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Inheritance of soluble solids content and sucrose in melon

Juliana Maria C da Silva ¹; Elaine Renata de C Viana ²; Patrícia Lígia D de Moraes ¹; Francisco L de S Tomaz ¹; Adriano F Martins ¹; Glauber Henrique de S Nunes ¹

¹Universidade Federal Rural do Semi-Árido (UFERSA), Mossoró-RN, Brasil; julianacosta@ufersa.edu.br; plmoraishotmail.com; lincotomaz@gmail.com; adrianomartinsfe@gmail.com; glauber@ufersa.edu.br; ²Universidade Federal do Piauí (UFPI), Bom Jesus-PI, Brasil; ercviana@gmail.com

ABSTRACT

The main quality parameters of melon are related to sucrose accumulation and soluble solids content. Understanding the genetic control of these traits is essential to help breeders in the selection process. The aim of this study was to evaluate the inheritance of sucrose accumulation and soluble solids content in melon. A randomized block design with three replicates was used to evaluate AC-16 and Vedraltais parents, and F₁, F₂, BC₁ and BC₂ generations. We verified that sucrose is the main factor which is related to genetic and environmental variability observed in sugar content between parents. The inheritance of sucrose content involves a major effect gene with additive and dominance effects associated with polygenes with additive effects. The inheritance of soluble solids involves a major gene with additive and dominance effects associated with polygenes, with additive effects, and the presence of epistasis.

Keywords: *Cucumis melo*, sugar content, additive effect, polygenes.

RESUMO

Herança do teor de sólidos solúveis e sacarose em melão

Os principais parâmetros de qualidade do fruto de melão relacionam-se com o acúmulo de sacarose e o teor de sólidos solúveis. O conhecimento do controle genético desses caracteres é fundamental para auxiliar o melhorista no processo seletivo. Objetivou-se com este trabalho estudar a herança do acúmulo de sacarose e do teor de sólidos solúveis em melão. Utilizou-se o delineamento em blocos casualizados com três repetições para avaliar os genitores AC-16 e Vedraltais, e as gerações F₁, F₂, RC₁ e RC₂. Verificou-se que a sacarose é o principal fator que confere a variabilidade genética e ambiental observada no teor de açúcar entre os genitores. A herança do teor de sacarose envolve um gene de efeito maior com efeitos aditivos e de dominância associado aos poligenes com efeitos aditivos. A herança de sólidos solúveis envolve um gene maior com efeitos aditivos e de dominância associado aos poligenes com efeitos aditivos e a presença de epistasia.

Palavras-chave: *Cucumis melo*, teor de açúcar, efeito aditivo, poligenes.

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Melon (*Cucumis melo*) is the most economically important cucurbit worldwide. In Brazil, the production is carried out in the semi-arid northeastern region, an area characterized by high temperatures (>30°C), high luminosity and reduced rainfall (<600 mm/year) (Nunes *et al.*, 2011). The states of Rio Grande do Norte and Ceará are the largest producers, being responsible for over 99% of the national production destined for export, mainly to the European market (IBGE, 2020).

The importing countries require high-quality fruits. The main determinant of quality evaluated in melon fruits is sweetness, defined by sucrose accumulation in the final stages of fruit development (Freilich *et al.*, 2015).

However, for commercialization, the quality of the fruit is evaluated mainly by the soluble solid content (Li *et al.*, 2019). In this sense, breeding programs of melon plants aim at developing high-level sugar cultivars.

Studies on genetic control of agronomic traits, such as sucrose level and soluble solids content are fundamental to help out the researcher in selection process. In inheritance studies, genetic effects (additive and non-additive) are usually considered, the average degree of dominance and the number of genes or loci involved in character determination. This information is important to help the breeders choosing what strategy is more appropriate to achieve their goals (Cruz

et al., 2014).

Information on genetic control of sucrose accumulation and soluble solids content in melon is rare and discrepant. Burger *et al.* (2002) observed that sucrose accumulation is related to a recessive gene called *suc*. On the other hand, Hongxia *et al.* (2019) state that this is a polygenic inheritance. In relation to soluble solids, Pouyesh *et al.* (2017) did not verify any predominance of dominant gene effects; whereas other authors observed additive and dominance effects involved in the inheritance of the trait (Akrami & Arzani, 2019).

