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Genetic inheritance of pulp color, cracking and netting in melon fruits

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Abstract: The aim of this study was to investigate the genetic inheritance of pulp color, cracking, and netting in melon fruits in crosses of two non-sweet melon accessions with a long shelf-life sweet melon. Two trials were conducted under field conditions at the Didactic Orchard of the Federal Rural University of the Semiarid Region , in the municipality of Mossoró-RN, Brazil, from March to June 2021. The populations used originated from crosses between AC-02 (Momordica Group, white pulp, cracked fruit, not netted) and I-180 (Dudaim Group; white fruit, not netted) with Timeless Gold (Cantalupensis Group; salmon pulp, netted). Chi-square (X^2) was used to analyze phenotypic segregation frequencies of F2 populations for pulp color (salmon, green, or white), cracking (present or absent), and pericarp texture (smooth or netted), at 5% probability level. Genetic inheritance of pulp color was controlled by an epistatic interaction of dominance between two genes. Fruit cracking involves the gene interaction of two double recessive epistatic genes. Pericarp netting was under dominant monogenic control.

Index terms: *Cucumis melo*, pulp color, fruit cracking, genetic control, netting.

Herança da cor da polpa, cracking e rendilhamento em meloeiro

Resumo: O objetivo deste estudo foi investigar a herança genética da cor da polpa, rachaduras e rendilhamento em frutos de melão em cruzamentos de dois genótipos de melão não-doce com um melão doce e longa vida útil. Dois ensaios foram realizados em condições de campo no Pomar Didático da Universidade Federal Rural do Semiárido, no município de Mossoró-RN, Brasil, entre março e junho de 2021. As populações utilizadas foram provenientes de cruzamentos entre AC-02 (Grupo Momordica, polpa branca, frutos rachados, não reticulados) e I-180 (Grupo Dudaim; frutos brancos, não rendilhados) com Timeless Gold (Grupo Cantalupensis; polpa salmão, rendilhado). O teste de Qui-quadrado (X^2) foi utilizado para analisar as frequências de segregação fenotípica das popula-

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ções F2, segregando pela cor da polpa (salmão, verde ou branco), rachadura (presente ou ausente) e textura do pericarpo (lisa ou reticulada), utilizando um nível de 5% de probabilidade. A herança da cor da polpa é controlada por uma interação epistática de dominância entre dois genes. O controle genético das rachaduras envolve a interação gênica de dois genes do tipo epistasia dupla recessiva. O rendilhamento do pericarpo possui controle monogênico dominante.

Termos para indexação: *Cucumis melo*, cor da polpa, rachadura no fruto, controle genético, rendilhamento.

Introduction

Melon (*Cucumis melo* L.) is one of the main Brazilian exported fresh fruit. In 2021, the country exported 257,902 tons of cantaloupe melon, an increase of 9.2% compared to the previous year. Among the main importers are the European Community, United States, various Asian countries and Chile. Regarding the evolution of the cultivation area, in the period from 1970 to 2021, the area cultivated with melon increased from 4,777 ha to 23,000 ha, which represented an increase of 380%. In terms of productivity, it raised from 1.09 Mg ha^{-1} in 1970 to 25.9 Mg ha^{-1}, a substantial increase of 2,276% (BENNO et al., 2022).

The increase in productivity resulted from the efforts of research institutions dedicated to developing new production technologies. Another essential factor was the new and rigorous quality standards required by the national and international markets, in which the melon growing activity is more involved. This has led producers to choose cultivars with higher productivity and greater resistance to diseases and pests, in addition to using different types of melon cultivars (SALVIANO et al., 2017).

Melon classification has a long and confusing history (PITRAT et al., 2000), which currently recognizes the great horticultural melon diversity using nomenclature for cultivated plants (BRICKELL et al., 2009). Burger et al. (2010) revised melon classification within the two recognized subspecies: agrestis and melo. Pitrat (2016) more recently revised the melon diversity disregarding the two subspecies but considering features of botanical classification with regard to italicization of group and sub-group names. McCreight (2017) refined the horticultural melon classification.

