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Inheritance of beta-carotene content in melon

Abstract – The objective of this work was to determine the inheritance of beta-carotene content in melon (*Cucumis melo*). The AC-16 accession (*Cucumis melo* subsp. *melo* var. *acidulus*) – with a low beta-carotene content and white mesocarp – was crossed with the Vedrantais cultivar (*C. melo* subsp. *melo* var. *cantalupensis*) – with a high beta-carotene content and salmon colored mesocarp –, to obtain the F_1, F_2, BC_1, and BC_2 generations. The AC-16 and 'Vedrantais' parents, the F_1 and F_2 generations, and the BC_1 and BC_2 backcrosses of each parent were evaluated. The quantification of beta-carotene was carried out in a high-performance liquid chromatography system. Mean components related to the additive and dominance effects, additive and dominance variances, and heritability were estimated. The beta-carotene content was high in 'Vedrantais' (17.78 µg g^{-1}) and low in AC-16 (0.34 µg g^{-1}). The following results were observed: additive and dominance effects on the genetic control of the character, incomplete character dominance, estimated number of loci close to two, greater variance for segregating populations (F_2 and backcrosses), and heritability values in the broad (87.75%) and narrow (64.19%) senses. The beta-carotene content in melon is controlled by a major effect gene, with additive and dominance effects associated with polygenes with additive effects.

Index terms: *Cucumis melo*, plant breeding, polygenes, quality.

Herança do teor de betacaroteno em melão

Resumo – O objetivo deste trabalho foi determinar a herança do teor de betacaroteno em melão (*Cucumis melo*). O acesso AC-16 (*Cucumis melo* subsp. *melo* var. *acidulus*) – com baixo teor de betacaroteno e mesocarpo branco – foi cruzado com a cultivar Vedrantais (*C. melo* subsp. *melo* var. *cantalupensis*) – com alto teor de betacaroteno e mesocarpo de cor salmão –, para obtenção das gerações F_1, F_2, RC_1 e RC_2. Avaliaram-se os genitores AC-16 e 'Vedrantais', as gerações F_1 e F_2, e os retrocruzamentos de cada genitor RC_1 e RC_2. A quantificação do betacaroteno foi realizada em sistema de cromatografia líquida de alto desempenho. Foram estimados os componentes de média relacionados aos efeitos aditivos e de dominância, as variâncias aditiva e de dominância e a herdabilidade. O teor de betacaroteno foi alto (17,78 µg g^{-1}) em 'Vedrantais' e baixo em AC-16 (0,34 µg g^{-1}). Observaram-se os seguintes resultados: efeito aditivo e de dominância no controle genético do caráter, dominância de caráter incompleta, número estimado de loci próximo de dois, maior variância para populações segregantes (F_2 e retrocruzamentos), e valores de herdabilidade nos sentidos amplo (87,75%) e restrito (64,19%). O teor de betacaroteno em melão é controlado por um gene de efeito maior, com efeitos aditivos e de dominância associados a poligenes com efeitos aditivos.

Termos para indexação: *Cucumis melo*, melhoramento vegetal, poligenes, qualidade.

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Introduction

The Northeastern Semiarid Region is the major producer and exporter of melon in Brazil. The national production is concentrated in the state of Ceará, in the Vale do Jaguaribe, and in the state of Rio Grande do Norte, in the Mossoró-Açu Agricultural Pole. These states are responsible for more than 99% of the national production and exports of melon (IBGE, 2022). The edaphoclimatic conditions and the high technology used are the main reasons for the productive success of this species in the Northeast (Figueirêdo et al., 2017).

