Genetic Correlations and Path Analysis in Butternut Squash *Cucurbita moschata* Duch

Correlaciones Genéticas y Análisis de Sendero en Zapallo *Cucurbita moschata* Duch

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Abstract. *A genetic correlation and path analysis was carried out for yield and fruit quality components of diallel crosses of butternut squash Cucurbita moschata Duch, using open-pollinated introductions,* S_0 *and inbred lines* S_1 *and* S_2 *at two sites: Candelaria and Buga, located in the Department of Valle del Cauca, Colombia. A split-plot experimental design with arranged, random blocks and four replicates was used. The average fruit weight presented positive genetic correlations with the total production per plant in all three generations and at both test sites. The total plant dry matter and total production per plant presented a high genetic correlation, and the fruit dry matter was inversely correlated with the total carotene. The total carotene and fruit color were independent. The path analysis confirmed high genetic correlations between the number of fruits per plant, average fruit weight, and total plant dry matter, with direct, positive effects, that were significantly greater than zero for the variables of number of fruits per plant and average fruit weight in regards to the total plant dry matter. The total production per plant expressed a direct, negative effect on the total plant dry matter. The fruit dry matter presented an indirect, negative effect on the total plant dry matter through the average fruit weight and an indirect, positive effect through the total production per plant.*

Key words: Total carotene, fruit dry matter, dry matter per plant, starch.

Resumen. *Se estudiaron las correlaciones genéticas y el análisis de sendero para los componentes del rendimiento y calidad del fruto de zapallo Cucurbita moschata Duch, en cruzamientos dialélicos entre introducciones de libre polinización* S_0 *y sus líneas* S_1 *y* S_2 *en dos localidades, Candelaria y Buga, ubicadas en el Departamento del Valle del Cauca, Colombia. Se usó un diseño experimental en parcelas divididas, arregladas en bloques al azar con cuatro repeticiones. El peso promedio del fruto presentó correlación genética positiva con producción por planta en las tres generaciones y las dos localidades consideradas. La materia seca por planta y producción por planta presentaron correlación genética alta, la materia seca del fruto estuvo inversamente asociado con caroteno total. El caroteno total y color de fruto manifestaron independencia. El análisis de sendero confirmo correlaciones genéticas altas entre número de frutos por planta, peso promedio del fruto y materia seca por planta con efectos directos positivos y significativamente mayores que cero para las variables número de frutos por planta y peso promedio del fruto sobre la materia seca por planta. La producción por planta expresó efecto directo negativo sobre materia seca por planta. La materia seca del fruto presentó un efecto indirecto negativo sobre materia seca por planta vía peso promedio del fruto y un efecto indirecto positivo a través de producción por planta.*

Palabras clave: Caroteno total, materia seca en fruto, materia seca por planta, almidón.

Selecting Cucurbita| introductions by the oil content in the seeds. Plant selection is facilitated by the magnitude and nature of the correlations between different traits (Falconer and Mackay, 1996). Plant breeders strive to develop cultivars that perform well for several traits at the same time whenever the correlation between said traits can be irrefutably attributed to genetic and not environmental causes (Ceballos, 1998). It is risky to use phenotypic correlations because they do not clearly reflect the correlation between genetic and environmental causes (Espitia, 2004).

When two traits express a high genetic correlation, it is possible to select one by selecting the associated trait (Agrawal, 1998; Márquez, 1991). This proves advantageous when a trait has a high economic or agricultural value but low heritability as compared with that of the associated trait. In this case, the high-value, low-heritability trait should be selected through the low-value, high-heritability trait. Similarly, when two genetically correlated traits present different degrees of difficulty for assessment, then the selection should be based on the easiest trait to evaluate (Miranda and Cruz, 1988).

