), Ahmed *et al.* (2017), Singh *et al.* (2018), and Hatwal *et al.* (2018) reported the importance of both additive and non-additive effects in the expression and genetic control of the fruit pulp thickness. Following the impact of these effects, Mohsin *et al.* (2017) reported that only the non-additive gene effect was important, whereas other study found that neither of the effects was important (Begum *et al.*, 2016).

According to the background in this field, this study aimed to evaluate the effect of inbreeding on the combining ability for eight traits of butternut squash fruit (*C. moschata*) and identify parents or F_1 hybrids that are outstanding; not only in terms of their combining ability but in terms of the fruit traits.

MATERIALS AND METHODS
Three diallel crosses, each involving six *C. moschata* parents with three levels of inbreeding (S_0 parents, S_1 and S_2 inbred lines derived from S_0 parents), were evaluated at the Experimental Center of the Universidad Nacional de Colombia–Palmira Campus. Table 1 presents the fruit traits of the six S_0 parents. 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 was used to evaluate

genotypes (six parents and fifteen direct crosses in each of the diallel crosses). Each experimental plot consisted of a five-plant furrow. A weighted selection index composed of traits such as average fruit weight (2.0–4.0 kg), fruit pulp thickness (3.5–5.0 cm) and salmon-colored pulp was used to select the fruits.

Table 1. Fruit traits of the six *Cucurbita moschata* S_0 parents used in the study.

Parent	Name	Geographic origin	Fruit traits[1]							
			FPT (cm)	FPC	DM (%)	DPC (cm)	PDF (cm)	EDF (cm)	NSF	100-seed weight (g)
P1	UNAPAL-Abanico-75-1	Atlantic Coast (Colombia)	3.97	Bright yellow (10)	12.53	12.21	17.64	20.15	301	11.12
P2	UNAPAL-Abanico-75-2	Atlantic Coast (Colombia)	3.33	Medium orange (12)	15.43	10.96	15.79	17.19	283	16.02
P3	UNAPAL-Dorado	Patía, Cauca (Colombia)	4.00	Medium orange (12)	13.00	17.50	15.80	21.50	372	11.40
P4	IC3A	Costa Rica (Central America)	4.38	Medium orange (12)	9.35	10.44	20.48	16.53	345	10.25
P5	UNAPAL-Llanogrande-1	Patía, Cauca (Colombia)	3.80	Medium orange (12)	11.31	10.00	15.74	16.58	263	8.91
P6	UNAPAL-Llanogrande-2	Patía, Cauca (Colombia)	4.00	Medium orange (12)	9.89	11.90	16.81	18.35	336	10.68

[1] FPT: fruit pulp thickness; FPC: fruit pulp color; DM: dry matter; DPC: diameter of the placental cavity; PDF: polar diameter of fruits; EDF: equatorial diameter of fruits; NSF number of seeds per fruit.

The following traits were evaluated: fruit pulp thickness (FPT) measured in cm; fruit pulp color (FPC) ranked from 1 to 15 based on the Roche Yolk Color Fan scale (Vuilleumier, 1969); dry matter (DM) measured as %; diameter of placental cavity (DPC), polar diameter of fruits (PDF), and equatorial diameter of fruits (EDF), all three measured in cm; number of seeds per fruit (NSF); and 100-seed weight measured in g. DM was determined by measuring the fresh weight of fruits and then oven-drying the fruits at 105 °C for 24 hours (Leterme and Estrada, 2012).

Genetic and statistical analyses were performed to estimate the combining ability of the different genotypes, using the method proposed by Hallauer and Miranda (1981), which partitions variation among genotypes (entries) into three components: parents, crosses and the parents vs. crosses contrast. Variance analysis and estimation of genetic effects were performed using the SAS/STAT® package, version 9.4 (SAS system for Windows, SAS Institute Inc©, 2012) and GENES (version 2.1 for Windows©, 2004) developed by Cruz (2013). The F-test was used for several sources of variation during the analysis of variance, and the Student's t-test was used to estimate genetic effects.

RESULTS AND DISCUSSION
Analysis of variance (ANOVA)
Statistical differences were detected in the source of generational variation for all evaluated traits: FPT, FPC, DM, DPC, PDF, EDF, NSF, and 100-seed weight (Table 2), indicating that at least one of the inbred generations presented a mean value significantly different from the rest. Ortiz *et al.* (2013) reported similar results in *C. moschata* for FPC. On the other hand, significant differences were observed in the source of genotype variation in the three generations analyzed for all the traits. It can be inferred that there is at least one parent or hybrid that recorded an average value of FPT, FPC, DM, DPC, PDF, EDF, NSF, and 100-seed weight differed statistically from other averages in each of the generations (Table 2). Espitia (2004) also recorded statistical differences in the source of *C. moschata* genotypes for FPT, NSF, and 100-seed weight in the two inbreeding generations studied (S_0 and S_1). Ortiz *et al.* (2013) observed similar results in *C. moschata* for FPC, finding differences among genotypes in the three diallel crosses evaluated (S_0, S_1, and S_2).