AC-02 melon accession (Momordica Group), belonging to the active germplasm collection of the Federal Rural University of the Semiarid Region (UFERSA), has been highlighted in studies associated with its resistance to powdery mildew (*Podosphaera xanthii*) (NUNES et al., 2017). It does not produce sweet type fruits, reducing its acceptance in many major import markets. Another accession from the active germplasm collection of UFERSA with potential for use in breeding programs is I-180 (Dudaim Group), which is known as Tiger Melon, due to the presence of yellow and orange stripes resembling a tiger. Its small size, and low soluble solids (SS) content also impairs its commercialization. The Cantaloupe type melon is aromatic, has salmon-colored pulp and higher SS content (>=10%), and does not show cracks when ripe.

There has been a growing interest among producers in diversifying the products offered to the national and international markets through the introduction of different melon genotypes, especially the Cantaloupe and Gália lace market types, (NUNES et al., 2004). In this sense, the study of the genetic control of traits of interest is fundamental for breeding programs (SANTOS et al., 2015).

Knowing the genetic inheritance of important horticultural traits is of utmost importance for initiating a breeding program. Understanding the number of genes involved, as well as their modes of interaction, allows for determining the criteria and selection intensity , the method of handling segregating populations, and breeding methods to obtain a lineage that contains the genetic background of the recurrent parent used but with the genes of interest from the donor parent. Thus, these studies guide breeders in the process of introgressing alleles of interest from the sources into commercial parents (MACIEL; SILVA, 2008).

Information about the genetic inheritance of pulp color, fruit rejection and yield are important for defining strategies in breeding programs, being necessary in the initial stages. Studies have been carried out with the objective of evaluating the genetic inheritance of melon pulp color (HUGHES, 1948; IMAM et al., 1972; CLAYBERG 1992), which identified the presence of two genes controlling this characteristic. In contrast, Fukino et al. (2008) observed that the genetic inheritance of melon pulp color was controlled by a single dominant gene. For the genetic inheritance of fruit crack, Qi et al. (2015) point to the presence of two main genes with additive and dominance effects along with epistasis. For the presence of netting in the fruit peel, two genes were found (RAMASWAMY at al., 1977).

Some momordica Group accessions exhibit fruit cracking under all environmental conditions, indicating the presence of genetic effects (DHILLON et al., 2007; DHILLON et al., 2012). However, there is limited information on the genetic control of fruit cracking in melons. The same applies to the pericarp netting characteristic.

In view of the above, the aim of this work was to study the genetic inheritance of pulp color, cracking and netting in melon fruits in crosses of Momordica and Dudaim accessions with long shelf-life Cantalupensis types, specifically, ‘Timeless Gold’ in order to determine the genetic control of these characteristics.

Material and methods

Location

Two trials were conducted under field conditions at the Didactic Orchard of the Federal Rural University of the Semiarid Region (UFERSA) in the municipality of Mossoró-RN from March to June 2021. The average local temperature was 31.5 °C, and the relative humidity was 52.6%. According to the Köppen classification, the climate is categorized as BSwh’, being hot and dry with a rainy season in the summer, extending into the fall (CARMO FILHO; OLIVEIRA, 1995). The municipality is located at 5º12’48’’ South Latitude; 37º18’44’’ West Longitude and altitude of 37 m above sea level.

Obtaining populations

Two populations were produced. The first was generated by the crossing between the AC-02 accession (receptor pollen) and the ‘Timeless Gold’ cultivar (donor pollen) in September 2019. An F2 population was produced from the self-fertilization of the F1 generation in January 2020. The second population was produced by the crossing between the I-180 accession (receptor pollen) and ‘Timeless Gold’ (donor pollen), and F2 was obtained by self-fertilization of the F1 generation at the same time as the first population.

AC-02 (Figure 1a) belongs to the Momordica Group and is of Indian origin (DANTAS et al., 2015). It features elongated fruits with white pulp color and, low soluble solids (SS) content (~5%), showing cracks when ripe. The accession was collected in a melon production area located in the municipality of Mossoró-RN. I-180 (Figure 1b) belongs to the Dudaim Group, produces small fruits, with low soluble solids (SS) content (~6%), and yellow and red stripes resembling rust. The mesocarp has creamy texture, white color and small seeds. It is believed that the yellow and orange tiger stripes are the source of its name (LUVGARDEN, 2022). ‘Timeless Gold’ (TG) (Figure 1c), is a commercial hybrid belonging to the cantaloupensis Group developed for long post-harvest shelf life. In addition to its wide adaptation to growing regions, it has high productivity, full netting, and fruits with high soluble solids (SS) content (>= 10 %).

