*ARTICLE*

# Inheritance of leaf color in papaya

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**Abstract:** *Physiological disturbances are one of the major bottlenecks to the expansion of papaya crops due to the negative influence on fruit quality. Studies on genotypes of light-green color have become essential to the development of strategies of tolerance to the physiological disorder skin freckle. Understanding the inheritance of qualitative traits is crucial to selection and prediction of the behavior of segregating generations. Thus, this study aimed to determine the inheritance of the qualitative trait leaf color in segregating generations of crosses between the dark-green cultivar BSA and the light-green cultivar GPC. Inheritance was determined based on the Mendelian genetics laws, by evaluating the phenotypic proportions in the analysis of generations $P_1$ (BSA), $P_2$ (GPC), $F_1$, $F_2$, $BC_1$, $BC_2$, $BC_{21}$, and $F_{2:3}$. The inheritance of light-green leaves from the crossing between BSA and GPG is due to double recessive epistasis.*

**Keywords**: *Carica papaya L., plant breeding, genetic variability, genetic control.*

## INTRODUCTION

Papaya (*Carica papaya* L.) is native to Central America or, more precisely, southern Mexico and Costa Rica (Chen et al. 1991). It is one of the most important tropical fruits worldwide and finds in Brazil favorable climatic conditions for its commercial exploitation. Therefore, the country has become one of the leading countries in papaya production (FAOSTAT 2016).

The search for new promising genotypes is crucial for the improvement of the crop. Initially, the knowledge about the genetic diversity directs the exploitation of the existing variability to be used in papaya breeding, aiming at new cultivars with different genotypic compositions (Silva et al. 2017, Pereira et al. 2019).

The diversity among accessions from germplasm banks, such as that of Caliman Agricola SA in Linhares – ES, has been reported by other authors (Barbosa et al. 2011, Quintal et al. 2012). Also, contrasting phenotypes for the qualitative trait leaf color have been confirmed by different chlorophyll contents, including BSA, of dark-green color, and GPC, of light-green color (Silva et al. 2017).

Studies on generations analysis are scarce, and few qualitative traits of papaya regarding genetic control have been investigated (Costa et al. 2013a). Qualitative traits usually have oligogenic inheritance, that is, they are controlled by few genes and are little influenced by the environment, which allows them to be exploited in a breeding program using hybridization. The expression of

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traits governed by few genes of greater effect have been shown to be important for breeding programs of several crops, mainly for those that work on the resistance response of plants to some diseases (Junghans et al. 2003, Vijayalakshmi et al. 2005, Batista et al. 2017, Costa et al. 2018).

Studies aiming at obtaining genotypes with light-green color have been carried out for these genotypes have tolerance to the physiological disorder known as skin freckle (Oliveira and Vitoria 2011, Pinto et al. 2013a, Pinto et al. 2013b). Skin freckle has caused significant losses to the export market of papaya, which is much more demanding when it comes to the *external* appearance of the fruits. Therefore, this trait has become relevant for a crop breeding program and has been studied by several authors (Kaiser et al. 1996, Campostrini et al. 2005, Gomes Filho et al. 2006, Gomes Filho et al. 2007).

In a study with five papaya genotypes, Torres Netto et al. (2009) highlighted that cv. Golden, for its light-green color, was the only one without midday depression of photosynthesis. They also reported that this property is the most relevant since the high temperature and high light incidence are common in the main areas of papaya production in Brazil. Torres Netto et al. (2009) state that further papaya breeding programs should be planned to incorporate some qualitative traits from light-green leaves genotypes.

Understanding the inheritance of leaf color is crucial to breeding programs as it supports the release of new cultivars and favors research strategies to avoid wasting time with inefficient breeding methods. The knowledge of the nature and magnitude of the gene effects that control a given trait is fundamental for the selection and prediction of the behavior of segregating and hybrid generations (Cruz et al. 2012). Thus, this work aimed to analyze the inheritance of the qualitative trait leaf color in papaya.