For all evaluated traits, in most of the cases the parents and crosses variation sources presented statistical significance in all three generations, which confirmed that in general terms at least one of the S_0, S_1, or S_2 parents, or at least one of the crosses between said parents, showed an average performance of FPT, FPC, DM, DPC, PDF, EDF, NSF, and 100-seed weight that differed significantly from the others (Table 2). Based on these results, it is inferred that regardless of the inbreeding level, it is possible to identify at least one parent or a hybrid with

Rev. Fac. Nac. Agron. Medellín 72(3): 8983-8993. 2019

8985

a mean value, in any of the traits, that differs statistically from the others. Significant differences have also been reported in *C. moschata* by Espitia (2004) regarding FPT, NSF, and 100-seed weight as well as by Ortiz *et al.* (2013) regarding FPC in both parents and crosses as sources in the different inbred generations under study.

Table 2. Mean squares of ANOVA for fruit pulp thickness (FPT), fruit pulp color (FPC), dry matter (DM), diameter of placental cavity (DPC), polar diameter of fruits (PDF), equatorial diameter of fruits (EDF), number of seeds per fruit (NSF), and 100-seed weight in three inbred generations of *Cucurbita moschata*.

Sources of variation	DF	Traits							
		FPT	FPC	DM	DPC	PDF	EDF	NSF	100-seed weight
Replicates (R)	3	0.89 **	1.81 **	84.28 **	9.68 **	3.83	3.30	2,387.35	3.17 *
Generations (D)	2	1.48 **	1.03 **	12.66 **	3.96 *	17.13 **	12.15 **	13,200.79 **	37.03 **
R×D	6	0.51 **	1.03 **	1.79	0.52	3.30	2.75	3,113.44	2.79 **
Genotypes (G)	60	0.62 **	0.83 **	17.25 **	12.38 **	11.94 **	22.74 **	11,317.94 **	9.51 **
Genotypes (S_0 G)	20	0.47 **	0.91 **	14.17 **	5.12 **	5.39 **	10.51 **	4,173.42 **	10.88 **
Parents (P_0)	5	0.57 *	1.74 **	19.59 **	5.18 **	3.08	10.28 *	6,842.67 *	25.91 **
Crosses (C_0)	14	0.43 **	0.66 **	13.24 **	3.64 **	5.87 **	7.96 **	2,299.35	5.29 **
GCA[1]	5	1.00 **	1.04 **	32.61 **	6.87 **	9.68 **	17.03 **	2,298.02	10.58 **
SCA[2]	9	0.11	0.45 *	2.48	1.86	3.75	2.92	2,300.09	2.35 **
P_0 vs. C_0	1	0.55	0.20	0.01	25.55 **	10.14	47.52 **	17,064.04 **	14.07 *
Genotypes (S_1 G)	20	0.50 **	0.84 **	19.82 **	16.16 **	15.57 **	25.83 **	11,946.26 **	9.23 **
Parents (P_1)	5	0.03	1.57 **	28.27 **	17.66 **	5.71	21.25 **	8,003.38 **	12.52 **
Crosses (C_1)	14	0.43 **	0.35	16.67 **	11.96 **	13.01 **	17.56 **	7,342.93 **	5.57 **
GCA	5	0.55 **	0.35	37.44 **	24.20 **	26.52 **	29.88 **	10,339.30 **	6.32 **
SCA	9	0.36 **	0.35	5.15 *	5.16 **	5.50 **	10.74 **	5,678.28 **	5.13 **
P_1 vs. C_1	1	3.75 **	4.00 **	21.61	67.43 **	100.67 **	164.48 **	96,107.41 **	44.07 **
Genotypes (S_2 G)	20	0.88 **	0.73 **	17.76 **	15.85 **	14.85 **	31.86 **	17,834.13 **	8.43 **
Parents (P_2)	5	0.26	1.57 **	22.69 **	9.46 **	14.80 **	14.65 **	18,812.67 **	3.19 *
Crosses (C_2)	14	0.63 **	0.45 *	17.18 **	10.27 **	3.39	20.00 **	11,093.89 **	3.93 **
GCA	5	1.32 **	0.44	39.92 **	24.19 **	4.03	48.18 **	9,523.44 **	6.90 **
SCA	9	0.24 *	0.46 *	4.55 *	2.54 **	3.03	4.37 *	11,966.36 **	2.27 **
P_2 vs. C_2	1	7.49 **	0.48	1.35	125.98 **	175.63 **	284.09 **	107,304.80 **	97.53 **
Error	180	0.13	0.21	2.15	0.96	2.11	1.92	1,666.37	0.87
Means		4.23	12.34	11.42	12.16	17.48	20.21	353.47	10.95
CV[3](%)		8.40	3.68	12.83	8.07	8.31	6.85	11.55	8.52

* Significant at a probability level of 0.05; ** Significant at a probability level of 0.01.
[1] General combining ability. [2] Specific combining ability. [3] Coefficient of variation

In the source of variation corresponding to the contrast between parents vs. crosses (P vs. C), significant differences were detected for most of the traits of the inbred generations, S_1 (FPT, FPC, DPC, PDF, EDF, NSF, 100-seed weight) and S_2 (FPT, DPC, PDF, EDF, NSF, 100 seed-weight), indicating that, overall, the average performance of all F_1 crosses (between S_1 or S_2 inbred lines) was higher than the average performance of parents as a whole (Table 2). Similar results were found by Espitia (2004) in S_1 for FPT, NSF, and 100-seed weight. On the other hand, in the S_0 inbred generation, statistical differences were only observed in the P vs. C contrast for DPC, EDF, NSF, and 100-seed weight (Table 2). Espitia (2004) reported similar results in S_0 for NSF but did not record differences for 100-seed weight in the S_0 generation in the contrast P vs. C.