There is a wide variation in the germplasm of melon (*Cucumis melo* L., Cucurbitaceae) for its mesocarp color, which is determined by a combination of pigments such as chlorophylls and carotenoids (Abo Sedera et al., 2016; Gur et al., 2017). One of the first works on the inheritance of mesocarp color in melon was developed by Hughes (1948), who verified the presence of the genes named *gf* and *wf* which influence the green and white mesocarp colors, respectively. Subsequently, Clayberg (1992) reported that the orange color is dominant over the green and white colors. The main pigment accumulated in the orange or salmon mesocarp in melon is beta-carotene, a precursor substance of vitamin A with antioxidant potential (Chayut et al., 2017). Currently, there is a growing demand for the biofortification of vegetables for human consumption, aiming at improving their quality and helping to prevent and reduce the risk of diseases (Bae et al., 2019; Gómez-García et al., 2020). In this sense, melon breeding programs have sought productive cultivars with excellent fruit quality and higher beta-carotene content.

In order to improve a characteristic, it is important to know its genetic inheritance. This knowledge helps the plant breeder in the decision-making on which strategy is most appropriate to be used to obtain fruit desirable characteristics. In plant inheritance studies, the genetic effects (additive and non-additive), the average degree of dominance, and the number of genes or loci involved are commonly estimated (Cruz et al., 2014).

Some studies have shown a complex inheritance for the accumulation of beta-carotene in melon (Monforte et al., 2004; Cuevas et al., 2010). Other studies identified quantitative trait loci (QTLs) related to that characteristic (Monforte et al., 2004; Cuevas et al., 2009; Diaz et al., 2011; Perpiñá et al., 2016). Nevertheless, studies on the inheritance of beta-carotene content in melon are rare. Thus, research which seek a better understanding of the genetic mechanism involved in the accumulation of beta-carotene in melon mesocarp in Brazilian conditions are still necessary.

The objective of this work was to determine the inheritance of beta-carotene accumulation in melon.

Materials and Methods

The experiment was carried out in 2015, from planting date on May 30th to harvest date on August 4th, at the Fazenda Experimental Rafael Fernandes, located in Lagoinha district (5°03'37"S, 37°23'50"W, at 72 m altitude), rural area of the municipality of Mossoró, in the state of Rio Grande do Norte (RN), Brazil. The soil of the experimental area is classified as Latossolo Vermelho-Amarelo, according to the Brazilian Soil Classification System (Santos et al., 2018), i.e., Ferralsols, with a sandy loam texture. The climate of the region is typified as Bswh, that is, semi-arid tropical, very hot and dry, according to the Köppen-Geiger's classification, with a rainy season in the summer, extending to the autumn.

Vedrantais cultivar and the melo accession AC-16 were used as parents. Vedrantais is a French cultivar, belonging to the variety *cantalupensis*, developed by the Vilmorin Seed Company. This cultivar has round-shaped Charentais-type fruit (IF = 1.0), orange mesocarp color, high levels of sucrose and soluble solids (> 12º Brix). AC-16 accession belongs to the variety *acidulus*, shows a white mesocarp, a yellow exocarp and low levels of sucrose and soluble solids (< 4º Brix). The crossing these parents resulted in the branch generation F_1 and, subsequently, the generation F_2 and the backcrosses (BC_1 and BC_2). One fruit per plant was collected for analysis, discarding the border fruit.

An experimental design in randomized complete blocks was carried out with three replicates. The evaluated generations were the parents (AC-16 and 'Vedrantais'), the F_1 and F_2, and the backcrosses from each parent (BC_1 and BC_2). Due to the genetic variability present in each generation, the plots consisted of the following numbers of plants: 13 ('Vedrantais'), 15 (AC-16 and F_1), 172 (F_2), 43 (BC_1), and 46 (BC_2).

The preparation of the area performed by plowing and harrowing, with subsequent formation of 0.2 m high and 0.6 m wide ridges. The mineral nutrition of the crop was held by fertigation on the basis of the chemical analysis of the soil. Seeding was performed in expanded polystyrene trays with 200 cells, filled with a commercial substrate (Polifértil Nutrição Importação e Exportação, Uberaba, MG, Brazil). The seedlings were transplanted when they showed the first fully expanded true leaf. The experimental plot consisted of a 3.0 m long row, 2.0 m spacing between rows, and 0.3 m between pits, with one plant per pit. A localized drip irrigation system was used, with 1.5 L h^{-1} average flow rate, with one emitter per plant. The phytosanitary control and other cultural treatments were conducted in accordance with the technical recommendations adopted in the region for melon tree (Figueirêdo et al., 2017).