## MATERIAL AND METHODS

The study of the oligogenic inheritance requires some steps to be followed. The contrasting parents selected for the trait leaf color were the lines BSA, of dark-green leaves, and GPC, of light-green leaves. Seeds of BSA and GPC genotypes were obtained from potentially inbred populations, maintained for more than eight self-fertilization generations in the germplasm bank of Caliman Agrícola S.A. Both parents had their morpho-agronomic traits described by Silva et al. (2017).

The experiment was carried out at Santa Teresinha Farm, belonging to Caliman Agrícola SA, in the municipality of Linhares, Espírito Santo (lat 19° 11’ 49” S, long 40° 05’ 52” W, alt 30 m asl), between February 2012 and December 2014 (Figure 1). The climate of the region is classified as type AWi (tropical humid), with rainy summer and dry winter (Alvares et al. 2013).

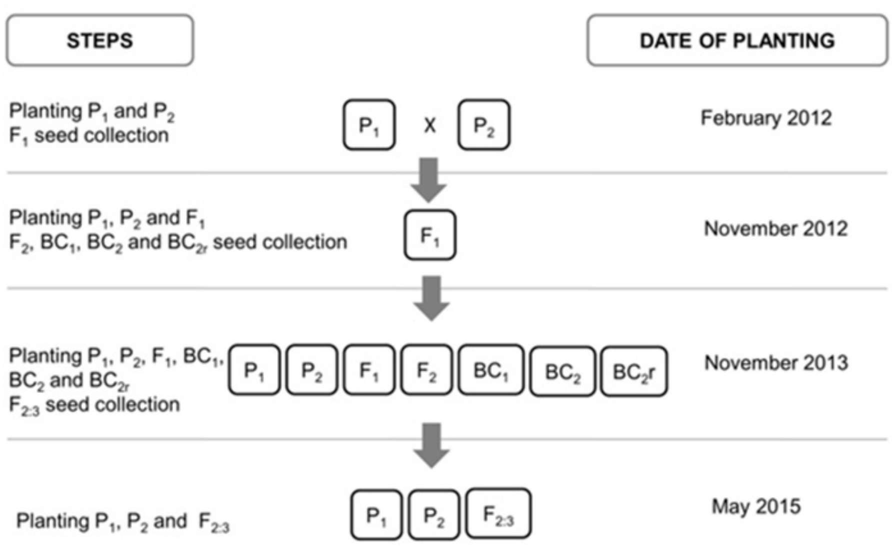


***Figure 1.*** Planting schedule and seed collection of the study generations from the cross $P_1$ (BSA) x $P_2$ (GPC).

The inheritance of leaf color in papaya was studied by the analysis of the generations $P_1$ (BSA), $P_2$ (GPC), $F_1$, $F_2$=, $BC_1$, $BC_2$, $BC_{2r}$ ($BC_2$ reciprocal), and $F_{2:3}$. The first planting of the parents was carried out in February 2012, and eight months later, GPC was used as a pollen donor to BSA to produce the $F_1$ population. Afterward, seeds were sown in November 2012, together with the parents, to produce populations $F_2$, $BC_1$, $BC_2$, and $BC_{2r}$, and to maintain $P_1$, $P_2$, and $F_1$ seeds in 2013.

The $F_1$ generation was *self-fertilized* to produce the $F_2$ generation. Backcrossings were performed as follows: $BC_1$ was obtained by crossing BSA, as the female parent, and $F_1$, as the male parent; $BC_2$ was obtained by crossing GPC, as the female parent, and $F_1$, as the male parent; and $BC_{2r}$ was obtained by crossing $F_1$, as the female parent, and GPC, as the male parent. The reciprocal cross was carried out to examine possible maternal control for the studied trait.

Seeds of all generations were planted in the field in November 2013. All hermaphroditic plants were evaluated: 16 from parent $P_1$; 16 from parent $P_2$; 23 from the $F_1$ generation, to evaluate the environmental effect; 168 from the $F_2$ generation; 41 from $BC_1$; 55 from $BC_2$; and 54 from $BC_{2r}$.