In the diallel cross between S_0 parents only, the additive effects (GCA) were important in the genetic expression and control of FPT (Table 2). In contrast, other authors have reported in S_0 parents that in *C. moschata* both additive and non-additive effects (SCA) are important in the genetic expression of FPT (Espitia, 2004; Nisha and Veeraragavathatham, 2014; Abdein *et al.*, 2017), while other authors have published that neither of the effects was important for FPT (Marxmathi *et al.*, 2018). Regarding diallel crosses between S_1 and S_2 inbred lines, results indicated the importance of the additive and non-additive gene effect in the genetic control of FPT (Table 2). Mohanty (2000), Pandey *et al.* (2010), El-Tahawey *et al.* (2015), Ahmed *et al.* (2017), Singh *et al.* (2018), and Hatwal *et al.* (2018) reported similar results in the cross between S_1 inbred lines of *C. moschata*. In contrast, a study conducted by Begum *et al.* (2016) involving crosses between S_1 inbred lines of *C. moschata* indicate that neither of the effects was important in the expression of FPT, whereas Mohsin *et al.* (2017) only reported the importance of non-additive effects.

In the diallel cross between S_0 parents, neither of the two types of effects was important in the genetic expression and control of NSF (Table 2). This result indicates, on the one hand, that there is not enough statistical evidence to conclude that some parents differ in its ability to transmit genes that allow its progeny to increase or decrease its NSF; on the other hand, it suggests that there is not enough evidence to conclude that some of the hybrids had a different behavior than expected based on combining ability of their parents and general mean. Espitia (2004) reported similar results in *C. moschata*, finding that the additive and non-additive effects did not contribute in statistical terms to the genetic expression of NSF. In contrast, Marxmathi *et al.* (2018) and Darrudi *et al.* (2018) found that both types of effects were important for NSF. The importance of additive and non-additive gene action in the control of NSF was observed in the case of diallel crosses between S_1 and S_2 inbred lines (Table 2). Espitia (2004), El-Tahawey *et al.* (2015), and Mohsin *et al.* (2017) also found a significant contribution of both types of effects on the genetic expression of NSF in diallel crosses between S_1 inbred lines of *C. moschata*.

Both additive and non-additive effects were important in the genetic control of the 100-seed weight in the three diallel crosses evaluated (Table 2). These results agree with those found by Nisha and Veeraragavathatham (2014) in diallel crosses of *C. moschata* between S_0 parents, and by Espitia (2004), Mohsin *et al.* (2017) and Hatwal *et al.* (2018) in diallel crosses between S_1 inbred lines. On the other hand, Espitia (2004) reported that only additive effects were important in the expression of 100-seed weight in diallel crosses between S_0 parents of *C. moschata*, while Darrudi *et al.* (2018) reported that only non-additive effects were important. Valdés *et al.* (2014) recorded a differential response in diallel crosses between S_0 parents of *C. moschata* evaluated during two different planting seasons, finding that both additive and non-additive effects were important in the genetic expression of 100-seed weight during one season, while only additive effects were responsible for its expression in the same genotypes during another season.

In the diallel cross between S_0 parents, only additive effects were important in the genetic expression and control of PDF and EDF (Table 2). In contrast, Abdein *et al.* (2017), Kakamari and Jagadeesha (2017), and Marxmathi *et al.* (2018) have reported that both additive and non-additive effects are important in the genetic expression of PDF and EDF in *C. moschata*. In the case of diallel crosses between S_1 inbred lines, this study indicates that both types of effects were important in the genetic control of both traits. These results are similar to those reported by Jha *et al.* (2009), Ahmed *et al.* (2017), Mohsin *et al.* (2017), and Singh *et al.* (2018) for diallel crosses between S_1 parents in *C. moschata* and by Rana *et al.* (2015) in diallel crosses between advanced inbred lines.

Additive effects were the only component of important variation in the genetic control of DPC and DM in the diallel cross between S_0 parents (Table 2). Marxmathi *et al.* (2018), on the other hand, reported that no effect was important for DM. Both additive and non-additive gene actions were observed to be important in the genetic control of DPC and DM in diallel crosses between S_1 and S_2 inbred lines (Table 2). Similar results were recorded by Rana *et al.* (2015) for DPC in diallel crosses between advanced lines of *C. moschata*; both types of effects were found to control these traits. Regarding DM, these same authors reported that only additive effects contributed significantly to its genetic expression. On the

other hand, the analysis of data for FPC indicated that additive effects were important in its genetic expression and control only in diallel crosses between S_0 parents, whereas non-additive effects were important in its control in diallel crosses between S_0 parents and between S_2 inbred lines (Table 2). In contrast, Ortiz et al. (2013) reported the importance of additive effects in all generations evaluated (S_0, S_1, S_2), while non-additive effects were only important in the expression of FPC in the S_0 generation.