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If target traits present a low genetic correlation, it is expensive to identify individuals or cultivars that present desirable traits simultaneously (Cruz and Regazzi, 1997; Espitia, 2004). Hallauer and Miranda (1988), Vencovsky and Barriga (1992), Falconer and Makay (1996), Cruz and Regazzi (1997), Ceballos (1998) and Cruz (2001) agreed that genetics correlations are useful for (1) achieving a quicker genetic advance through an indirect screening for character 'X', which is expensive, through another 'Y' trait, which is easy to identify and measure with higher heritability; (2) estimating the change and predicting the level of response related to a selection for two genetically correlated traits; (3) developing indices of simultaneous selection for several traits of economic interest; and (4) preparing path diagrams. The path coefficient is a standardized regression coefficient that estimates the direct influence of a variable on another, regardless of the other variables. This statistic helps break down correlation coefficients into their direct and indirect effects (Vencovsky and Barriga, 1992).

In butternut squash *Cucurbita moschata* Duch. and winter squash *Cucurbita maxima*, the dry matter in fruit (DMF) is traditionally low (Baena *et al.,* 2010; Jacobo *et al*., 2011) and the gold color of the fruit flesh is the most conspicuous attribute correlated with the total carotene (Ortiz *et al.,* 2009a) that is dependent on the concentration of α and β-carotene (Ortiz, *et al.,* 2008; Konopacka *et al*., 2010; Souza *et al.,* 2012).

In *C. maxima*, a significant and high phenotypic correlation has been identified between the length of main vine and the yield components in parental and F_1 populations, but not in segregating populations (Vinasco *et al.,* 1998). Wessel and Carbonell (1989), working with *C. moschata*, found that the total number of fruits per plant was highly correlated with the yield, whereas the fruit size was not correlated with the number of fruits per plant.

Espitia (2004), also working with *C. moschata*, found that genetic correlations (r_G) were superior in both magnitude and significance when compared with phenotypic (r_P) and environmental (r_E) correlations. The fruit weight per plant presented high phenotypic and genetic correlations with the average fruit weight and number of fruits per plant. In the path analysis, all of the direct effects were positive and superior to the indirect ones. The estimation and importance of the direct effects were higher in the diallel crosses of the lines, as compared with the varieties. The direct effects were higher when genetic correlations were used, as compared with those of phenotypic correlations. The average fruit weight was the causal variable that showed the largest direct effect on the fruit weight per plant, with values 3.2 to 4.9 times greater than the residual effect.

This paper aimed to analyze the genetic and path correlations for traits related to butternut squash production and fruit quality in diallel crosses using open-pollinated introductions S_0, and inbred lines S_1 and S_2.

MATERIALS AND METHODS

Study sites. This study was carried out at two sites in the Department of Valle del Cauca, Colombia, during the semesters 2005A, 2005B; 2006B and 2007A. The first was the Experimental Center of the Universidad Nacional de Colombia - Palmira campus, located in the municipality of Candelaria (3°25 'N, 76°25' W) at 973 masl, with a mean annual temperature of 26 °C, 1,100 mm of annual precipitation, and 76% relative humidity. The second was the Servicio Nacional de Aprendizaje (SENA), located in the municipality of Buga (3°53' N, 76°18' W) at 969 masl, with a mean annual temperature of 23 °C, 980 mm of annual precipitation, and 75% relative humidity.

Genetic materials. A total of 133 Colombian butternut squash introductions belonging to the research collection of the Universidad Nacional de Colombia Palmira's Vegetable Breeding, Agronomy, and Seed Production Program were evaluated. Each introduction was self-pollinated to generate S_1 seeds. Ten S_1 lines were then selected for high fruit dry matter yield and inbreeding was again performed to generate S_2 seeds. Six S_0 populations and the inbred S_1 and S_2 lines were selected for three diallel crosses (S_0 x S_0, S_1 x S_1, and S_2 x S_2), following method 2 and model I as proposed by Griffing (1956). The hybrids and progenitors were evaluated during the semesters 2006B and 2007A.