For the qualitative analysis of beta-carotene, the company's standard Sigma-Aldrich with 95% purity was used. Methanol, acetonitrile, and ethyl acetate were used to perform the chromatographic analyses. Melon pulp used to quantify beta-carotene was homogenized and stored at -20°C. Beta-carotene was extracted in a 15 mL Falcon tube, protected from light, by adding 3 g of pulp and 3 mL of isopropyl alcohol. This mixture was homogenized in a vortex and centrifuged (10,000 RCF) for 5 min at 4°C. Supernatant was collected, and the precipitate was reextracted with 6 mL acetone, and then reextracted with 3 mL ethyl acetate. At each reextraction, the mixture was homogenized in a vortex (Shanghai Hannuo Instrument Co. Ltd., XH-B, Shanghai, China) and centrifuged (Shanghai Surgical Instrument Factory, 80-2, Shanghai, China) at 10,000 RCF for 5 min at 4°C.

Supernatants were pooled and concentrated in an evaporator (Sigma Aldrich, Laborota 4003, Saint Louis, MO, USA), at 30°C, 0.09 MPa, protected from light. After the evaporation of the solvents, beta-carotene was resuspended in 2 mL ethyl acetate and filtered through 0.45 μm membrane of polyvinylidene fluoride (PVDF). The quantification of beta-carotene was performed in a high-performance liquid chromatography system (HP 1090, Hewlett-Packard, Orsay, France). The mobile phase was formed by methanol, ethyl acetate and acetonitrile, at 2:1:1 ratio; with 3 μL injection volume, 0.3 mL min^{-1} flow rate, 40°C column temperature, and 450 nm maximum wavelength.

To perform the genetic parameter estimations and the adjustment of the additive-dominant model, the mixed model method proposed by Piepho & Möhring (2010) was used. The test implementation of the additive-dominant model was performed using the method proposed by Kearsey & Pooni (1996), according to the following expression:

$$\mu_i = m + [a]x_{i1} + [d]x_{i2} + \lambda_i,$$

in which: μ_i is the value of the i^{th} generation under the additive-dominant model i = 1, G; m is the intercept; [a] is the additive effect; [d] is the dominance effect; x_{i1} and x_{i2} are the coefficients of additive and dominance effects, respectively; λ_i is the nonadjustment effect.

As the generations were evaluated in a randomized complete block design, the model for plant k, 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 error of the plot p_{ij} and the plant error e_{ijk} have normal distribution with zero average and variances σ^2_p and σ^2_e, respectively. The genetic variation within generation was modeled by the genetic effect g_{ijk} at the plant-specific level. The SAS code used for all analyses was adapted from Piepho & Möhring (2010). The adjustment of the genetic variance structure was performed by the MIXED procedure in the SAS Version 9.2 program (SAS Institute Inc., Cary, NC, USA).

According to the method proposed by Piepho & Möhring (2010), the average components related to the additive [a] and dominance [d] effects were estimated, as well as the variances of addition, dominance, and heritability. The average degree of dominance (ADD) and the minimum number of genes (η) involved in the expression of the character were also estimated.