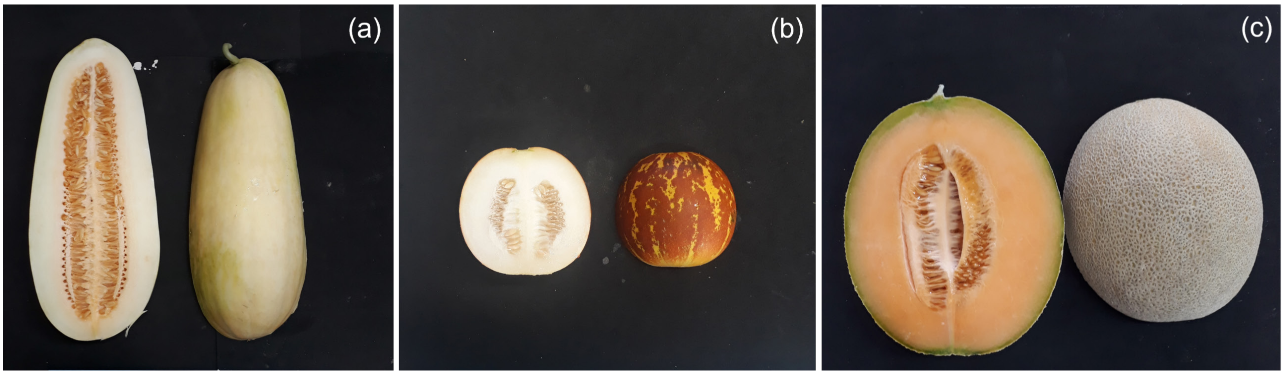

Figure 1. Fruits of genotypes used in the study of the genetic inheritance of pulp color, pericarp texture and cracking. (a) AC-02; (b) I-180 and (c) Timeless Gold (TG).

Genetic inheritance Study

The seeds from populations generated by crosses (F1, F2, and parents) were sown in polyethylene trays filled with substrate (Tropstrato®). Twelve days after sowing, they were transplanted to the field in beds with spacing of 2 m between beds, covered with plastic mulch, and plant spacing of 0.3 m. The classic genetic design was applied, involving these populations. Crop management practices were suggested by Nunes et al. (2004). At the time of harvest, performed 65 days after transplanting, the following characteristics were evaluated: pulp color, considered the predominant one, presence or absence of cracking, and pericarp texture (smooth or netted).

Statistical Analysis

From the frequencies observed in plants of segregating populations defined for pulp color (salmon, green or white), *cracking* (present or absent) and pericarp texture (smooth or netted), the Chi-square (X^2) test was used to analyze the phenotyping data of F2 individuals and test the genetic models in order to describe the genetic inheritance of traits using nominal error of 5% ($\alpha = 0.05$).

Results

Pulp color inheritance

The pulp coloration observed in all AC-02, TG and I-180 fruits were as expected with their original descriptions (white, salmon and white color, respectively), indicating the purity of seeds used (Figure 1).