Evaluated variables. The following variables were evaluated: fruits per plant; average fruit weight (kg); plant production (kg); dry matter per fruit; dry matter per plant (kg); total carotene (μg g^{-1}), using the extraction technique with petroleum ether-acetone-washing with decanted water and spectrophotometry at 450 nm, as developed by HarvestPlus (Rodríguez and Kimura 2004; Rodríguez *et al.,* 2008); total starch in pulp (mg g^{-1}), determined by starch gelatinization and dispersion in 4M KOH followed by hydrolysis mediated by a heat-resistant amyloglucosidase and specific determination of glucose using a glucose oxidase reactive and spectrophotometry at 500 nm (Faisant *et al.,* 1995; Cumarasamy *et al.,* 2002); and crude protein in the fruit, estimated as total N by the Kjeldahl method, multiplied by the constant 6.25 (Nielsen, 1998).

Experimental design. A split-plot experimental design was used, arranged in randomized blocks with four repetitions, five plants per repetition. Three vigorous plants are selected and each two fruits per plant was taken. The main plot corresponded to the S_0, S_1 and S_2 generations and the subplot corresponded to the hybrids resulting from the diallel combinations of S_0 x S_0, S_1 x S_1 and S_2 x S_2.

Estimation of genotypic correlations. The genetic correlation coefficient (r_G) for each pair of traits was calculated using the GENES software for Windows. This program uses the matrices of variances and co-variances of each pair of target variables and applies the conventional genetic correlation model (Gallais, 2003).

Path analysis. The following path analyses were conducted: (1) the dry matter per plant in relation to the number of fruits per plant, fruit dry matter, and average fruit weight, and (2) the fruit dry matter content in relation to the starch, crude protein, and total carotene in the dry matter. Data processing was performed with SAS-9.1 (2000) and Genes software.

RESULTS AND DISCUSSION

Genetic correlations. The genetic correlation coefficients (r_G) for the different traits evaluated in the three diallel crosses (S_0, S_1 and S_2) in the two test sites are listed in Table 1. The higher and significant correlations between the variables were: First, plant production with the average fruit weight per plant was positive and significant, indicating that selecting for fruit weight guarantees cultivars with higher production per plant and dry matter per plant. Second, yield per plant and dry matter per plant, this involves identifying the best genotypes for dry matter per plant by only measuring the production per plant in the field. Third, the fruit dry matter and starch in fruit expressed the highest genetic correlation; thus, to determine dry matter (twenty times less expensive), selecting genotypes for starch production can be used. Fourth, carotene per plant and fruit crude protein, where it is clear that an improvement can be achieved in one of two characteristics, probably, may be enhanced if one of them. However, the monetary cost to value these two variables, forced to seek indirect associations with other characteristics that are lower cost determination. The strong correlation of starch content and dry matter content (r>0.8) was reported by Cervantes et al. (2011) in sweet potato storage roots.

Production. Furthermore, the genetic advances in production per plant resulting from a higher number of fruits can be achieved without affecting the average fruit weight because these two variables do not present a statistically significant genetic correlation. However, they can be affected by the dry matter content in fruit, which is highly correlated with the dry matter per plant (Table 1) (Ortiz *et al*., 2009a; Baena *et al*., 2010; Valdes *et al*., 2013).

This result contrasts with the negative correlation obtained by other researchers working with different species of Cucurbita such as Doijode and Sulladmath

Table 1. Genetic correlations for several traits of *Cucurbit moschata* based on three diallel crosses at two sites in Valle del Cauca, Colombia.

Trait	Number of fruits per plant	Average fruit weight	Plant production	Fruit dry matter	Plant dry matter	Carotene per plant	Starch	Crude Protein
Number of fruits per plant	1	–0.14	0.457*	–0.044	0.384*	0.135	–0.039	0.178
Average fruit weight		1	0.818**	–0.485*	0.450 *	0.545*	–0.471*	0.375*
Plant production			1	0.483*	0.627**	0.552*	–0.467*	0.367*
Fruit dry matter				1	0.343*	–0.908**	0.998**	–0.498*
Plant dry matter					1	–0.278*	0.369*	–0.086
Carotene per plant						1	–0.901**	0.647**
Starch							1	–0.521**
Crude protein								1

*, ** = Significant at P<0.05 and 0.01, respectively.