The joint analysis of the results of the three diallel crosses indicates that, in general terms, additive effects were responsible for the genetic expression and control for most of the traits in crosses made between the different inbred generations evaluated. Non-additive effects, on the other hand, were also responsible for the genetic control for most of the traits, but almost exclusively in the crosses made between S_1 and S_2 inbred lines. This could be attributed to the greater genetic divergence occurring in crosses between parents with a narrow genetic base in contrast to crosses between broad-based parents. Espitia (2004) observed similar results in C. moschata for 100-seed weight, yield, and yield components in diallel crosses between S_0 parents and between S_1 lines.

General combining ability (GCA) effects

A differential response was observed in parents in their

general combining ability (GCA) effects for FPT, indicating the highly significant differences in additive effects detected by ANOVA in the three diallel crosses (Table 2). The S_0 parents (P3 and P4) and the S_2 inbred lines (P1, P2, and P3) presented significant GCA effects values as well as highest FPT values (Table 3). Espitia (2004), Nisha and Veeraragavathatham (2014), and Abdein et al. (2017) also recorded at least one S_0 parent with significant GCA effects values. Other authors (Mohanty, 2000; Espitia, 2004; Pandey et al., 2010; El-Tahawey et al.; 2015, Ahmed et al., 2017; Singh et al., 2018; Hatwal et al., 2018) have also reported the existence of at least one S_1 line with significant GCA effects values. However, Rana et al. (2015) and Begum et al. (2016) did not find any inbred line of C. moschata with significant GCA effects values. Of the outstanding genotypes mentioned previously, S_0 parents (P3 and P4) are recommended to genetically improve FPT for the fresh consumption market formed by consumers who prefer whole, non-sliced fruits, taking advantage of the additive effects of intrapopulation recurrent selection (IRS). The S_2 inbred line (P2) is recommended for the improvement of FPT for agro-industrial use or the fresh consumption market formed by consumers for whom fruit weight is not a limiting characteristic for purchase (Table 3).

When evaluating FPC, almost all the S_0 parents and S_1 and S_2 inbred lines recorded significant GCA effects values

Table 3. Cucurbita moschata parents showing general combining ability (GCA) effects that are significant for fruit pulp thickness (FPT), fruit pulp color (FPC), polar diameter of fruits (PDF), and 100-seed weight, obtained in diallel crosses between S_0 parents and between S_1 and S_2 inbred lines.

Trait	Generation								
	S_0			S_1			S_2		
FPT	P2	**-0.21** **	*3.96*	P6×P6	**-0.28** *	*4.17*	P1×P1	**0.21** *	*4.69*
	P3	**0.38** **	*4.44*				P2×P2	**0.22** *	*4.70*
	P4	**0.21** **	*4.30*				P3×P3	**0.30** **	*4.78*
	P6	**-0.25** **	*3.94*				P5×P5	**-0.37** **	*4.22*
							P6×P6	**-0.28** **	*4.29*
FPC	P2	**-0.21** **	*12.17*	P1×P1	**-0.13** **	*12.27*	P2×P2	**-0.08** *	*12.47*
	P3	**-0.15** *	*12.09*	P2×P2	**0.18** **	*12.50*	P3×P3	**-0.27** **	*12.32*
	P4	**-0.21** **	*12.23*	P3×P3	**-0.19** **	*12.31*	P4×P4	**0.16** **	*12.59*
	P5	**0.29** **	*12.48*	P4×P4	**0.06** *	*12.49*	P5×P5	**0.16** **	*12.56*
	P6	**0.35** **	*12.51*	P5×P5	**-0.06** *	*12.41*			
				P6×P6	**0.12** **	*12.55*			
PDF							P5×P5	**0.88** **	*18.52*
100-seed weight				P2×P2	**0.98** *	*11.73*	P5×P5	**-0.99** *	*10.54*

* Significant at a probability level of 0.05. ** Significant at a probability level of 0.01
Values in bold: GCA effects values. Values in italics: average values of hybrids in diallel crosses between S_0 parents and S_1 and S_2 inbred lines.

and a medium orange color according to the Roche Yolk Color Fan scale (Vuilleumier, 1969) (Table 3). Of these genotypes, S_0 parents (P3 and P4) are recommended for the genetic improvement of FPC destined for the fresh consumption market. This market is formed by consumers who prefer whole, non-sliced, fruits. The S_2 inbred line (P2) is recommended for agro-industrial use or the fresh consumption market formed by consumers for whom fruit weight is not a limiting characteristic for purchase. Ortiz *et al.* (2013) also identified in *C. moschata* at least one S_0 parent or S_1 and S_2 lines with significant GCA effects values for FPC.

In the case of 100-seed weight, the only genotypes that reported significant GCA effects values were the S_1 inbred line (P2) and the S_2 inbred line (P5) (Table 3). These genotypes, however, did not show high 100-seed weight values. Other authors haver reported similar results for 100-seed weight in S_1 lines (Espitia, 2004; Mohsin, 2017; Hatwal *et al.*, 2018). Espitia (2004) found at least one S_0 parent of *C. moschata* with significant GCA effects values for 100-seed weight, whereas Valdés *et al.* (2014) did not find any S_0 parent with significant GCA effects values.