Given the above, the aim of this study is to evaluate inheritance of

sucrose accumulation and soluble solids content in melon.

MATERIAL AND METHODS

Location of the experiment

The experiment was carried out at Fazenda Experimental Rafael Fernandes, located in Alagoinha, rural zone of Mossoró-RN (5°03'37"S, 37°23'50"W, 72 m altitude), in Red Yellow Argisol with sandy loam texture (Embrapa, 2018). According to Köppen classification, the climate in Mossoró is 'BSWh', hot and dry, with two climatic seasons: one dry, from June to January, and the other one rainy, from February to May (Carmo Filho *et al.*, 1991).

Germplasm

Accession AC-16 and Vdrantais cultivar were used as parents. Accession AC-16, from the Germplasm Bank of Universidade Federal Rural do Semi-Árido, belongs to the botanic group "acidulus". The accession has white mesocarp, yellow exocarp, elongated fruit shape and low levels of sucrose and soluble solids (<4°Brix). Vdrantais is a French cultivar, belonging to the botanic group "cantaloupensis", developed by Vilmorin Seed Company. This cultivar has round-shaped Charentais fruits (IF = 1.0), orange mesocarp, high levels of sucrose and soluble solids (>12°Brix). The parents were crossed to obtain F₁ filial generation, then this generation was self-fertilized, giving rise to the F₂ generation and, later, both parents were backcrossed (BC₁ and BC₂).

Experimental procedure

The generations were sown in 200-cell polystyrene trays containing commercial substrate Polifertil®. The seedlings were transplanted when the first true leaf was fully expanded. The experimental plot consisted of a 3.0-m long row, spaced 2.0 m between rows

and 0.3 m between pits, with one plant per pit. A drip irrigation system was used, with emitters spaced 0.3 m apart. Soil preparation and cultural practices were carried out according to the standard recommendation for melon cultivation in the state of Rio Grande do Norte (Nunes *et al.*, 2011).

Quantification of sugars and soluble solids

Standards for sucrose, glucose and fructose (chromatographic purity ≤99%) were purchased from Sigma-Aldrich®. For chromatographic analysis, type I ultrapure water was used both for sample dilution and for running the chromatogram. The sugar standards were prepared in a single solution at a concentration of 10 mg/mL.

A 40-mL aliquot of homogenized melon pulp was centrifugated for five minutes to 10.000 RCF at 15°C and filtered using 0.45 µm PVDF membrane. The sugars were separated on a chromatographic column, Technologies type, measuring 300 x 7.7 mm, model PL Hi-Plex H Agilent molecular exclusion with 8 µm particles and a Waters Refractive Index (IR) 2414 detector. Mobile phase dilution was performed in gradient mode, with a flow of 0.6 mL/min (Corrêa *et al.*, 2013).

Soluble solid content was determined with the aid of Atago® digital refractometer, PR-Palette 100 model, using the average value of three readings in a slice cut longitudinally, and the results were expressed in °Brix.

Design and statistical analysis

We evaluated parents (AC-16 and Vdrantais) and also F₁, F₂, BC₁ and BC₂ generations using a randomized block design, with three replicates. Due to the genetic variability verified in each generation, the plots consisted of 15

(AC-16, Vdrantais and F₁), 172 (F₂), 43 (BC₁) and 46 (BC₂), totalizing 306 plants evaluated in this study.

To estimate the genetic parameters and the adjustment of additive-dominant model, we used Piepho & Möhring's mixed model methodology (2010). The variance structure is presented in detail by Kearsey & Pooni (1996).

As the generations were evaluated in randomized block design, the model for k plant, evaluated in plot i in block j was the following: $y_{ijk} = b_j + \mu_i + p_{ij} + g_{ijk} + e_{ijk}$ in which the plot error p_{ij} and plant error e_{ijk} have normal distribution with zero average and variances σ_p^2 and σ_e^2 , respectively. The genetic variation within generation was modeled using the genetic effect g_{ijk} at the plant-specific level. The adjustment of the genetic variance structure was performed through MIXED procedure using SAS® 9.2 software (SAS Institute, 2004).