(1984), Rana *et al.* (1985), Pandita *et al.* (1989), Wessel and Carbonell (1989). Singh *et al.* (1992), Amaral *et al.* (1994), Cui *et al*. (1996), Gwanama *et al.* (1998), Vinasco *et al.* (1998), Kumaran *et al.* (1998), Devadas *et al*. (1999), Mohanty (2001), Pandey *et al.* (2002), Espitia (2004),) and Aliu *et al.* (2012) for maize, with a negative correlation between the yield and protein content.The inverse association that generally occurs between the number of fruits per plant and average fruit weight, which was characterized by low and not significant probably results from the physiological phenomenon of fruits competing for photosynthates and for vital space to develop; so that plants either produce a high number of small fruits or a low number of large fruits (Azcon and Talon, 1993).

The average fruit weight presented a positive and highly significant genetic correlation with the production per plant, indicating that the selection of cultivars with heavier fruits ensures a higher production per plant, regardless of the selection method used for the number of fruits. Likewise, very heavy fruits tend to present a lower percentage of dry matter, which, in turn, can be compensated for by a higher dry matter per plant and per unit area.

The fruit dry matter content was inversely related to the total carotene and crude protein contents and directly related to the starch percentage. This relationship is complex and reflects the study of the growth dynamics of the fruit as well as the monitoring of nutrient accumulation throughout fruit growth. The same results for a negative correlation were found between yield and total protein content in maize (Aliu *et al.,* 2012).

Although this study focused on the fruit dry matter content, the expression of this trait is conditioned by the fruit starch content, which is the natural physiological contributor for the origin of starch in the chloroplast to the sink organ (fruit), where it is stored (Salisbury and Ross, 2000).

Starch is a fruit macromolecule on which the selection for fruit dry matter should focus, taking advantage of the highly significant genetic correlation between both traits (Table 1). Its importance is clear, especially because it is more expensive to measure starch for industrial quality control than it is to measure fruit dry matter, in monetary terms as well as in terms of technique protocols and scheduling. Furthermore, the shelf life of butternut squash during prolonged periods is directly proportional to the dry matter, starch, and sugar contents in the mesocarp (Lacuzzo and Dalla Costa, 2009).

Increasing the fruit starch content and, as a result, the fruit dry matter content significantly reduces total carotene levels, which could be attributed to the fact that, under normal conditions, the leaf lamina sends an extremely diluted nutrient-containing solution to the developing fruit, which acts as a protection mechanism against the desiccation of developing fruit or as a nutrient-rich substratum for the future development of new seedlings. In such cases, the concentration of carotenoids and antioxidant pigments will probably be high in fruits with a low dry matter content.

In fruits with 15% dry matter or more, the concentration of total carotene decreases because most of it has probably been diverted to a more oxidative state because of redox potential imbalance (Salisbury and Ross, 2000); however, carotene continues to promote yellow pulp color, in particular because other colored molecules intervene in fruit color (Rodríguez and Kimura, 2004; Konopacka *et al.,* 2010).

In fruits with 15% dry matter or more, the concentration of total carotene decreases because most of the carotene has probably been diverted to a more oxidative state due to a redox potential imbalance (Salisbury and Ross, 2000); however, carotene continues to promote a yellow pulp color, in particular because other colored molecules probably are involved in fruit color (Rodríguez and Kimura, 2004; Konopacka *et al.,* 2010).

The high genetic correlation between dry matter per plant and starch content is attributed to a dependency ratio between both variables. Starch is synthesized in chloroplasts as a direct product of photosynthesis (Azcon and Talon, 1993; Salisbury and Ross, 2000) and transported to the sink organ (fruit) by plant transport systems. The hypertonicity caused by a solute concentration in crib tubes induces the entrance of water by osmosis, generating a pressure that pushes the solution up to the sink organ. In Cucurbits, this solution is highly diluted (Azcon and Talon, 1993). As a result, starch is deposited differentially in the fruit, depending on each genotype's capacity to return moisture to the plant's vascular system. This induces an "abnormal" accumulation of starch that differs from the diluted condition that is typical of Cucurbits. The starch therefore becomes the most important photosynthate reserve for reproductive purposes and is directly responsible for fruit dry matter.