Only the S_2 line (P5) recorded significant GCA effects value for PDF (Table 3). Similar results have been reported in *C. moschata* by several authors (Jha *et al.*, 2009; Rana *et al.*, 2015; Ahmed *et al.*, 2017; Mohsin *et al.*, 2017; Singh *et al.*, 2018), who found at least one inbred line with significant GCA effects values, indicating that for this specific trait, only a few genotypes evaluated had the ability to transmit favorable genes to their progenies. Kakamari and Jagadeesha (2017) and Marxmathi *et al.* (2018) reported at least one S_0 parent with significant GCA effects values for PDF. Finally, in the case of DM, DPC, EDF, and NSF, no parent was genetically superior to the other parents under this study (Table 3). Rana *et al.* (2015) did not find any inbred line of *C. moschata* with significant GCA effects values for DPC and EDF; however, they did record at least one inbred line with a significant GCA effects value for DM. Jha *et al.* (2009) also reported the non-existence of *C. moschata* lines with significant GCA effects values for EDF. However, Ahmed *et al.* (2017), Mohsin *et al.* (2017), and Singh *et al.* (2018) recorded significant GCA effects for this trait in inbred lines, whereas Kakamari and Jagadeesha (2017), and Marxmathi *et al.* (2018) reported at least one S_0 parent

with significant GCA effects values for EDF. Furthermore, other authors (Espitia, 2004; El-Tahawey *et al.*, 2015; Mohsin *et al.*, 2017) identified at least one inbred line of *C. moschata* with significant GCA effects values for NSF, differing from the results found in the current study.

The joint analysis of all the traits evaluated in this study indicated that, for butternut squash destined to the fresh consumption market formed by consumers who prefer whole, non-sliced, fruits, S_0 parents (P3 and P4) can be suggested as genotypes to improve FPT and FPC genetically, taking advantage of the additive effects of IRS. These parents presented significant GCA effects values for both traits, with P3 presenting an FPT of 4.40 cm and P4, one of 4.30 cm; both presented a medium orange FPC (Table 3). In addition, they presented acceptable average values for the other studied traits. On the other hand, in the case of butternut squash for agro-industrial use or the fresh consumption market consisting of consumers for whom fruit weight is not a limiting characteristic for purchase, S_2 parent (P2) can be recommended for the simultaneous improvement of FPT and FPC, taking advantage of both additive and non-additive effects by IRS. This genotype reported significant GCA effects values for both traits, with an FPT of 4.70 cm and a medium orange FPC (Table 3). It also presented acceptable average values for the other traits under study.

Specific combining ability (SCA) effects
Several crosses between S_0 parents or between S_1 and S_2 inbred lines presented significant SCA effects for FPT (Table 4), presenting values above the expected average based on the GCA effects values of parents and the overall average. Similar results were observed in *C. moschata* by Espitia (2004), who reported at least one cross between S_0 parents with significant SCA effects values. Other authors have also reported the existence of at least one inbred line with significant SCA effects values for FPT in *C. moschata* (Mohanty, 2000; Pandey *et al.*, 2010; El-Tahawey *et al.*, 2015; Rana *et al.*, 2015; Ahmed *et al.*, 2017; Mohsin *et al.*, 2017; Singh *et al.* 2018; Hatwal *et al.*, 2018). However, Espitia (2004) and Begum *et al.* (2016) did not find any S_1 inbred line of *C. moschata* with significant SCA effects values for FPT. Of the outstanding hybrids mentioned; in the case of the fresh consumption market formed by consumers who prefer whole, non-sliced fruit. The hybrids between S_0 parents (P1×P4) and (P2×P3) are the genotypes

recommended to improve FPT, taking advantage of additive effects and allowing superior-performance varieties or lines obtained by transgressive segregation. The S_2 hybrid (P1×P6) is recommended to improve FPT for the same market, using reciprocal recurrent selection (RRS) to take advantage of both types of effects. In the case of genotypes for agricultural use or for the fresh consumption market formed by consumers for whom fruit weight is not a limiting characteristic for purchase, the between S_1 inbred line hybrids (P1×P5), the S_2 inbred line hybrids (P1×P3), and (P2×P6) are recommended for improving FPT by RRS (Table 4).

Table 4. Hybrids of *Cucurbita moschata* obtained by diallel crosses between S_0 parents and between S_1 and S_2 inbred lines, showing significant combining ability effects (SCA effects) for fruit pulp thickness (FPT), fruit pulp color (FPC), dry matter (DM), diameter of placental cavity (DPC), polar diameter of fruits (PDF), equatorial diameter of fruits (EDF) and 100-seed weight.