Using the method described in Piepho & Möhring (2010), the authors estimated the average components related to additive [a] and dominance effects [d], as well as the additive, dominance and heritability variances. The average degree of dominance (ADD) and the minimum number of genes (n) involved in the character expression according to Wright (1934) were also estimated.

Genetic models were tested using the maximum likelihood method in mixtures of normal density functions described by Silva (2003). The distributions of each of the population were as follows (see Box 1), in which: μ : constant reference; A: additive effect of the major-effect gene; D: dominance effect of the major-effect gene; [a]: additive polygenic component; [d]: dominance polygenic component; V_A : additive variance; V_D : variance attributed to dominance deviations of polygenic effects; S_{AD} :

$$P_1: N(\mu - [a] - A, \sigma^2); P_2: N(\mu - [a] + A, \sigma^2); F_1: N(\mu - [d] - D, \sigma^2);$$

$$F_2: \frac{1}{4}N\left(\mu + \frac{[d]}{2} - A, \sigma^2 + V_A + V_D\right) + \frac{1}{2}N\left(\mu + \frac{[d]}{2} + D, \sigma^2 + V_A + V_D\right) + \frac{1}{4}N\left(\mu + \frac{[d]}{2} + A, \sigma^2 + V_A + V_D\right);$$

$$BC_{11}: \frac{1}{2}N\left(\mu + \frac{[a]}{2} + \frac{[d]}{2} - A, \sigma^2 + \frac{V_A}{2} + V_D - S_{AD}\right) + \frac{1}{2}N\left(\mu - \frac{[a]}{2} + \frac{[d]}{2} + D, \sigma^2 + \frac{V_A}{2} + V_D - S_{AD}\right);$$

$$BC_{12}: \frac{1}{2}N\left(\mu + \frac{[a]}{2} + \frac{[d]}{2} + A, \sigma^2 + \frac{V_A}{2} + V_D + S_{AD}\right) + \frac{1}{2}N\left(\mu + \frac{[a]}{2} + \frac{[d]}{2} + D, \sigma^2 + \frac{V_A}{2} + V_D + S_{AD}\right)$$

Box 1. Inheritance model carried out using Monogen v.0.1 software (Silva, 2003). Mossoró, UFERSA, 2021.

Model	Parameter
1: Major gene with additive and dominance effects + polygenes with additive and dominance effects	$\mu, A, D, [a], [d], V_A, V_D, S_{AD}, \sigma^2$
2: Major gene with additive and dominance effects + polygenes with additive effects	$\mu, A, D, [a], V_A, \sigma^2$
3: Major gene with additive effects + polygenes with additive and dominance effects	$\mu, A, [a], [d], V_A, V_D, S_{AD}, \sigma^2$
4: Major gene with additive effects + polygenes with additive effects	$\mu, A, [a], V_A, \sigma^2$
5: Polygenes with additive and dominance effects	$\mu, [a], [d], V_A, V_D, S_{AD}, \sigma^2$
6: Polygenes with additive effects	$\mu, [a], V_A, \sigma^2$
7: Major gene with additive and dominance effects	μ, A, D, σ^2
8: Major gene with additive effects	μ, A, σ^2
9: Environmental effect	μ, σ^2

A: additive effect of the major gene; D: dominance effect of the major gene; [a]: additive polygenic component; [d]: dominance polygenic component; V_A : additive variance; V_D : variance attributed to dominance deviations of polygenic effects; S_{AD} : variance component related to the products of additive polygenic effects by polygenic dominance effects; σ^2 : environmental variance.

component of variation related to products of additive polygenic effects by polygenic dominance effects; σ^2 : environmental variance.

Density functions for BC_{11} and BC_{12} are formed by mixing two normal densities and F_2 by mixing three normal distributions. Using the likelihood functions for each model, it was possible to compose tests of interest, considering different hypotheses.