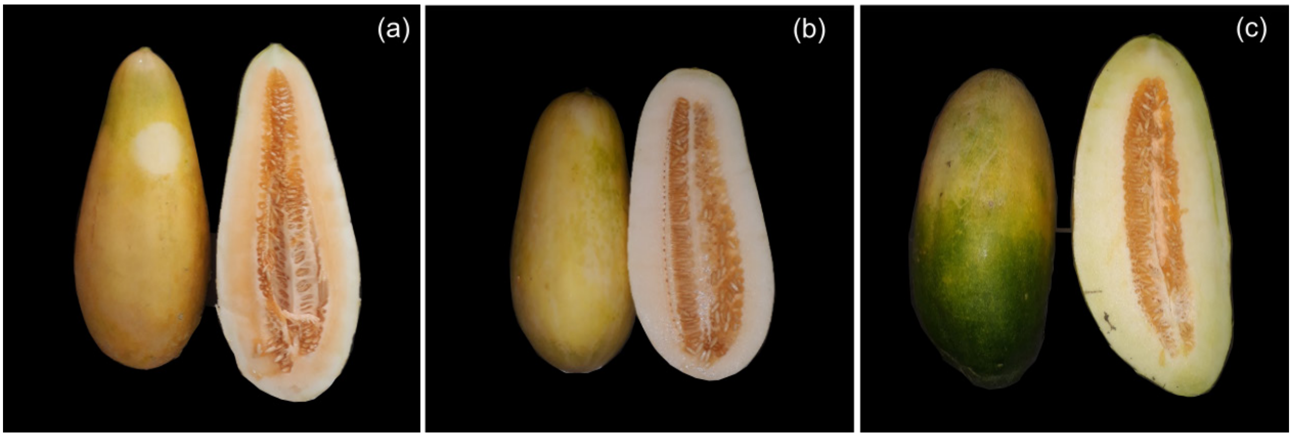

Figure 2. Fruits with pulp colorations found in the F2 AC-02 x Timeless Gold cross: salmon (a), white (b) and green (c).

The F1 generation of both populations produced only fruits with salmon pulp. F2 AC-02 x TG was segregated for flesh color: 133 salmon: 25 white: 9 green (Table 1 and Figure 2). This distribution approximated a phenotypic ratio of 12:3:1 for salmon, white, and green, respectively. Based on these frequencies, a model was suggested to describe the genetic control involved in the inheritance of fruit pulp color in this cross.

The genetic model suggested the expression of two genes with dominant epistatic allelic interaction. In this interaction, the salmon color is dominant in the presence of pulp color, and the white color is dominant over the green color. The chi-square test confirmed this finding (Table 1). The *p*-value ≥ 0.05 indicates that the test was not significant, which means that the observed frequency does not differ from the expected frequency, and any deviations are purely due to chance. Thus, the null hypothesis was accepted, indicating that the genetic inheritance of pulp color in this cross involves two genes with dominant epistasis.

Table 1. Segregation of pulp color from AC-02 and I-180 x 197 Timeless Gold (TG) crosses.

	Generation	Observed segregation			Expected ratio	X^2	p
		Salmon	White	Green			
AC-02 x TG	AC-02 (P1)	0	10	0	0:1:0		
	TG (P2)	10	0	0	1:0:0		
	F1 (P1 X P2)	10	0	0	1:0:0		
	F2 (F1 X F1)	133	25	9	12:3:1	1.950^{ns}	0.377
I-180 x TG	I-180 (P1)	0	10	0	0:1:0		
	TG (P2)	10	0	0	1:0:0		
	F1 (P1 X P2)	10	0	0	1:0:0		
	F2 (F1 X F1)	115	37	13	12:3:1	2.237^{ns}	0.326
	F2 combined	248	62	22	12:3:1	0.080^{ns}	0.961
	F2 homogeneity					4.457	0.108

ns: Non-significant

I-180 x Timeless Gold F1 also exhibited salmon color pulp. The segregated F2 generation exhibited 115 salmon color pulp, 37 white color pulp, and 13 green color pulp (Table 1 and Figure 3), an acceptable fit to the expected phenotypic ratio of 12:3:1 for salmon, white, and green color pulp, respectively, and aligns with what was observed for the AC-02 x Timeless Gold population. These results support the null hypothesis that genetic inheritance of pulp color in these two crosses of diverse melons is conditioned by the epistatic dominance interaction between two genes, as observed in the F2 generation.