Trait	Generation								
	S_0			S_1			S_2		
FPT	P1×P2	**-0.19** **	*3.69*	P1×P2	**-0.40** **	*4.07*	P1×P3	**0.30** **	*5.36*
	P1×P4	**0.23** **	*4.54*	P1×P4	**0.17** *	*4.54*	P1×P4	**0.13** *	*4.79*
	P1×P6	**-0.15** **	*3.71*	P1×P5	**0.41** **	*5.09*	P1×P6	**-0.43** **	*4.01*
	P2×P3	**0.07** **	*4.37*	P1×P6	**-0.18** *	*4.02*	P2×P3	**0.24** **	*5.09*
	P2×P4	**-0.16** **	*3.99*	P2×P3	**0.23** **	*4.77*	P2×P5	**-0.15** **	*4.23*
	P2×P5	**0.06** *	*3.89*	P2×P4	**-0.16** *	*4.07*	P2×P6	**0.17** **	*4.62*
	P2×P6	**0.20** **	*3.87*	P2×P5	**0.18** *	*4.76*	P3×P4	**-0.34** **	*4.41*
	P3×P4	**-0.10** **	*4.60*	P3×P4	**-0.19** *	*4.20*	P3×P5	**-0.13** *	*4.33*
	P3×P5	**-0.13** **	*4.28*	P3×P5	**-0.15** *	*4.61*	P3×P6	**0.14** **	*4.70*
	P4×P5	**0.09** **	*4.32*	P4×P6	**0.27** **	*4.26*	P4×P5	**0.18** **	*4.24*
	P4×P6	**-0.07** **	*4.05*	P5×P6	**-0.35** **	*3.98*			
FPC	P1×P2	**0.22** *	*12.22*	P1×P3	**0.16** *	*12.25*	P1×P2	**-0.31** **	*12.18*
	P1×P3	**-0.59** **	*11.36*	P1×P4	**-0.59** **	*11.78*	P1×P4	**-0.31** **	*12.31*
	P1×P5	**0.22** *	*12.58*	P1×P5	**0.28** **	*12.53*	P1×P5	**0.43** **	*12.86*
	P2×P6	**-0.21** *	*12.31*	P2×P3	**-0.15** *	*12.35*	P1×P6	**0.31** **	*12.64*
	P3×P4	**0.53** **	*12.44*	P2×P4	**0.35** **	*13.00*	P2×P4	**0.25** **	*12.81*
	P4×P5	**-0.40** **	*12.19*	P2×P5	**-0.28** **	*12.32*	P3×P4	**0.43** **	*12.64*
				P3×P4	**0.22** **	*12.51*	P3×P5	**-0.31** **	*12.02*
				P3×P5	**-0.15** *	*12.11*	P4×P6	**-0.38** **	*12.39*
DM	P3×P6	**-1.29** *	*10.96*	P1×P3	**2.19** *	*17.55*			
DPC	P1×P2	**-0.83** *	*12.26*				P1×P4	**1.09** *	*14.24*
	P2×P6	**1.12** **	*13.06*				P2×P6	**1.27** *	*15.03*
	P5×P6	**-1.04** *	*9.71*						
PDF							P5×P6	**-1.46** *	*17.52*
EDF	P2×P6	**1.67** *	*20.53*						
	P5×P6	**-1.25** *	*16.77*						
100-seed weight	P1×P2	**-1.15** *	*12.48*	P1×P2	**-2.43** *	*9.93*	P3×P4	**1.53** **	*13.24*
	P3×P4	**0.98** *	*12.89*						

* Significant at a probability level of 0.05. ** Significant at a probability level of 0.01
Values in boldface: SCA effects values. Values in italics: Average values of hybrids.

The analysis of FPC indicated that several crosses between S_0 parents or between S_1 and S_2 inbred lines were identified with significant SCA effects values (Table 4). Of these crosses, the hybrid between S_2 inbred line (P1×P6) is recommended to genetically improve FPC for the fresh consumption market formed by consumers who prefer whole, non-sliced fruits. Ortiz *et al.* (2013) had also reported the existence of at least one cross between S_0 parents in *C. moschata* with a significant SCA effects value.

In the case of DPC, three hybrids between S_0 parents and two between S_2 inbred lines presented significant SCA effects values (Table 4). Of these, the hybrid S_2 inbred line (P2×P6) is recommended to improve DPC by RRS for agro-industrial use or for the fresh consumption market formed by consumers for whom fruit weight is not a limiting characteristic for purchase. Rana *et al.* (2015) also reported the existence of at least one hybrid between advanced inbred lines of *C. moschata* with significant SCA effects values for DPC.

In the case of 100-seed weight, two hybrids between S_0 parents, one between S_1 inbred lines and another between S_2 inbred lines showed significant SCA effects values (Table 4). Similar results were reported in *C. moschata* by several authors (Espitia, 2004; Valdés *et al.*, 2014; Nisha and Veeraragavathatham, 2014), who observed at least one cross between S_0 parents with significant SCA effects values. Other authors have also reported the existence of at least one inbred line of *C. moschata* with significant SCA effects values for 100-seed weight (Espitia, 2004; El-Tahawey *et al.*, 2015; Mohsin *et al.*, 2017; Hatwal *et al.*, 2018).

One hybrid between S_0 parents and another between S_1 inbred lines presented significant SCA effects values for DM (-1.29* and 2.19*, respectively) (Table 4), indicating that their DM contents were lower in the first hybrid and higher in the second one, with respect to expected mean with base in GCA effects of its parents and general mean. Rana *et al.* (2015) had also observed the existence of at least one hybrid between advanced inbred lines of *C. moschata* with significant SCA effects values for DM.

Only two crosses with significant SCA effects values were identified in the case of EDF. These corresponded to hybrids between the S_0 parents (P2×P6) and (P5×P6)

(Table 4). Kakamari and Jagadeesha (2017) and Marxmathi *et al.* (2018) found similar results in hybrids between S_0 parents for EDF. On the other hand, the existence of at least one hybrid between inbred lines of *C. moschata*, with significant SCA effects values for EDF, has been reported by other authors (Jha *et al.*, 2009; Rana *et al.*, 2015; Ahmed *et al.*, 2017; Mohsin *et al.*, 2017; Singh *et al.*, 2018).