To build the genetic model, we considered as the most general model the one which shows the existence of major-gene effect + polygenes with additive and dominance effects and equal environmental variances in all generations (Box 1). Independent genes were also admitted (both polygenes and those of major effect). The likelihood tests were performed using LR statistics. In general, LR statistic is given by:

$$LR = -2 \ln \frac{L(M_i)}{L(M_j)}$$

in which $L(M_i)$ and $L(M_j)$ are the likelihood functions of models i and j ; where model i shall be hierarchical to model j . The tests were performed using the statistical software Monogen v.0.1 (Silva, 2003).

RESULTS AND DISCUSSION

Sucrose

The authors verified significant

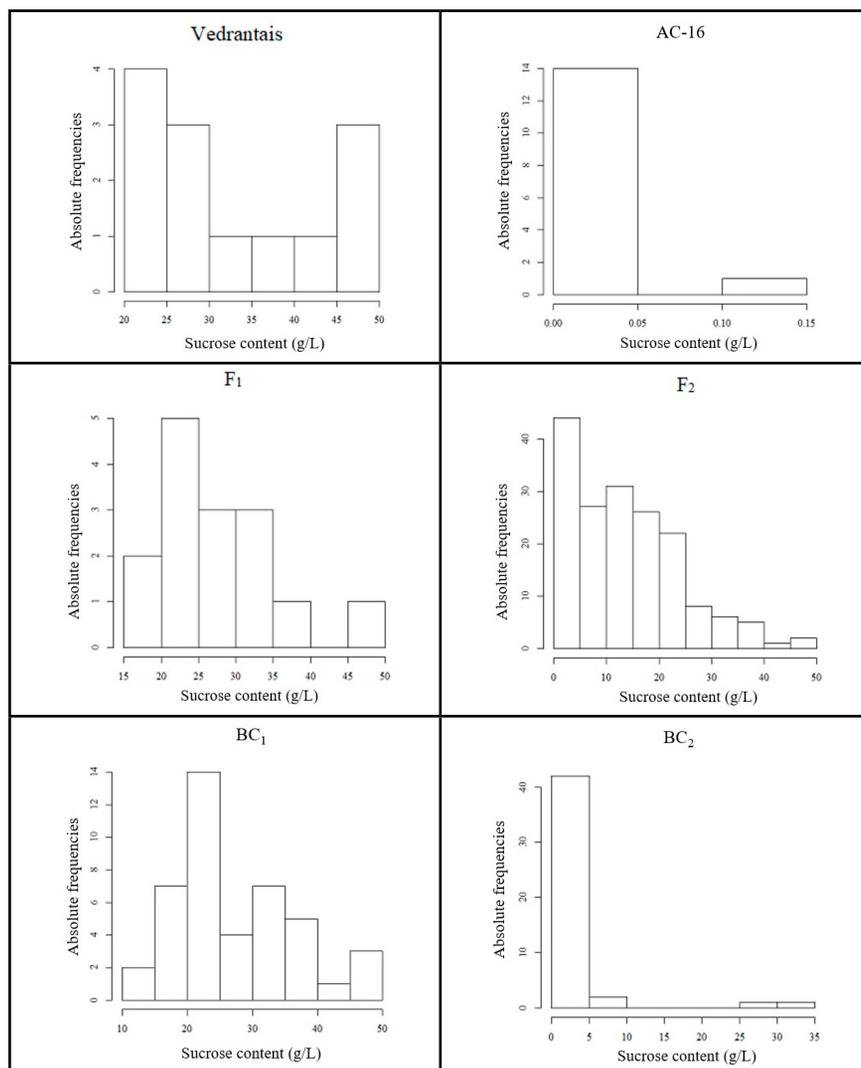


Figure 1. Distribution of absolute frequencies of sucrose content in melon fruits obtained from Vedrantaís x AC-16 crossing, parents, F_1 generation and segregating generations (F_2 and backcrossing). Mossoró, UFERSA, 2021.

contrast between parents for sucrose content. Vedrantaís showed 15 times more sucrose than AC-16 (Table 1). This result justifies the reason why the authors have chosen these contrasting parents to study this trait.

The estimates of generation variances used in this study are in accordance with what was expected: greater variances of segregating populations (F₂ and backcrosses), considering F₂ generation superior to the others both for sucrose and soluble solids contents (Table 1).