A nonlinear regression model was adjusted between the fruit dry matter and starch contents in the fresh pulp for each test site and averaged for the S_0, S_1 and S_2 generations. In the case of Candelaria (Figure 1a), the starch content of the fresh pulp (mg g^{-1}) was equal to $0.1347X^{1.5232}$ fruit dry matter with R^2 =0.8463; in the case of Buga (Figure 1b), the starch content of the fresh pulp (mg g^{-1}) was equal to $0.0954X^{1.6438}$ fruit dry matter with R^2=0.7994. The regression model expressed a direct relationship between the fruit dry matter and starch content in the fresh pulp. The correlation between these two traits is useful because: (1) it is simpler, quicker, and less expensive to determine dry matter than to determine starch, given the cost of the enzymatic methods required for starch determination; and (2) if genotypes are selected for high dry matter content in the fruit, they would be simultaneously selected for high starch content.

This model can be used to estimate starch content based on fruit dry matter content or, in its absence, to define selection criteria for fruit dry matter, given certain minimum thresholds of fruit starch content required for agroindustrial uses.

The inverse correlation of the total carotene and crude protein contents with the dry matter per plant, dry matter per fruit, and starch percentage poses a challenge for genetic improvement because the selection for the former traits acts in contraposition to the selection for the latter traits. The same conclusion for the genetic correlation (r_G = 0.6–0.8) between a high b-carotene accumulation and a low dry matter (low starch) content has been reported, although it is not clear whether this is based on functional links between starch and carotenoid accumulations in sweet potatoes (Tomlins *et al.*, 2012). A probable explanation of the genetic correlation of these two macromolecules, which are so chemically and biochemically different, is that, during photosynthesis, both carotenoids and chlorophyll serve as photon receptors, protectors from excess light, and antioxidants. These functions of carotenoids require the support of a specific protein known as the orange carotenoid protein (Wilson *et al.*, 2008), which allows carotenoids to capture oxidizing radicals (Meléndez *et al.*, 2007). Therefore, the flow of carotenoids and proteins through the diluted solution circulating through the phloem up to the fruit can possibly explain the significant correlation between the two macromolecules; especially

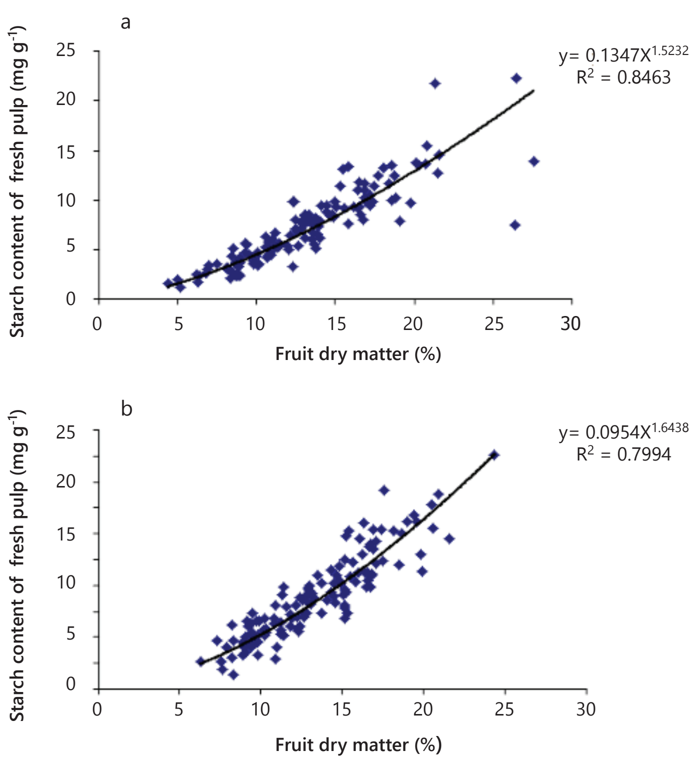

Figure 1. Correlation between fruit starch and fruit dry matter in butternut squash in (a) Candelaria and (b) Buga, both in the Department of Valle del Cauca, Colombia.