In the $F_2$ generation, seven plants of different colors were selected: dark-green leaves (5, 7, 8, and 9) and light-green leaves (1, 2, and 4) leaves. These plants were crossed and self-fertilized to obtain the $F_{2:3}$ generation ($F_3$ generation derived from the $F_2$ generation selected). The self-fertilized plants 1, 5, 7, and 9 and the three 2x1, 2x4, and 8x7 crosses were planted in the field in May 2015. Hermaphroditic plants from each treatment of the $F_{2:3}$ generation (15, 27, 26, 36, 31, 32, and 26 hermaphroditic plants) were evaluated to confirm the phenotypic segregation and the genetic control of the trait, based on the Mendelian laws.

Manual pollination was performed by transferring the pollen from a hermaphroditic plant to the stigma of a female plant. Hermaphroditic plants that did natural pollination were used for the self-fertilization. All procedures were performed before anthesis, preventing the pollination from other plants. Flowers were marked and protected with paper bags. All populations were obtained in the field.

The experiment was carried out with one hermaphroditic plant per hole, which were spaced at 3.6 m between rows and 1.5 m within rows, following cultural practices recommended for the crop (Costa et al. 2013b).

The analysis of the inheritance of the qualitative trait was based on the Mendelian laws, where the phenotypic proportions in $F_2$, backcross, and subsequent generations were evaluated. This procedure was carried out for leaf color in the segregating generations and was divided into two classes (dark-green and light-green), the same pattern shown by the parents BSA (dark-green) and GPC (light-green).

Plant phenotypes were analyzed at 300 days after planting when the plants were clearly distinguished between dark-green and light-green leaves. The description of each phenotype was confirmed by the chlorophyll content index (CCI), quantified with a portable chlorophyll meter ClorofiLOG® CFL 1030, according to the manufacturer's instructions (Falker 2008), and the frequency distribution for BSA and GPC was graphically displayed. The leaf color variability in papaya was confirmed by the CCI and analyzed for the physiological traits, based on Castro et al. (2011), who observed that the light-green color of the papaya leaves could be confirmed by the lower CCI values.

The analysis of the color, with a discrete distribution, was carried out by the genetic hypothesis test. This test allows determining the predominant segregation pattern that indicates whether it is governed by one, two, or more genes, as well as the predominant type of interaction (Liu 1997). The chi-square test has been proven to be practical and efficient in testing the hypotheses of segregation patterns (Batista et al. 2017) for it considers the deviations between expected and observed values and the number evaluated (Schuster and Cruz 2004).

The chi-square test ($\boldsymbol{\chi}^2$) used to verify the ratio of segregation in all populations with its particularities is given by:

$$\boldsymbol{\chi}^2 = \sum_{i=1}^{n} \frac{(Obs_i - Exp_i)^2}{Exp_i}$$

where:

$\boldsymbol{\chi}^2$ is the calculated chi-square value;

$Obs_i$ and $Exp_i$ are the observed and expected values for the $i^{th}$ phenotypic class (i = 1, 2, ... n), respectively.

Analyses were performed for non-parametric chi-square test at 5% of probability, using the Genes software (Cruz 2016).

## RESULTS AND DISCUSSION

Table 1 shows the phenotypic frequencies based on the leaf color (dark-green or light-green). The BSA parent (dark-green leaf) had a mean CCI of 58.50 ± 2.32, while the GPC parent (light-green color), had CCI of 47.19 ± 2.86. The CCI is a continuous random variable, and its frequency distribution is shown in Figure 2, where the light- and dark-green colors form very distinct classes. A normal distribution is observed for the CCI data (BSA with p-value = 0.7733 and GPC p-value = 0.6994 by the Shapiro-Wilk test). All the plants in the $F_1$ generation had dark-green leaves, indicating that the light-green color is controlled by recessive gene(s).