The estimates in Vedrantaís ranged from low (20 g/L) to high values (50 g/L), whereas the parent showing low sucrose accumulation (AC-16) showed

a narrow range of values, between 0.00 and 0.15 g/L (Figure 1). Burger *et al.* (2002) also observed greater variation in the parent with a high level of sucrose ('Noy Yizre'el') when compared with the parent with a low level of sucrose ('Faqqous'). Variation in both parents is due to environment, being not inheritable.

The F₁ generation showed a distribution of values from 15 to 50 g/L in sucrose accumulation (Figure 1). We verified wide distribution of F₂ generation with values which ranged from 0.00 to 50 g/L. The F₂ generation showed a left-skewed distribution trend with more than 60% of the values with

estimates up to 25 g/L (Figure 1). The variation in backcross BC₁ was superior to those verified for backcross BC₂ (Table 1, Figure 1).

Additive variance was superior to dominance variance. Narrow-sense heritability was, as expected, inferior to broad-sense heritability, since narrow-sense heritability contains only the contribution of additive genetic variance (Table 1). Additive variance is one of the determinant factors of covariance between parents, considering that its magnitude is an indication of the relationship between the selection unit and the improved unit (Cruz *et al.*, 2014).

The additive variance was all transmitted to the filial generation and is directly related to selection gain. The greater the estimate of additive variance, the greater the narrow-sense heritability. High heritability provides greater confidence that phenotypic values represent genetic values (Cruz *et al.*, 2014). When compared with the heritability estimates observed by Burger *et al.* (2002) (63.50 and 53.66 for broad and narrow-sense heritability, respectively), the values found in this study were similar (Table 1). We highlight that despite of the fact that comparing heritability estimates is particularly important, we shall proceed carefully, though, as heritability depends on the population being tested and environmental conditions.

The average degree of dominance was 1.06 showing the presence of dominance for sucrose content and estimates of two loci involved in the inheritance of the trait (Table 1). We highlight that the value obtained is close to that presented by Burger *et al.* (2002). However, Zhang *et al.* (2016) reported that 83 genes are related to sugar metabolism during melon ripening. Recently, 47,666 expressed genes were identified during fruit development. Among these genes, 48 were associated with starch and sucrose metabolism (Shin *et al.*, 2017). However, we point out that the estimate of the number of loci in this study is underestimated due to the assumptions required in the method used and in the number of

Table 1. Estimates of average and variance of generations, average and variance components of the additive-dominant model and F Test (Wald) for the content of sucrose and soluble solid contents in melon, obtained studying inheritance using generations of Vedrantaís x AC-16 crossing. Mossoró, UFERSA, 2021.

Generations	Sucrose content (g/L)		Soluble solids (%)	
	Average	Variance	Average	Variance
P ₁ (Vedrantaís)	32.44	0.23	10.05	0.56
P ₂ (AC-16)	0.02	0.23	4.06	0.24
F ₁	27.33	58.03	7.89	1.15
F ₂	13.43	97.61	6.75	2.10
BC ₁	27.25	85.71	7.69	1.84
BC ₂	1.89	69.84	4.61	1.47
Components of variance				
σ ² _A	39.67		0.87	
σ ² _D	21.02		0.58	
σ ² _G	12.69		0.00	
σ ² _E	36.92		0.66	
h ² _n (%)	40.64		41.23	
h ² _b (%)	60.69		68.72	
ADD	1.06		1.15	
h	2.10		3.54	
Components of averages				
SV	Estimate	F (Wald)	Estimate	F (Wald)
Block	-	7.21**	-	3.83*
[a]	16.21	122.22**	2.99	401.62**
[d]	-5.59	5.62*	-9.20	11.73**
[aa]	-	-	-2.38	12.72**
[dd]	-	-	7.65	33.81**
[ad]	-	-	0.17	1.07 ^{ns}

** , * : Significant at p<0.01 and p<0 by F test (Wald). σ²_A: additive variance; σ²_D: dominance variance; σ²_G: genetic variance; σ²_E: environmental variance; h²_n: narrow-sense heritability; h²_b: broad-sense heritability [a]: additive effect; [d]: dominance effect; [aa] additive-additive effect; [dd] dominance-dominance effect; [ad] additive-dominance effect.

non-segregating loci in both parents for sucrose accumulation.