when trying to understand the role of carotenoids in heat tolerance in squashes belong to the "Cucurbits" family, which are adapted to warmer climates and mostly grown in tropical regions (Ara *et al.,* 2013). However, the true explanation is yet to be revealed.

A nonlinear regression model was adjusted to express the total carotene content in relation to the fruit dry matter content. In the case of Candelaria (Figure 2a), the starch content in the fresh pulp (mg g^{-1}) was equal to 1,670.2$X^{-0.951}$ dry matter with R^2 =0.9101; in the case of Buga (Figure 2b), the starch content in the fresh pulp (mg g^{-1}) was equal to 1,570.6$X^{-0.958}$ dry matter with R^2=0.847. The same results of a negative correlation between these two variables pose a risk of loss of total carotene with increasing fruit dry matter, unless the number of genes that control the expression of carotene in pumpkin is identified, as in the case with the inheritance of B-carotene in the cucumber and melon, which is recessive and controlled by at least two genes that, in the case of melon, are influenced by epistatic interactions (Cuevas *et al.,* 2010). However, the amount of carotene in squash fruit is so high that, even in breeding processes with dry matter levels as high as 30–40%, the total carotene should be around 100 µg g^{-1} fresh matter of fruit, which is still high for this macronutrient.

Path analysis. The genetic correlation (r_G) given in Table 1 was used for the path analyses. The response variables were plant dry matter and fruit dry matter and the causal factors were the number of fruits per plant, average fruit weight, production per plant, and fruit dry matter in the first analysis (Table 2) and total carotenes, starch, and crude protein in the second analysis (Table 3). The effects were positive, direct, and significantly greater than zero for the variables of number of fruits per plant and average fruit weight in