The genetic models were tested using the maximum likelihood in mixtures of normal density functions as described by Silva (2003). The distributions for each population was evaluated as follows:

P_1: N (μ – [a] – A, σ^2); P_2: N (μ – [a] + A, σ^2);

F_1: N (μ – [d] – D, σ^2);

F_2: N/4 (μ + [d]/2 – A, $\sigma^2 + V_A + V_D$) + N/2 (μ + [d]/2 + D,

$\sigma^2 + V_A + V_D) + N/4 (\mu + [d]/2 + A, \sigma^2 + V_A + V_D)$;

BC_1: $N/2 (\mu + [a]/2 + [d]/2 - A, \sigma^2 + V_A/2 + V_D - S_{AD}) + N/2 (\mu - [a]/2 + [d]/2 + D, \sigma^2 + V_A/2 - S_{AD})$;

BC_2: $N/2 (\mu + [a]/2 + [d]/2 + A, \sigma^2 + V_A/2 + V_D + S_{AD}) + N/2 (\mu + [a]/2 + [d]/2 + D, \sigma^2 + V_A/2 + S_{AD})$;

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

In order to complement the study of classical inheritance carried out by the components of average and variances, another study was conducted with models that consider the effect of a major gene and polygenes (Table 1). During the construction of the genetic model, the most general model was considered to be the one with the existence of a gene with a greater effect plus polygenes with additive and dominance effects and equal environmental variances, in all generations. Independent genes were also admitted (both polygenes and genes with greater effect). From the likelihood functions for each model, it was possible to compose tests of interest, considering different hypotheses. The tests were performed using the statistical software Monogen v.0.1 (Silva, 2003).

Table 1. Inheritance models used by the Monogen v.0.1 program (Silva, 2003).

Model	Parameter
1. Major gene with additive and dominance effects + polygenes with additive and dominance effects	μ, A, D, [a], [d], V_A, V_D, S_{AD}, σ^2
2. Major gene with additive and dominance effects + polygenes with additive effects	μ, A, D, [a], V_A, σ^2
3. Major gene with additive effect + polygenes with additive and dominance effects	μ, A, [a], [d], V_A, V_D, S_{AD}, σ^2
4. Major gene with additive effect + polygenes with additive effect	μ, A, [a], V_A, σ^2
5. Polygenes with additive and dominance effects	μ, [a], [d], V_A, V_D, S_{AD}, σ^2
6. Polygenes with additive effect	μ, [a], V_A, σ^2
7. Major gene with additive and dominance effects	μ, A, D, σ^2
8. Major gene with additive effect	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], polygenic additive component; [d], polygenic dominance component; V_A, additive variance; V_D, variance attributed to dominance deviations of polygenic effects; S_{AD}, variance component related to the products of polygenic additive effects by the polygenic dominance effects; σ^2, environmental variance.

Results and Discussion

Regarding the mesocarp color of the parents, 'Vedrantais' – with orange mesocarp – showed a high content of beta-carotene (17.78 μg g^{-1}), while the parent AC-16 – with white mesocarp – showed very low content of beta-carotene (0.34 μg g^{-1}), which confirms the contrast between parents, indicating that their choice to obtain segregating generations was adequate (Figure 1). In a study on the inheritance of beta-carotene content and its association with the mesocarp color in melon, Cuevas et al. (2010) used the American line 'Top Mark' (orange mesocarp) and the Chinese line 'Q 3-2-2' (white mesocarp) as parents. The beta-carotene content levels in these parents were 6.56 and 0.15 μg g^{-1}, respectively, which are lower values than those observed in the present work. It is underlined that beta-carotene content is influenced by the genotype, the stage of fruit development and environmental conditions (Sharma et al., 2020; Singh et al., 2021).

Clayberg (1992) checked epistasis between the genes *gf* and *wf* for the genotypic combinations (*wf* $^+$*_/gf* $^+$*_*) and (*wf* $^+$*_/gfgf*) to produce fruit with orange mesocarp, as well as for combinations (*wfwf / gf* $^+$*_*) to produce fruit with white mesocarp, and the combination (*wfwf/gfgf*) which is responsible for the green color. Thus, the parents 'Vedrantais' and AC-16 are (*wf* $^+$ *wf* $^+$*/gfgf*) and (*wfwf /gf* $^+$ *gf* $^+$), respectively.