This study only revealed one cross with a significant SCA effects value for PDF, the hybrid between S_2 inbred lines (P5×P6) (Table 4). Jha *et al.* (2009), Ahmed *et al.* (2017), Mohsin *et al.* (2017) and Singh et al. (2018) had also recorded the presence of at least one hybrid between inbred lines with significant SCA effects values for PDF. Kakamari and Jagadeesha (2017) and Marxmathi *et al.* (2018), on the other hand, reported at least one hybrid between S_0 parents with significant SCA effects values for PDF.

No crosses presented significant SCA effects values for NSF. Espitia (2004) had not reported the existence in *C. moschata* of crosses between S_1 inbred lines with significant SCA effects values. However, the presence of at least one cross between inbred lines with significant SCA effects values has been observed by other authors (El-Tahawey *et al.*, 2015; Mohsin *et al.*, 2017). Espitia (2004), Marxmathi *et al.* (2018), and Darrudi *et al.* (2018), on the other hand, reported at least one cross between S_0 parents with significant SCA effects values for NSF.

The joint evaluation these results indicated that in the case of the fresh consumption market formed by consumers who prefer whole, non-sliced fruits; the hybrid between S_2 inbred lines (P1×P6) is the cross recommended for the simultaneous genetic improvement of FPT and FPC. It takes advantage of both additive and non-additive effects by RRS and records a significant SCA effects value for both traits, presenting an FPT of 4.01 cm and a medium orange FPC (Table 4). In addition, this hybrid presented acceptable average values for the other traits studied.

CONCLUSIONS
Additive effects were responsible for the genetic expression and control for most of the fruit traits evaluated in the three diallel crosses. Non-additive effects were also responsible for the genetic control of most of the

Rev. Fac. Nac. Agron. Medellín 72(3): 8983-8993. 2019

8991

traits, but almost exclusively in crosses between S_1 and S_2 inbred lines. In the case of the fresh consumption market formed by consumers who prefer whole, non-sliced fruits, the S_0 parents UNAPAL-Dorado and IC3A (P3 and P4) were recommended for the simultaneous genetic improvement of traits fruit pulp thickness and fruit pulp color, taking advantage of additive effects. In the case of genotypes destined for agro-industrial use or for the fresh consumption market formed by consumers for whom fruit weight is not a limiting characteristic for purchase, the S_2 parent UNAPAL-Abanico-75-2 (P2) is recommended for the simultaneous improvement of traits fruit pulp thickness and fruit pulp color, taking advantage of additive effects. In the case of the fresh consumption market formed by consumers who prefer whole, non-sliced fruits, the hybrid between S_2 inbred lines   UNAPAL-Abanico-75-1×UNAPAL-Llanogrande-2 (P1×P6) is recommended for the simultaneous genetic improvement of traits FPT and FPC, taking advantage of both additive and non-additive effects. After evaluating the effect of inbreeding on the genetic expression and control of fruit traits analyzed in this study, it was found that non-additive effects are important in diallel crosses between inbred lines than in those between S_0 parents.

ACKNOWLEDGEMENTS

REFERENCES

Abdein MAE, Hassan HMF and Dalia HM. 2017. General performance, combining abilities and heritability of yield and yield component traits in pumpkin (*Cucurbita moschata* Poir.) at different conditions. Current Applied Science and Technology 17(1): 121–129.

Ahmed B, Masud MAT, Zakaria M, Hossain MM and Mian MAK. 2017. Heterosis and combining ability of pumpkin (*Cucurbita moschata* Duch Ex Poir.). Journal of Agricultural Studies 5(3): 132–139. doi: 10.5296/jas.v5i3.11920

Begum F, Akanda AM, Masud MAT, Rasul MDG and Islam MA. 2016. Combining ability and heterosis for PRSV-W resistance in pumpkin (*Cucurbita moschata*). Journal of International Academic Research for Multidisciplinary 4(1): 92–102.

Crossa J, Vasal SK and Beck DL. 1990. Combining ability in diallel crosses of CIMMYT's tropical late yellow maize germplasm. Maydica 35: 273–278.

Cruz CD. 2013. GENES - a software package for analysis in experimental statistics and quantitative genetics. Acta Scientiarum Agronomy 35(3): 271–276. doi: 10.4025/actasciagron.v35i3.21251

Darrudi R, Nazeri V, Soltani F, Shokrpour M and Ercolano MR. 2018. Evaluation of combining ability in *Cucurbita pepo* L. and *Cucurbita moschata* Duchesne accessions for fruit and seed quantitative traits. Journal of Applied Research on Medicinal and Aromatic Plants 9: 70-77. doi: 10.1016/j.jarmap.2018.02.006

El-Tahawey MAFA, Kandeel AM, Youssef SMS and Abd El-Salam MMM. 2015. Heterosis, potence ratio, combining ability and correlation of some economic traits in diallel crosses of pumpkins. Egyptian Journal of Plant Breeding 19(2): 419–439. doi: 10.12816/0011721

Espitia M. 2004. Estimación y análisis de parámetros genéticos en cruzamientos dialélicos de zapallo (*Cucurbita moschata* Duch. ex Poir.). Tesis Doctoral en Ciencias Agropecuarias-Mejoramiento Genético Vegetal. Facultad de Ciencias Agropecuarias. Universidad Nacional de Colombia. Palmira. 206 p.

