

Combining ability of recombined F_4 papaya lines: a strategy to select hybrid combination

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ABSTRACT: The growing demand for quality of papaya by the domestic and international markets requires the development of genotypes that are capable of incorporating traits, such as high yield and fruit quality. This study estimated the genetic parameters and the specific combining ability of F_4 papaya lines crossed to the SS-72/12 tester to identify genotypes with higher genetic value for hybrid production. We evaluated 169 treatments consisting of 62 topcross hybrid combinations, 97 F_5 lines, and 10 controls in a 13×13 lattice design with five replicates and two plants per plot. The following traits were evaluated: plant height (PH), stem diameter (SD), first-fruit insertion height (FFIH), number of marketable fruits (NMF), number of deformed fruits (NDF), number of fruitless nodes (NFN), average fruit weight (FW), and yield (YLD). Differences $p < 0.05$ were found in most traits evaluated. The specific combining ability estimates indicate that hybrids formed by the cross between SS-72/12 tester and the following lines are promising, considering the multiple traits: UCLA08-088, UCLA08-101, UCLA08-071, UCLA08-014, UCLA08-025, UCLA08-028, UCLA08-122, UCLA08-055, UCLA08-026, and UCLA08-092. These hybrids meet the demands for domestic and international markets and may be available to producers as new papaya cultivars.

Keywords: *Carica papaya* L., papaya breeding, topcross, genetic parameter

Introduction

Papaya (*Carica papaya* L.) is one of the most widely grown and consumed fruits in tropical and subtropical regions of the world and its production is directly related to the use of high-yielding cultivars adapted to the different growing regions.

The UENF/CALIMAN is the main breeding program of papaya in Brazil. The program was started in 1996 and has produced 21 hybrids. One of the most important and the first hybrid developed in the country is 'Calimosa' (UENF/CALIMAN - 01), cultivated in various papaya growing regions across Brazil (Pereira et al., 2019).

However, the growing demand for superior genotypes by the domestic and international markets requires continuous development of cultivars that encompass traits, such as high yield, high fruit quality, and disease resistance.

New cultivars usually originate from segregating populations through breeding programs. In those populations, the breeder generates several lines and/or hybrid combinations. To evaluate those lines and/or hybrid combinations, methods such as the Topcross (Fountain et al., 2019) and diallel cross (Liang et al., 2019) are used for studies of general (GCA) and specific (SCA) combining ability to select the most promising genotypes. Those methods allow determining the lines with the best average behavior within the set of tested parents, or with the specific performance in a hybrid combination.

Throughout the progress of UENF papaya breeding program, studies were undertaken on GCA and SCA to

select new hybrids. Some of these studies examined traits related to fruit yield and quality (Ide et al., 2009; Cardoso et al., 2014; 2015; Barros et al., 2017), fruit deformity (Cardoso et al., 2017), and disease resistance (Vivas et al., 2014).

This study estimated genetic parameters and the specific combining ability effects of new hybrid combinations generated from crosses of recombined F_4 lines to SS-72/12 tester (topcross). Additionally, it aimed to identify lines with high genetic value for the production of hybrids that could be used as alternatives in terms of fruit size and yield for producers and consumers.

Materials and Methods

Genetic material

The genetic material comprised 97 F_5 lines, 62 topcross hybrids and 10 controls (UC-Sekati, UC-JS12, SS-72/12, Maradol, Waimanalo, 'UENF/CALIMAN 01', 'Tainung', 'Golden', 'Aliança' and 'UC10'), totaling 169 papaya genotypes.

The F_5 lines originated from a cross population between UC-Sekati and UC-JS12 parents of the Germplasm Bank of the UENF/CALIMAN breeding program. The parents belong to the same heterotic group (Formosa group), but are contrasting for agronomic and sensory traits. The UC-Sekati parent has large fruits, optimum pulp firmness, and medium soluble solids content. The UC-JS12 parent, in turn, diverges from UC-Sekati in relation to the last two traits, exhibiting moderate pulp firmness and elevated soluble solids content (Cortes et al., 2019). Accordingly, the UC-Sekati parent was used as a source of pulp thickness, whereas

UC-JS12 was used as a source of flavor. After the crosses, F₁ plants were self-pollinated, originating the F₂ segregating population, which was advanced up to F₄ generation by the SSD (single-seed descent) method. From that generation, F₄ lines were self-pollinated to obtain F₅ lines, which were used in the study. In the same generation (F₄), the same lines were crossed to the SS-72/12 parent (Solo group tester) to obtain 62 topcross hybrids. A flowchart with all the stages to obtain the recombined lines and hybrid combinations is shown in Figure 1.