The three parameters ([m], [a], and [d]) which constitute the average components of the additive-dominant model were significant, indicating the presence of additive and dominance effects in the genetic control of the character (Table 2). The negative value of [d] is explained by the fact that the dominance occurs towards the phenotypic manifestation of lower character magnitude, that is, the occurrence of lower beta-carotene content.

The average degree of dominance, obtained from the variance components, was lower than the

unity (0.86), indicating the presence of incomplete dominance. The number of estimated loci was close to two (Table 2). Cuevas et al. (2010) estimated four loci in the genetic control of beta-carotene content in the cross between the Chinese lineage 'Q 3-2-2' (white mesocarp) and the line 'Top Mark' (salmon mesocarp). The differences basically occur due to the parents used and the environmental conditions.

Regarding the variance components, the estimates are in line with the expectations: greater variances of segregating populations (F_2 and backcrosses), in which the variance of the generation F_2 was greater than the others (Table 2). The additive variance was greater than the dominance variance. According to Cruz et al. (2014), the additive variance is one of the determining factors of covariance between relatives, and its magnitude is indicative of the relationship between the selection unit and the improved unit.

Heritability values in the broad and narrow senses were 87.75 and 64.19%, respectively (Table 2). The narrow-sense heritability was, as expected, lower than the broad-sense heritability, since the former contains only the contribution of additive genetic variance. In this case, the greater the additive variance estimate, the greater the heritability in the narrow sense. The estimates obtained in this work are an indication of a favorable condition for selection because most of the phenotypic variation is due to genetic causes.

Differences were found between the model 1 and the others (Table 3), indicating that the model 1 should be used to test the effect of greater gene and polygenes. When comparing models 1 and 5, the presence of the greater gene with additive and dominance effects was tested, to check their presence in the genetic control of beta-carotene content in melon. When comparing models 1 and 7, the presence of polygenes with additive effects and dominance was tested. In this case, the presence of polygenes in the inheritance of beta-carotene content in melon was also checked.

Regarding the comparison of models which consider the effect of a major gene and polygenes (Table 3), it can be inferred that the inheritance of beta-carotene content in melon is complex, as observed by Monforte et al. (2004) and Cuevas et al. (2010). According to Monforte et al. (2004), the production of beta-carotene (orange mesocarp) is independent of the genes related to green (*gf*) and white (*wf*) colors. In a study with microsatellite molecular markers in the cross 'Shongwan Charmi PI 161375' (green mesocarp) and a line type 'Frog Skin' (white mesocarp), the same authors identified three QTLs associated with the orange color. The authors reported that the orange color is associated with the accumulation of beta-carotene.

Vedrantais (17.78 μg g^{-1}) AC-16 (0.34 μg g^{-1})

Figure 1. Mesocarp color and average value of beta-carotene content in parents ('Vedrantais' x AC-16) used to obtain segregating populations. Photos by Juliana Maria Costa da Silva

As checked by Cuevas et al. (2010), the quantitative variation of beta-carotene content is strictly associated with the variation of orange mesocarp tones. Thus, there must be genes related to the production of beta-carotene and polygenes which affect this character content in melon. Perpiñá et al. (2016) identified a high-effect QTL on chromosome 9 from studies with introgression lines derived from the cross between 'Vedrantais' and 'Ginsen-makuwa', an oriental cultivar. Ramamurthy & Water (2015), when studying the F_2 generation from the cross between melons of the varieties *flexuosus* and *cantalupensis*, detected two QTLs influencing the pulp color, both co-located with QTLs already registered for the concentration of beta-carotene. By this result, the pulp color can serve as a selection index for the concentration of beta-carotene in melon.

Tzuri et al. (2015) identified the gene *CmOr*, an allele previously described as *gf* gene, as responsible for the orange color of melon mesocarp. The authors identified salmon *CmOr* haplotypes capable of inducing beta-carotene accumulation in melon, while the green/white haplotypes do not act this way. Therefore, the accumulation of beta-carotene is closely related to the polymorphism of the *CmOr* (Monforte et al., 2014; Chayut et al., 2015; Feder et al., 2015; Lian et al., 2021). An identified SNP marker for *CmOr* may allow the use of new genomic tools to understand the accumulation of beta-carotene and allow to obtain biofortified cultivars.