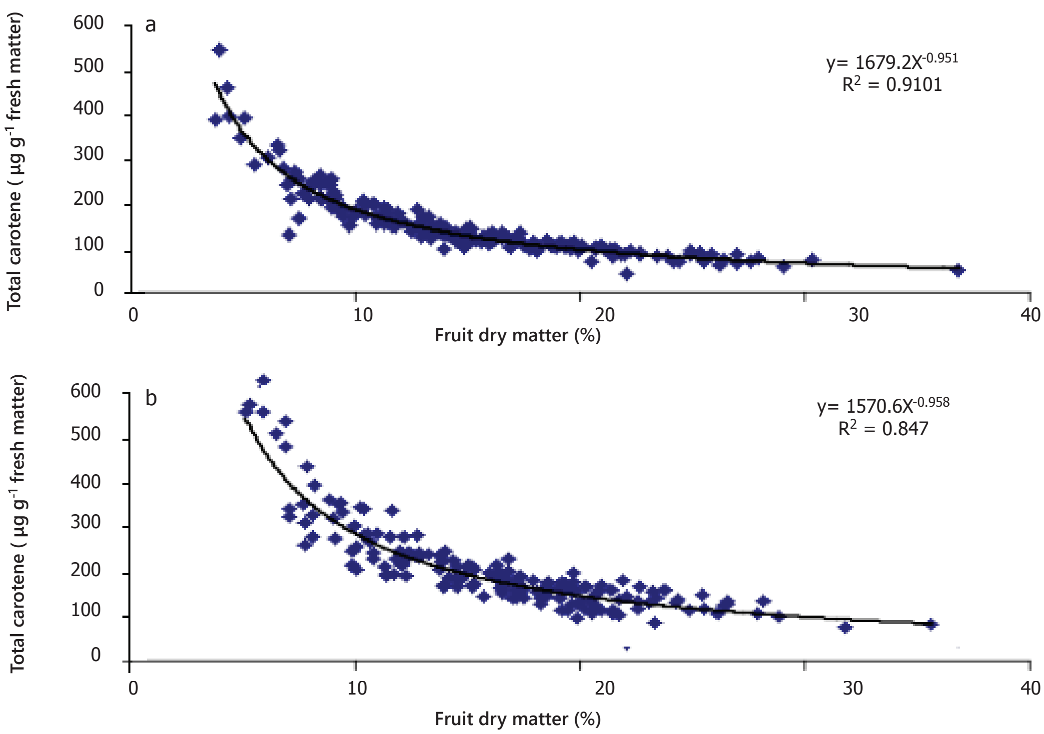

Figure 2. Correlation between the total carotene and fruit dry matter in butternut squash in Candelaria (a) and Buga (b), both in the Department of Valle del Cauca, Colombia.

regards to the plant dry matter, confirming previously obtained results. A genotype selection for a higher dry matter production per plant can be achieved by selecting for a high number of fruits per plant, regardless of the selection for a higher average fruit weight.

The significant, direct but negative effect of the production per plant on the dry matter per plant indicated that selecting for a high dry matter per plant should not be done using genotypes with a higher production per plant as a referent, but rather using genotypes with a high number of fruits or with a superior average fruit weight.

The dry matter in the fruit presented a negative, indirect effect on the dry matter per plant regarding the average fruit weight and a positive, indirect effect regarding the production per plant. This means that very heavy fruits contain a low fruit dry matter (r_G = –0.485), causing a significant decrease in dry matter per plant. Nevertheless, if the plant biomass is high, the higher dry matter content of light fruits compensates for the lower dry matter content of heavy fruits.

Table 2. Direct (main diagonal)[a] and indirect (elements outside the diagonal) effects of the causal factors number of fruits per plant, average fruit weight, plant production and fruit dry matter on the variable of plant dry matter in *Cucurbita moschata*.

	Number of fruits per plant	Average fruit weight	Plant production	Fruit dry matter	r_G
Plant dry matter	**3.662**	–0.795	–2.454	–0.029	0.384
	–0.513	**5.677**	–4.392	–0.322	0.450
	1.674	4.644	**–5.37**	–0.321	0.627
	–0.161	–2.753	2.594	**0.664**	0.343

[a] Direct effects appear in bold in the main diagonal. An explicit significance was not reported for direct and indirect effects; however, any effect higher than|0.70|is considered high.

Table 3 presents the path analysis results for the variable of fruit dry matter in relation to the total carotene, starch and crude protein. In this case, a departure was made from the assumption that fruit dry matter is an aggregate of components such as total carotene, crude protein, and starch.

The negative genetic correlation between the fruit dry matter and total carotene content can be basically attributed to the negative, indirect effect of the starch content, which means that, by increasing the fruit dry matter, the starch content also increases (r_G = 0.998), but the total carotene content decreases. A similar situation occurs with crude protein; however, the effect is less noticeable because the genetic correlation with fruit dry matter is lower (r_G = –0.498). Apparently, the negative relationship between the fruit dry matter and the B-carotene is similar to the behavior seen in sweet potatoes (Cervantes *et al.,* 2011).

Table 3. Direct[a] and indirect effects of the causal factors of total carotene, starch, and crude protein on the variable of dry matter per fruit in *Cucurbita moschata*.

	Total carotene	Starch	Crude protein	r_G
Fruit dry matter	**–0.098**	–0.845	0.035	–0.908
	0.088	**0.938**	–0.028	0.998
	–0.063	–0.489	**0.054**	–0.498

[a] Direct effects appear in bold in the main diagonal. An explicit significance was not reported for direct and indirect effects; however, any effect higher than|0.70|is considered high.

The path analysis results for the total carotene are given in Table 4, where the total carotene content is expressed in relation to the fruit dry matter yield, plant dry matter, starch of content, and crude protein content.