Evaluation trial

The experiment was carried out in the municipality of Linhares - ES, Brazil, (19°23'28" S, 40°04'20" W, altitude of 33 m). The climate of the region is classified

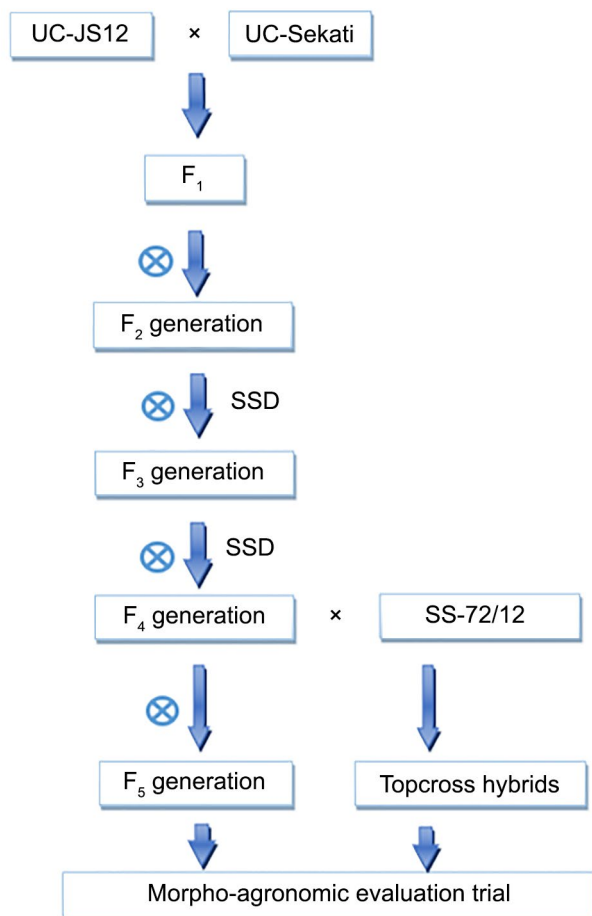


Figure 1 – Flowchart of the pedigree and stages to obtain recombined lines and new hybrids. A biparental cross between the UC-JS12 and UC-Sekati genotypes was formed, forming F₁ generation. This generation was conducted by single seed descent up to the fourth generation, the lines of this generation were crossed with the SS-72/12 tester to obtain the hybrid combinations, and the same lines were self-fertilized to obtain F₅ lines.

as type AWi (tropical humid), with rainy summers and dry winters, the average annual temperature in the region is 23.4 °C (Alvares et al., 2013). The genotypes were evaluated in a competition assay, using a 13 × 13 lattice square experimental design with five replicates, with two plants per plot, at a spacing 3.6 m between the rows and 1.5 m between the plants.

Seedlings were produced in 96-tube plastic trays, using a commercial substrate. After germination and acclimatization (30 days), the seedlings were transplanted to the experimental unit in the commercial area of the company. Fertilization, management, pest/disease control, and cultivation treatments were the same adopted in the commercial plantings of the company. Evaluations were performed at 210 (Oct 2017), 300 (Jan 2018), and 390 (May 2018) days after planting.

Field phenotyping

We used an image-based phenotyping methodology, validated and described by Cortes et al. (2017) to phenotyping papaya plants, to measure the following traits: plant height - PH (cm), measured from the ground base to the insertion of the last pair of leaves; stem diameter - SD (cm), measured at 20 cm from the ground; first-fruit insertion height - FFIH (cm), measured from the ground base to the first fruit insertion into the stem; number of marketable fruits - NMF, determined by counting fruits with commercial traits; number of deformed fruits - NDF, determined by the count of carpeloid and pentandric fruits in each plant; number of fruitless nodes - NFN, by counting fruitless nodes in each plant; average fruit weight - FW (g), determined by weighing five fruits on a digital analytical scale; and yield - YLD (kg per plant).

For the traits NMF, NDF, NFN, the plugin cell counter of ImageJ software was used to count the traits and the results of the three evaluations were summed. Plant height and SD were expressed as the average of three evaluations. Average fruit weight was determined as the average weighted by the NMF of each season. Lastly, YLD was calculated as the weighted FW multiplied by NMF. The NDF and NFN data were $\sqrt{x + 0.5}$ transformed for normalization.

Statistical analysis

Genetic parameters

The agronomic data were analyzed in the "PROC GLM" module of SAS Studio software. The analyses of variance were performed according to the following model:

$$Y = \mu + R_{(j)} + B / R_{(k)(j)} + T_{(i)} + e_{ijk}$$

where: μ = overall constant; $R_{(j)}$ = effect of replicate $j \sim \text{NID}(0, \sigma^2_r)$; $B/R_{(k)(j)}$ = effect of block k within replicate $j \sim \text{NID}(0, \sigma^2_b)$; $T_{(i)}$ = effect of treatment $i \sim \text{NID}(0, \sigma^2_t)$; e_{ijk} = experimental error $\sim \text{NID}(0, \sigma^2)$. Furthermore, the

following parameters were estimated:

a) Heritability: $h^2 = \frac{\sigma_g^2}{\sigma_f^2}$

b) Experimental coefficient of variation: $CV_e = \frac{\sqrt{MSE}}{\bar{X}}$

c) Genetic coefficient of variation: $CV_{g(\%)} = \left[\frac{100\sqrt{\sigma_g^2}}{\bar{X}} \right]$

d) Variation index: $V_{i(\%)} = 100 \frac{CV_g}{CV_e}$

Specific combining ability

The specific combining ability (SCA) was estimated as the difference between the mean of each hybrid from the tester and the overall mean of the crosses with that tester, using a formula described by Hallauer et al. (2010), as follows:

$$SCA_g T_i = X_e T_i - X_g T_i$$

where: X_e is the mean of the hybrid obtained from tester i ; X_g is the overall mean of the crosses with tester i .