For inheritance (using the average sucrose content), the authors verified the presence of additive and dominance effects in genetic control of sucrose content (Table 1). The negative value for the component [d] shows dominance to reduce this trait value. The model did not include epistatic effects.

We used the genetic models via maximum likelihood to study inheritance. First, we compared the complete model with major gene with additive and dominance effects + polygenes with additive and dominance effects (Model 1) with a model with major genes with additive and dominance effects + polygenes with additive effects (Model 2). No difference was noticed concerning these models (Table 2), showing that model 2 is sufficient, that means, the polygenes do not show additive effects, only for the major-effect gene.

Afterwards, we compared model 2 with models 4 and 7. Comparing models 2 and 4, we could test the dominance effect of the major gene, observing that this is a significant effect (Table 2). Comparing models 2 and 7, we tested the presence of additive-effect polygenes, verifying its significance. Thus, considering the genetic control of sucrose content, a major-effect gene with additive and dominance effects associated with polygenes with only additive effects can be observed.

Reports on inheritance of sucrose content in melon is rare to find in literature. One of the first studies on the subject was published by Burger *et al.* (2002), in which they verified that one gene, composed of two alleles in which the recessive allele with incomplete dominance, called *suc*, is responsible for the accumulation of sucrose. However, more recent studies confirm as polygenic, the inheritance of sucrose content in melon (Hongxia *et al.*, 2019). We highlight that the discrepancies in results are mainly due to the difference in parents involved in the studies.

The results in this study are partially in accordance with those reported

by Burger *et al.* (2002), in relation to the presence of a major gene with additive and dominance effects (Table 2). Considering that the frequency distributions presented in this study are very similar to those presented by Burger *et al.* (2002), we can conclude that the difference in relation to results is strictly related to the genetic-statistical treatment applied to the dataset. Thus, as sucrose content is a quantitative trait, it shall be studied using statistical techniques suitable for this trait.

From a pragmatic point of view, breeding program for high sucrose content in melon can be carried out using methods which seek the gradual accumulation of this sugar as recurrent selection. Due to the presence of additive and dominance effects, heterosis for this trait can be explored. Currently, melon cultivars around the world are single hybrids due to the homogeneity and presence of heterosis for traits of interest.

Soluble solid content

Table 2. Hypothesis tests of hierarchical genetic models obtained in the study of inheritance for sucrose content and soluble solids in melon fruits. Mossoró, UFERSA, 2021.

Tests	GL	Sucrose (g/L)		Soluble solids (%)	
		χ^2_c	Probability	χ^2_c	Probability
1 vs 2	3	1.64	0.65	6.93	0.04
1 vs 3	1	1.45	0.73	5.89	*
1 vs 4	4	2.92	0.57	10.54	0.03
1 vs 5	5	1.57	0.58	10.56	*
1 vs 6	6	2.92	0.71	10.54	0.06
1 vs 7	5	51.56	0.00	45.46	0.00
1 vs 8	6	52.53	0.00	45.51	0.00
1 vs 9	7	193.51	0.00	167.19	0.00
2 vs 4	1	33.29	0.00	3.60	0.05
2 vs 6	2	31.29	0.00	3.60	0.16
2 vs 7	2	49.92	0.00	38.53	0.00
2 vs 8	3	50.90	0.00	38.58	0.00
2 vs 9	4	191.87	0.00	160.26	0.00
3 vs 5	1	0.00	1.00	*	*
3 vs 6	4	3.70	0.44	10.66	0.03
3 vs 8	5	53.31	0.00	45.63	0.00
3 vs 9	6	194.28	0.00	167.31	0.00
4 vs 6	1	35.65	0.00	32.76	*
4 vs 8	2	49.61	0.00	34.98	0.00
4 vs 9	3	190.58	0.00	156.66	0.00
5 vs 6	3	3.70	0.29	10.66	0.01
5 vs 9	5	194.28	0.00	167.31	0.00
6 vs 9	2	190.58	0.00	156.66	0.00
7 vs 8	1	0.97	0.32	0.05	0.82
7 vs 9	2	141.95	0.00	121.73	0.00
8 vs 9	1	1.64	0.20	6.93	0.00