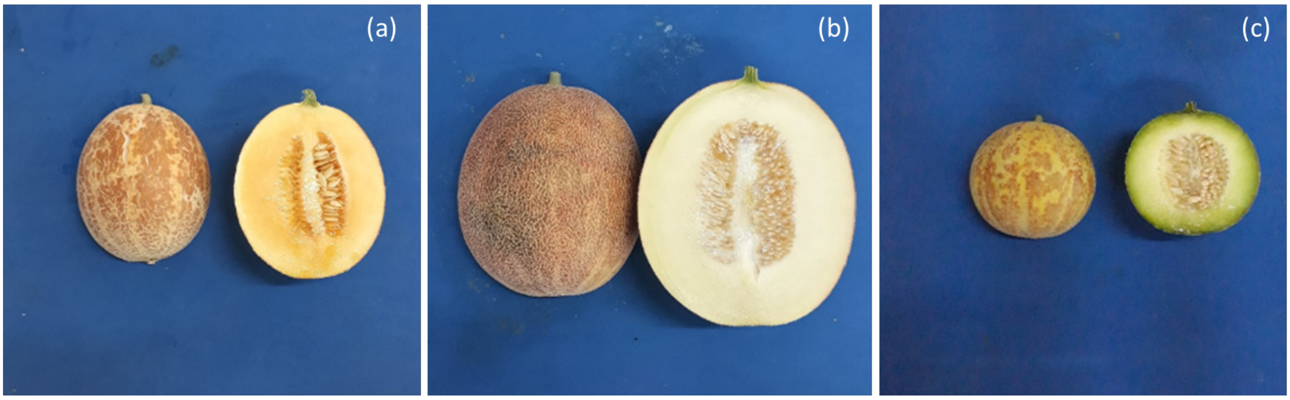

Figure 3. Fruits with different pulp colors observed in the F2 generation of the I-180 x Timeless Gold cross: salmon (a), white (b) and green (c).

Cracking inheritance

All AC-02 fruits exhibited this feature through cracks that extended to more than 50% of their length (Table 2). On the other hand, the Timeless Gold parent, consistent with the Cantalupensis Group did not show cracks. In the F1 generation, all cracked fruits indicated dominance of this trait in this cross.

The F2 generation segregated 95 cracked and 72 individuals without cracks (Table 2). The segregation in this population indicates an expected 9:7 ratio. The proposed model for the genetic inheritance of this characteristic involves the genetic interaction of two genes of the double recessive epistasis type. The X^2 values support this theory (Table 2). In this case, the genetic inheritance would be controlled by two genes, each composed of two alleles, with the epistatic alleles being recessive. The presence of dominant alleles at both loci produces individuals with the presence of cracks.

Table 2. Segregation of pericarp cracking in the AC-02 x Timeless Gold cross.

Progeny	Observed segregation		Expected ratio	X^2	p
	Present	Absent			
AC-02 (P1)	10	0	1:0		
TG (P2)	0	10	0:1		
F1 (P1 X P2)	10	0	1:0		
F2 (F1 X F1)	95	72	9:7	0.024^{ns}	0.876

ns: non-significant

Netting inheritance

Pericarp netting is characteristic of Timeless Gold fruits. No netting was observed in AC-02 or I-180 fruits (Table 3). The F1 of both crosses exhibited netting. Both populations segregated for fruit netting in close approximations to an expected 3 netted: 1 non-netted ratio (Table 3), where a completely dominant allele confers the presence of netting is dominant over the recessive allele that confers absence. This type of inheritance impairs the attainment of smooth fruits in breeding programs involving crossbreeding with melons from the Cantalupensis group.

Table 3. Segregation of pericarp netting in populations from AC-02 x Timeless Gold and I-180 x Timeless Gold crosses.

	Progeny	Observed segregation		Expected ratio	X^2	p
		Present	Absent			
AC-02 x TG	AC-02 (P1)	0	10	1:0		
	TG (P2)	10	0	0:1		
	F1 (P1 X P2)	10	0	1:0		
	F2 (F1 X F1)	130	37	3:1	0.517^{ns}	0.472
I-180 x TG	I-180 (P1)	0	10	1:0		
	TG (P2)	10	0	0:1		
	F1 (P1 X P2)	10	0	1:0		
	F2 (F1 X F1)	132	33	3:1	2.587^{ns}	0.108
	F2 combined	262	70	3:1	2.715^{ns}	0.099
	F2 homogeneity				2.920	0.087

ns: non-significant

Discussion

In dominant epistasis, a dominant allele (*A*) inhibits the expression of the (B) allele. For (*B*) to be expressed, a pair of alleles (*aa*) must be present at another locus. Thus, the Timeless Gold parent showed salmon-colored fruits due to the presence of the dominant allele (*A*). On the other hand, AC-02 and I-180, due to the presence of allele pair the (*aa*), allows the expression of (*B*). In the F1 of both crosses, salmon-colored pulp fruits are observed, since the presence of a dominant allele in Timeless Gold prevents white pulp. In the F2 generation, 12 individuals are expected with genotype *A*___ (salmon), 3 individuals *aa/B_* (white), and 1 individual *aabb* (green).