Lee (1988), in a study with grape, reported that the chlorophyll content varies greatly between species and between genotypes of the same species. This variability was also found in papaya and is likely to be explored in breeding programs, and its physiological aspect has been studied by several authors (Torres Netto et al. 2002, Castro et al. 2011).

Castro et al. (2014) found that papaya genotypes with different leaf colors had CCIs related to total chlorophyll concentrations, quantified by a destructive method. The genotype with light-green leaf partitioned less nitrogen for chlorophyll synthesis when compared with the genotype with dark-green leaf. Moreover, the latter was more sensitive to PSII (photosystem II) damage when nitrogen was scarce.

In the $F_2$ generation, the segregation for the color trait was 9 dark-green: 7 light-green ($\chi^2$ =0.732, p-value=0.3923) indicating digenic inheritance with double recessive epistasis (Phillips 2008, Griffiths et al. 2015). This result shows that the dark-green color is controlled by at least one dominant allele, simultaneously in the two loci. The light-green color includes genotypes with a dominant allele in only one of the loci and the genotype with double recessive alleles. The inheritance hypothesis that the characteristic leaf color is controlled by a gene that segregates 3 dark- green: 1 light-green in $F_2$ and the hypothesis that it is controlled by three genes that segregate 27 dark-green: 37 light-green in $F_2$ were also tested. The segregation shown in this study did not fit into any of these hypotheses by the chi-square test (Table 1).

The genotypes in each generation are represented in Table 1, where the dark-green color shows at least one dominant allele for each locus (AABB; AaBb; AABb; AaBB) and the light-green color shows at least one locus with all recessive

***Table 1.*** Summary of frequencies observed, chi-square test, and genotypes for the seven generations in the study of leaf color in papaya in the analysis of generations, with plants evaluated at 300 days after planting

| Generation | Frequency of phenotype observed | | CCI [1] | $H_0$ hypothesis | $\chi^2_C$ [2] | Genotypes | |
|---|---|---|---|---|---|---|---|
| | Dark-green | Light-green | | | | Dark-green | Light-green |
| BSA | 16 | 0 | 58.50 ± 2.32 | | | AABB | |
| GPC | 0 | 16 | 47.19 ± 2.86 | | | | aabb |
| $F_1$ | 23 | 0 | | | | AaBb | |
| $F_2$ one gene, complete dominance | 89 | 79 | | 3 Dark-green: 1 Light-green | 43.460* (0.00%) | 1AA; 2Aa | 1aa |
| $F_2$ two genes, complete dominance | 89 | 79 | | 9 Dark-green: 7 Light-green | 0.732 (39.23%) | 1AABB; 2AABb; 2AaBB; 4AaBb | 1AAbb; 2Aabb; 1aaBB; 2aaBb; 1aabb |
| $F_2$ three genes, complete dominance | 89 | 79 | | 27 Dark-green: 37 Light-green | 8.018* (0.46%) | 27A-B-C- | 9A-bbC-; 9aaB-C-; 9A-B-cc; 3aabbC-; 3A-bbcc; 3aaB-cc; 1aabbcc |
| $BC_1$ | 41 | 0 | | | | 1AABB; 1AABb; 1AaBB; 1AaBb | |
| $BC_2$ | 14 | 41 | | 1 Dark-green: 3 Light-green | 0.006 (93.79%) | 1 AaBb | 1Aabb; 1aaBb; 1aabb |
| $BC_{2r}$ | 15 | 39 | | 1 Dark-green: 3 Light-green | 0.223 (63.74%) | 1 AaBb | 1Aabb; 1aaBb; 1aabb |

[1] CCI - chlorophyll content index measured with a portable chlorophyll meter ± standard deviation.

[2] $\chi^2_C$ = calculated chi-square, where * is significant at p-value = 0.05 for chi-square test, respectively; the probability is indicated between parenthesis.