GL: degree of freedom; χ^2_c : Chi-square *: Value not obtained due to convergence problems. 1: major gene with additive and dominance effects + polygenes with additive and dominance effects; 2: major gene with additive and dominance effects + polygenes with additive effects; 3: major gene with additive effects + polygenes with additive and dominance effects; 4) major gene with additive effects + polygenes with additive effects; 5) polygenes with additive and dominance effects; 6) polygenes with additive effects; 7) major gene with additive and dominance effects; 8) major gene with additive effects; 9: environmental effect.

The parents were contrasting for soluble solid content. Vedrantaís cultivar shows high content of soluble solids (10.05%) and AC-16 showed low content of soluble solids (4.06%) (Table 1). As for sucrose, the variance estimates in the generations evaluated in this study are in accordance with the expected result: greater variances of segregating populations (F_2 and backcrosses), being the F_2 generation variance superior when compared with the others (Table 1). The variation observed in Vedrantaís parent was superior to the one observed in AC-16 (Table 1).

The estimates of parent Vedrantaís ranged from low values (9%) to high values (12%), whereas the parent with

low sucrose accumulation (AC-16) presented a narrow range of values between 3.0 and 5.0% (Figure 2). The F_1 generation showed amplitude ranging from 6.0 to 10.0%. The authors verified wide range of distribution in F_2 generation, from 3.0 to 11.0%. The distribution of F_2 generation showed a tendency towards symmetry. The variation in backcross generation BC_1 was superior to the one verified for backcross generation BC_2 (Table 1, Figure 2).

Additive variance was higher than dominance variance, therefore estimates of narrow-sense heritability were lower than broad-sense heritability (Table 1). The estimate of narrow-sense

heritability (41.23%) was reduced, indicating, as for sucrose, a strong environmental influence. Few estimates of narrow-sense heritability in melon were observed, Melo *et al.* (2011) obtained an estimate of less than 20%. For broad-sense heritabilities, estimates varied from 0.23 to 0.75 (Kalb & Davis, 1984; Burger *et al.*, 2002; Melo *et al.*, 2011; Akrami & Arzani, 2019). We highlight that the heritability values vary according to the type of population, the estimation method and the environment, which justifies the differences found in the literature.

The average degree of dominance was 1.15, showing the presence of dominance for soluble solids content and number of loci involved in the inheritance of this trait close to four (Table 2). Melo *et al.* (2011), evaluating the F_2 generation and the backcrosses of the population generated by an “inodorus” lineage of the Honey Dew type, with a high content of soluble solids and an “acidulus” lineage with a low content of soluble solids, estimated 28 loci involved in the inheritance of soluble solids in melon and average degree of dominance 1.54. Pereira *et al.* (2018) identified six QTLs influencing the soluble solids content in progeny from the cross between two commercial cultivars: Pele de Sapó (inodorus) and Vedrantaís (cantaloupensis).

For soluble solids, the additive-dominant model was more complex since it involved the presence of additive, dominance and epistatic effects (additive x additive and dominant x dominant) (Table 1). The inheritance study with genetic models using maximum likelihood identified the presence of a major-effect gene with additive and dominant effects when testing the hypothesis of comparison of models 1 and 5 (Table 2). The test between models 1 and 7, which confronts the existence of a major gene + polygenes with only a major-effect gene, was significant, evidencing the presence of polygenes in controlling this trait.