Due to the complexity of inheritance, the genetic improvement for a high content of beta-carotene in melon can be done by means of backcrossing for the introgression of the gene with greater effect and, also, by methods that seek the gradual accumulation of that pigment, such as recurrent selection. Due

Table 2. Estimates of average and variance components of beta-carotene content in melon (*Cucumis melo*) obtained in the inheritance study (additive-dominant model) from generations derived from the cross 'Vedrantais' x AC-16.

Source of variation	DF	Average (µg g^{-1})		Variance	
		Estimative	F (Wald)	Parameter	Estimative
Block	2	-	0.70^{ns}	σ^2_A	47.81
[a]	1	8.72	128.72**	σ^2_D	17.55
[d]	1	-1.57	4.68*	σ^2_p	3.24
[aa]		-	-	σ^2_e	9.12
[dd]		-	-	h^2_n (%)	64.19
[ad]		-	-	h^2_b (%)	87.75
η		1.34		ADD	0.86
Generation		Average		Variance	
P_1-'Vedrantais'		17.78		6.05	
P_2 (AC-16)		0.34		0.02	
F_1		14.78		21.30	
F_2		8.28		74.49	
BC_1		15.26		67.29	
BC_2		1.27		33.88	

DF, degree of freedom; [a], additive model; [d], dominant model; [aa], additive-additive model; [dd], dominant-dominant model; [ad], additive-dominant model; η, number of loci; σ^2_A, additive variance; σ^2_D, dominance variance; σ^2_p, plot variance; σ^2_e, error variance; h^2_n, heritability in narrow sense; h^2_b, heritability in broad sense; ADD, average degree of dominance. ^{ns}Nonsignificant. **, *Significant at 1% and 5% probability, respectively, by Wald's F-test.

Table 3. Hypothesis tests of hierarchical genetic models obtained in the study of the inheritance of beta-carotene contents in melon (*Cucumis melo*), from generations derived from the cross 'Vedrantais' x AC-16.

Test	DF	χ^2_c	Probability
1 vs 2	3	176.09	0.0000
1 vs 3	1	148.62	0.0000
1 vs 4	4	178.89	0.0000
1 vs 5	5	169.74	0.0000
1 vs 6	6	190.24	0.0000
1 vs 7	5	152.40	0.0000
1 vs 8	6	182.05	0.0000
1 vs 9	7	261.78	0.0000
2 vs 4	1	2.84	0.0940
2 vs 6	2	14.16	0.0008
2 vs 7	2	-	-
2 vs 8	3	5.97	0.1132
2 vs 9	4	85.70	0.0000
3 vs 5	1	21.12	0.0000
3 vs 6	4	41.62	0.0000
3 vs 8	5	33.43	0.0000
3 vs 9	6	113.16	0.0000
4 vs 6	1	11.35	0.0007
4 vs 8	2	3.16	0.2057
4 vs 9	3	82.90	0.0000
5 vs 6	3	20.51	0.0000
5 vs 9	5	92.05	0.0000
6 vs 9	2	71.54	0.0000
7 vs 8	1	29.65	0.0000
7 vs 9	2	109.38	0.0000
8 vs 9	1	176.09	0.0000

DF, degree of freedom; χ^2_c, chi-square. $^{(-)}$Value not obtained due to convergence problems.

to the presence of additive and dominance effects, the exploration of heterosis is recommended for this character. In fact, currently, melon cultivars around the world are simple hybrids due to their homogeneity and the presence of heterosis in characteristics of interest.

Conclusion

The inheritance of beta-carotene content in melon is complex, with the presence of a greater effect gene, and additive effects and dominance associated with polygenes with additive effects.

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