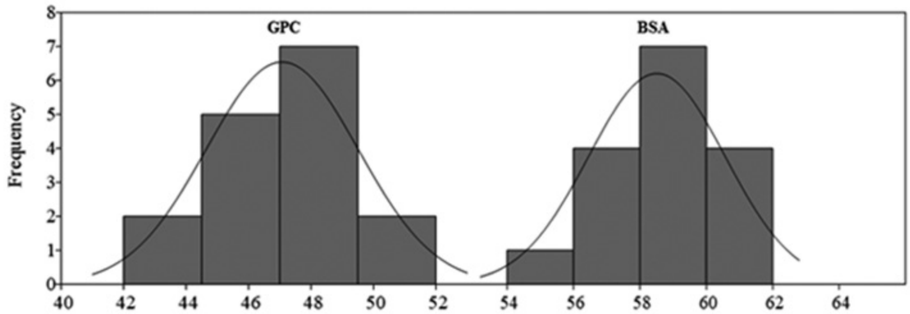


***Figure 2.*** Frequency distribution of CCI values of papaya leaves of BSA and GPC genotypes.


***Figure 3.*** Difference in leaf color of papaya originated from self-fertilization of plant 5 at seven months after planting; in the foreground, dark-green plant to the left and light-green plant to the right.

alleles (AAbb; Aabb; aaBB; aaBb; aabb).

The dark-green color of all plants in $BC_1$ indicates that the genotypes of this generation have at least one dominant allele in each locus. When adjusting to the proportion of 1 dark-green: 3 light-green in $BC_2$ ($\chi^2$ =0.006, p-value=0.9379), the dark-green color is represented by the genotype with both loci in heterozygosity, while the color of the light-green plants is controlled by a locus with both recessive alleles. The $BC_{2r}$ generation had plants at the proportion of 1 dark-green: 3 light-green, indicating the absence of maternal effects in the expression of the leaf color.

Cassetari et al. (2015) studied lettuce and reported different shades of green and a relative number of deleterious mutants. These mutants were genetically identified, and all of them indicated that the reduction in the green color (chlorophyll) corresponds to recessive alleles.

The phenotypic frequencies of the $F_{2:3}$ are shown in Table 2. Four plants selected in the $F_2$ (1, 5, 7, and 9) were self-fertilized. In the self-fertilization of plant 1 (light-green phenotype), all progenies had light-green color (45.74 ± 2.41 CCI) since they showed at least one locus in recessive homozygosity. Conversely, in the self-fertilization of plant 9 (dark-green phenotype), all progenies had dark-green color (58.97 ± 3.83 CCI), indicating that their plant has all dominant alleles.

The dark-green plants 5 and 7 had progenies with segregation of 3 dark-green: 1 light-green (60.28 ± 2.59 and 45.57 ± 2.45; 60.84 ± 3.64; and 45.88 ± 2.55 CCI) ($\chi^2$ =0.111, p-value=0.7389; $\chi^2$ =0.461, p-value=0.4669) (Table 2), indicating that plants 5 and 7 have one locus with all dominant alleles and the other locus with one dominant allele and one recessive allele. Figure 3 shows the dark-green and light-green leaves progenies from plant 5.

***Table 2.*** Summary of frequencies observed, chi-square test, and genotypes at generation $F_{2:3}$, for the seven genotypes and crosses selected in $F_2$ in the study of leaf color in papaya, at 300 days after planting