The inheritance of the soluble solid content is controversial among authors. Pouyesh *et al.* (2017) found a predominance of additive effects;

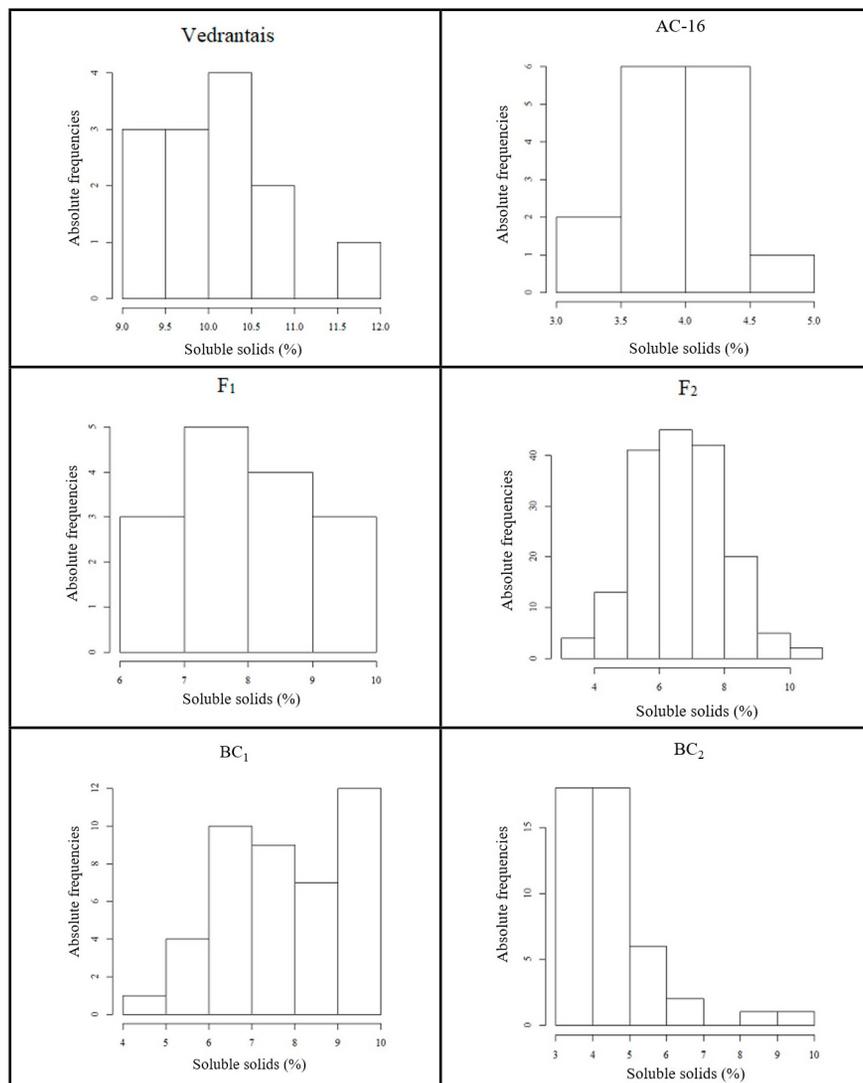


Figure 2. Distribution of absolute frequencies of soluble solids in melon obtained from Vedrantaís x AC-16 crossing, parents, F_1 generation and segregating generations (F_2 and backcrossing). Mossoró, UFERSA, 2021.

Shashikumar & Pitchaimuthu (2016) and Akrami & Arzani (2019) verified additive and dominance effects involved in the inheritance of the trait. No articles were found showing the participation of epistasis in the inheritance of soluble solids in melons. Discordant reports in literature can be explained by the different parents involved in the studies. The segregating population of each cross is a function of the background of the parents, that is, of the constituent alleles of each one of them. In addition, environmental variations are remarkable in the case of traits heavily influenced by the environment.

To perform the crossing technique in this study, the best strategy would be to use a recurrent selection program in order to increase the frequency of favorable alleles continuously, until reaching a satisfactory level of soluble solids. This breeding process is time consuming and demands higher effort, furthermore, the breeder also needs to be more careful. Families with half-siblings and even inbred families could be used. The intention is to carry out the population improvement and then select lines from the improved population, as the probability of extracting lines with higher frequency of favorable alleles is greater.

Given the results above, we can conclude that inheritance of sucrose content involves a major effect gene with additive and dominance effects associated with polygenes with additive effects. We understand that inheritance of soluble solids is determined by a major gene with additive and dominance effects associated with polygenes with additive effects and the presence of epistasis.

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