The initial studies on the genetic inheritance of pulp color were conducted by Hughes (1948) and Imam et al. (1972). They identified the presence of two genes, designated as gf (green fresh) and wf (white fresh), determining green and white colors, respectively. Clayberg (1992) reported that salmon color is dominant over both green and white colors. Additionally, the author reported epistasis between gf and wf, so that genotypic combinations result in fruits with salmon, white, and green pulp color. Salmon is dominant among these colors, and white color is dominant over green color. These findings align with results observed in AC-02 x Timeless Gold and I-180 x Timeless Gold crosses.

However, Fukino et al. (2008) observed that melon pulp color was controlled by a single dominant gene in an inheritance analysis involving the PMAR No. 5 (salmon pulp color) x Harukei No. 3 (green pulp color) cross. In the F1 generation, all fruits had salmon mesocarp, and in the F2 generation, only melons with salmon and green pulp color were found. This simple inheritance was attributed to the *gf* gene located in the IX linkage group.

Subsequently, Tzuri et al. (2015) designated an allele in CmOr as the 'Golden' SNP, which was responsible for both non-salmon and salmon phenotypes. They suggested editing the genome of the Or gene for the nutritional biofortification of melons. Silva (2022), in a study on the genetic inheritance of β-carotene content in a cross derived from the A-16 lineage (white pulp color) x Védrantais (salmon pulp color), suggested that segregation in this trait is controlled by a major gene with additive and dominance effects associated with polygenes of additive effects.

Two independent genes (A and B) with double recessive epistasis are associated with cracking in the AC-02 x Timeless Gold cross. In this case, each gene has two alleles (*A* and *a* for gene A; *B* and *b* for gene B), and there is complete dominance. The genotypes are characterized as follows: AC-02 (P1), *AABB* (crack), 'Timeless Gold' (P2), *aabb* (no crack), F1 *AaBb* (crack), F2 (9) *A_B_* (crack): (3) *A_bb* (no crack): (3) *aaB_* (no crack): (1) *aabb* (no crack). It is evident that cracking only occurs when at least one dominant allele is present at each locus (*A_B_*). In this case, the presence of dominant alleles at each locus is necessary for the cracking expression .

The occurrence of cracking varies among melon cultivars. This condition is often attributed to temperature fluctuations, irrigation, and nutrition variations during the maturation stage, predisposing fruits to cracking (Fernández-Trujillo et al., 2013).

However, there is limited evidence that this anomaly has a genetic basis. Qi et al. (2015), studied genetic inheritance models in a cross involving the 'RE-33' variety (cracking-resistant) and the 'MOIN-10' variety (cracking-susceptible) and demonstrated that the most suitable model for explaining this trait involves two major genes with additive and dominance effects along with epistasis. Additionally, the heritability found suggests environmental influence or genotype-environment interaction.

Important information on the molecular and metabolic bases of netting and its close association with ligno-suberization of the rind during melon development was obtained by Cohen et al. (2019). Reticulated rind is characterized by induced expression of biosynthetic genes acting in the central pathways of phenylpropanoid, suberin, lignin, and lignan. Transcriptions of genes associated with lipid polymer assembly, cell wall organization, and loosening are highly enriched in reticulated tissue. These signatures are exclusive to reticulated structures and absent in smooth surfaces observed between reticulated regions and on the skin of smooth fruits.

Conclusions

The genetic inheritance of pulp color is conditioned by the epistatic interaction of dominance between two genes.

Genetic control associated with cracking involves the gene interaction of two genes of the double recessive epistasis type.

The melon pericarp netting has dominant monogenic control.

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