| $F_2$ plants | $F_2$ genotypes | Frequency of phenotype observed $F_{2:3}$ Dark-green (DG) | Light-green (LG) | CCI [1] | $H_0$ hypothesis | $\chi^2_C$ [4] | $F_{2:3}$ genotypes |
|---|---|---|---|---|---|---|---|
| 1[2] | AAbb | 0 | 15 | 45.74 ± 2.41 | - | - | AAbb |
| | Aabb | | | | | | 1AAbb:2Aabb:1aabb |
| | aaBB | | | | | | aaBB |
| | aaBb | | | | | | 1aaBB:2aaBb:1aabb |
| | aabb | | | | | | aabb |
| 5[2] | AABb | 21 | 6 | 60.28 ± 2.59 | 3: 1 | 0.111 (73.89%) | 1AABB:2AABb:1AAbb |
| | AaBB | | | 45.57 ± 2.45 | | | 1AABB:2AaBB:1aaBB |
| 7[2] | AABb | 18 | 8 | 60.84 ± 3.64 | 3: 1 | 0.462 (46.69%) | 1AABB:2AABb:1AAbb |
| | AaBB | | | 45.88 ± 2.55 | | | 1AABB:2AaBB:1aaBB |
| 9[2] | AABB | 36 | 0 | 58.97 ± 3.83 | - | - | AABB |
| 2 x 1[3] | AAbb x AAbb | 0 | 31 | 46.69 ± 2.83 | - | - | AAbb |
| | Aabb x Aabb | | | | | | 1AAbb:2Aabb:1aabb |
| | aaBB x aaBB | | | | | | aaBB |
| | aaBb x aaBb | | | | | | 1aaBB:2aaBb:1aabb |
| | aabb x aabb | | | | | | aabb |
| 2 x 4[3] | AAbb x AAbb | 0 | 32 | 46.34 ± 2.80 | - | - | AAbb |
| | Aabb x Aabb | | | | | | 1AAbb:2Aabb:1aabb |
| | aaBB x aaBB | | | | | | aaBB |
| | aaBb x aaBb | | | | | | 1aaBB:2aaBb:1aabb |
| | aabb x aabb | | | | | | aabb |
| 8 x 7[3] | AaBB x AaBB | 18 | 8 | 62.15 ± 2.75 | 3: 1 | 0.462 (46.69%) | 1AABB:2AaBB:1aaBB |
| | AABb xAABb | | | 44.56 ± 1.00 | | | 1AABB:2AABb:1AAbb |

[1] CCI - chlorophyll content index, measured with a portable chlorophyll meter ± standard deviation

[2] Hermaphroditic genotypes selected and self-fertilized in $F_2$ to produce the $F_{2:3}$ generation

[3] Genotypes selected with the same traits of interest in $F_2$ and cross between female genotype and hermaphroditic genotype to produce generation $F_{2:3}$

[4] $\chi^2_C$ = calculated chi-square, where is significant at p-value = 0.05 for the chi-square test; the probability is indicated between parenthesis.

Plants 1, 2, and 4 (light-green color) and 8 and 7 (dark-green color) generated crosses (2x1, 2x4 and 8x7). For 2x1 and 2x4, all light-green progenies were obtained, showing mean CCI values of 46.69 ± 2.83 and 46.34 ± 2.80, respectively. This result indicates that all the parents have the same locus with two recessive alleles (AAbb or aaBB) and that when crossing all their progenies, the latter has a locus in recessive homozygosity, which controls the light-green color. However, the cross between light-green parents with different loci with recessive alleles (AAbb x aaBB) would produce all progenies with dark-green color, and therefore, after the selection of the light-green color genotype, self-fertilization favors the fixation of this trait. The segregation in the cross 8x7 was 3 dark-green: 1 light-green (62.15 ± 2.75 and 44.56 ± 1.00 CCI) ($\chi^2$ =0.605, p-value=0.4669), showing that the two plants have the same locus with dominant alleles and a heterozygous locus.

The lowest means for the CCI variable were found for the genotypes with light-green leaf of the cross 8x7 (44.56 ± 1.00). All means were higher than 40, which is associated with high photosynthetic pigment values (chlorophylls a and b and carotenoids) and nitrogen content in papaya leaves (Torres Netto et al. 2002).

Knowing the digenic inheritance with dual recessive epistasis, from crosses between BSA and GPC, the possibility of incorporating the light-green color into new commercial cultivars becomes an interesting prospect for the papaya breeding.

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