The negative, direct effect of the fruit dry matter on the total carotene content again evidenced the difficulty of breeding for a high total carotene content without reducing the fruit dry matter content. The study results seem to indicate that much of the total carotene diluted in fruits with a high moisture content (Jacobo *et al.*, 2011; Kim *et al.,* 2012) undergoes degradation or transformation during postharvest dehydration (Ortiz *et al*., 2008).

Although the correlation between the starch content and total carotene was negative (r_G = –0.901), the direct effect of the starch on the total carotene was

Table 4. Direct[a] and indirect effects of the causal factors of fruit dry matter, dry matter per plant, starch content, and crude plant on the variable of total carotenes in the fruit pulp of *Cucurbita moschata*.

	Fruit dry plant	Plant dry plant	Starch	Crude protein	r_G
Total carotenes	**–5.546**	–0.052	4.906	–0.216	–0.908
	–1.902	**–0.152**	1.814	–0.037	–0.278
	–5.535	–0.056	**4.916**	–0.226	–0.901
	2.762	0.013	–2.561	**0.433**	0.647

[a] Direct effects appear in bold in the main diagonal. An explicit significance was not reported for the direct and indirect effects; however, any effect higher than|0.70|is considered high.

positive and considerably high, opening the possibility of improving total carotene content by increasing starch content if the linkage between starch and fruit dry matter can be broken (r_G = 0.998).

When the total carotene content is expressed as a function of the variables of fruit dry matter, dry matter per plant, and starch (Table 5), the direct effect of starch content on the total carotene is confirmed once more, suggesting that a selection for a high starch content should be used as a breeding strategy for a high total carotene content by inbreeding with a recurrent selection program that could serve as a strategy to increase the frequencies of genes that promote the expression of these traits (Ortiz, *et al.*, 2014).

CONCLUSIONS

A highly significant genetic correlation was detected between the fruit dry matter content and starch content.

Taking into account that the total carotene and crude protein contents were inversely correlated with the dry matter per plant, dry matter per fruit, and percentage starch, this poses a challenge for genetic improvement because selecting for the former traits acts in contraposition to the selection of the latter traits. The absence of a genetic correlation between the number of fruits per plant and average fruit weight opens the possibility of simultaneously selecting for a high number of fruits and high fruit weight, guaranteeing cultivars with increased fruit yield and total plant dry matter.

Table 5. Direct[a] and indirect effects of the causal factors of fruit dry matter, dry matter per plant, and starch content on the variable of total carotenes in the pulp of *Cucurbita moschata*.

	Fruit dry matter	Dry matter per plant	Starch	r_G
Total carotenes	**–2.213**	–0.000	1.305	–0.908
	–0.759	**–0.001**	0.482	–0.278
	–2.208	0.000	**1.308**	–0.901

[a] Direct effects appear in bold in the main diagonal. An explicit significance was not reported for direct and indirect effects; however, any effect higher than|0.70|is considered high.

The significant, direct but negative effect of the production per plant on the dry matter per plant indicates that selecting for a high dry matter content per plant should not be performed using genotypes with a higher production per plant as a referent, but rather using genotypes with a high number of fruits or superior average fruit weight.

Genetic improvement still must address the negative genetic correlations between fruit dry matter versus total carotene and starch versus total carotene, because efforts to increase fruit dry matter and starch content trigger a decreased production of total carotene.

Heavy, voluminous fruits contain a low percentage of dry matter, inducing a significant reduction in dry matter per plant. The goal is to identify genotypes with a high number of heavy but small fruits.

A reciprocal recurrent selection program between populations with a high carotene content and a low starch content versus populations with a low carotene content and a high starch content could prove to be a genetic strategy to improve these traits. Another possibility is to perform backcrossing between a parent with a high starch content (donor) and one with a high carotene content (recurrent parent). This process could break the linkage between starch and the fruit dry matter while concentrating on favorable genes for both total carotenes and starch in a single population.

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