Hallauer AR and Miranda JB. 1981. Quantitative genetics in maize breeding. First Edition. The Iowa State University Press, Ames. 468 p.

Hatwal PK, Yadav VS, Thakur R and Mahawar AK. 2018. Estimation of heterosis in relation to combining ability for earliness, yield and quality attributes in pumpkin (*Cucurbita moschata* Duch. ex Poir). Indian Journal of Agricultural Research 52(5): 548-553. doi: 10.18805/IJARe.A-5012

Jha A, Pandey S, Rai M, Yadav DS and Singh TB. 2009. Heterosis in relation to combining ability for flowering behaviors and yield parameters in pumpkin. Vegetable Science 36(3): 332–335.

Kakamari GS and Jagadeesha RC. 2017. Estimation of combining ability for growth, yield and its components in pumpkin (*Cucurbita moschata* Duch. Ex. Poir). Research in Environment and Life Sciences 10(3): 280-283.

Kim HY, Nam SY, Yang SY, Kim HM and Jeong HJ. 2016. *Cucurbita moschata* Duch. and its active component, β-carotene effectively promote the immune responses through the activation of splenocytes and macrophages. Immunopharmacology and Immunotoxicology 38(5): 319-326. doi: 10.1080/08923973.2016.1202960

Leterme P y Estrada F. 2012. Análisis de alimentos y forrajes, protocolos de laboratorio. Universidad Nacional de Colombia, Facultad de Ciencias Agropecuarias, Palmira. 57 p.

Marxmathi P, Krishnamoorthy V and Thankaraj P. 2018. Combining ability studies in pumpkin (*Cucurbita moschata* Duch ex Poir). International Journal of Microbiology and Applied Sciences 7(3): 3033-3039. doi: 10.20546/ijcmas.2018.703.352

Mohanty BK. 2000. Combining ability for yield and its components in pumpkin. The Indian Journal of Genetics and Plant Breeding 60(3): 373–379.

Mohsin GM, Doullah MAU, Hasanuzzaman M, Biswas BK, Islam MS, Rahman S and Islam AKMA. 2017. Combining ability analysis in pumpkin (*Cucurbita moschata* Duch Ex Poir). Contemporary Research in India 7(3): 176–181.

Nisha SK and Veeraragavathatham D. 2014. Heterosis and combining ability for fruit yield and its component traits in pumpkin (*Cucurbita moschata* Duch. ex Poir.). Advances in Applied Research 6(2): 158–162. doi: 10.5958/2349-2104.2014.00008.4

Ortiz GS, Vallejo FA, Baena D, Estrada EI y Valdés MP. 2013. Zapallo para consumo en fresco y fines agroindustriales: investigación y desarrollo. Universidad Nacional de Colombia, Palmira. 255 p.

Pandey S, Jha A, Kumar S and Rai M. 2010. Genetics and heterosis of quality and yield of pumpkin. Indian Journal of Horticulture 67(3): 333–338.

Rana MS, Rasul MG, Islam AKMA and Hossain MM. 2015. Combining ability of quality traits in pumpkin (*Cucurbita moschata* Duch. Ex Poir.). Bangladesh Research Publications Journal 11(3): 233–236.

Restrepo-Salazar JA, Vallejo-Cabrera FA and Restrepo-Salazar EF. 2018a. Habilidad combinatoria en función de la endogamia para producción y peso del fruto en *Cucurbita moschata* Duch. ex Poir. Revista Colombiana de Ciencias Hortícolas 12(1): 126–135. doi: 10.17584/rcch.2018v12i1.7032

Restrepo J, Vallejo F and Restrepo E. 2018b. Yield Heterosis and average fruit weight as a function of inbreeding in *Cucurbita moschata* Duch. ex Poir. Agronomía Colombiana 36(1): 5-12. doi: 10.15446/agron.colomb.v36n1.66312

Rezende GSP and Souza-Junior CL. 2000. A reciprocal recurrent selection procedure outlined to integrate hybrid breeding program in maize. Journal of Genetics and Breeding 54(1): 57–66.

SAS Institute Inc. 2012. SAS/STAT® Guide for Personal Computers. Version 9.4 Edition. SAS Institute Inc., Cary, NC. 378 p.

Singh N, Sidhu MK and Dhatt AJ. 2018. Heterosis and combining ability for bushy and butternut traits in pumpkin (*Cucurbita moschata*). Indian Journal of Agricultural Sciences 88(6): 877-883.

Valdés MP, Ortiz S y Vallejo FA. 2014. Efectos heteróticos para el carácter extracto etéreo en la semilla de zapallo *Cucurbita moschata* Duch. Revista U.D.C.A Actualidad & Divulgación Científica 17 (2): 371–379.

Vuilleumier JP. 1969. The 'Roche Yolk Colour Fan' – An instrument for measuring yolk colour. Poultry Science 48(3): 767–779. doi: 10.3382/ps.0480767

Yadav M, Jain S, Tomar R, Prasad GBKS and Yadav H. 2010. Medicinal and biological potential of pumpkin: an updated review. Nutrition Research Reviews 23(2): 184–190. doi: 10.1017/S0954422410000107

Rev. Fac. Nac. Agron. Medellín 72(3): 8983-8993. 2019

8993