Results

Estimates of genetic parameters

All treatments showed a difference $p < 0.05$ and were decomposed into categories, as lines, hybrids, and controls. The F test revealed a difference $p < 0.01$ for all traits in all categories, except for NDF and NFN related to the controls, which did not present difference $p > 0.05$. The differences $p < 0.01$ indicate the existence of genetic variation between and within categories, which enable the selection of hybrids and/or lines.

The experimental coefficient of variation (CVe) ranged from 10 % (PH) to 37 % (YLD). The traits FFIH, PH, SD, NFN, and FW showed CVe values lower than 20 %, indicating good experimental precision. The NMF (33 %), NDF (28 %) and YLD (37 %), in turn, presented elevated values due to their nature, as these variables are highly influenced by environmental variations.

The FW, PH, NMF, and FFIH showed heritability (h^2) values higher than 80 %. For the other traits (SD, NDF, NFN and YLD), the h^2 values ranged from 60 to 68 %.

Lattice efficiency was higher than 100 % for FFIH, PH, SD, NMF, NFN, FW, and YLD, which showed respective efficiency values of 113, 126, 120, 121, 114, 111 and 129 %. For NMF, lattice efficiency was 100 %.

The genetic coefficient of variation (CVg) ranged from 8 % (SD) to 33 % (NMF). The variation index (Vi) is another parameter that can help the decision making during the selection process. In this study, FFIH, SD, NDF, NFN, and YLD showed Vi values of 88, 66, 61, 55 and 63 %, respectively, all lower than a unity.

Estimates of SCA

In the study of combining ability, the best hybrid combinations considering traits like SD, NMF, FW and YLD presented positive combining ability estimates. For traits like FFIH, PH, NDF, and NFN, negative estimates showed the best hybrid combinations.

The results allowed the hybrid combinations to be separated into two main groups, considering that the initial cross was between the SS-72/12 tester, belonging to the Solo group, and a set of lines belonging to the Formosa group. Given the predominant additive gene action for FW, hybrid combinations with the Formosa genetic profile and with an intermediate profile between Solo and Formosa were expected. According to Pereira et al. (2019), crosses between large- and small-fruit parents result in hybrids that produce medium-sized fruits.

The first group comprised combinations and its fruit weight ranged from 746 to 980 g, termed as the 'Intermediate' group. It included only the combinations whose weight was higher than that of the Solo profile and lower than that of the Formosa profile. The second group, named 'Formosa', contained combinations whose weight ranged from 1000 to 1400 g.

The 31 hybrid combinations pertaining to the Intermediate group and their SCA estimates for the eight evaluated traits, shown in Figure 2. Each segment reflects the quantitative value of the SCA estimate for the traits under study.

For YLD, the combining ability estimates ranged from -18.30 to 20.03, with the hybrid combinations formed by the SS-72/12 tester and the UCLA08-101, UCLA08-097, UCLA08-088, UCLA08-014 and UCLA08-071 lines standing out. For FW, in turn, estimates varied from -166.85 to 87.50. For this trait, the outstanding hybrid combinations involved the UCLA08-062, UCLA08-066, UCLA08-111, UCLA08-088 and UCLA08-087 lines.

For NMF, combining ability estimates ranged from -16.90 to 18.14, with hybrid combinations involving the UCLA08-101, UCLA08-025, UCLA08-097, UCLA08-125 and UCLA08-014 lines standing out. For SD, in turn, combining ability estimates ranged from -1.01 to 2.99. The combinations between the tester and the UCLA08-025, UCLA08-014, UCLA08-101, UCLA08-043 and UCLA08-118 lines stood out for this trait.

Combining ability estimates of -19.07 to 18.76 were found for the FFIH trait, with the hybrid combinations involving the UCLA08-025, UCLA08-043, UCLA08-125, UCLA08-082 and UCLA08-119 lines standing out. For PH, estimates ranged from -24.09 to 21.53. For this trait, the combinations with the UCLA08-001, UCLA08-082, UCLA08-119, UCLA08-043 and UCLA08-097 lines were superior.

The combining ability estimates for NDF ranged from -7.49 to 12.12, with the hybrid combinations formed by the UCLA08-069, UCLA08-125, UCLA08-128, UCLA08-101 and UCLA08-021 lines standing out. For NFN, in turn, estimates ranged from -3.14 to 3.64

multiple traits: SS-72/12 × UCLA08-028, SS-72/12 × UCLA08-122, SS-72/12 × UCLA08-055, SS-72/12 × UCLA08-026 and SS-72/12 × UCLA08-092. The SS-72/12 × UCLA08-028 combination showed estimates for FW, YLD, NDF and NFN; SS-72/12 × UCLA08-122, for NMF, FW, YLD, NDF and NFN; SS-72/12 × UCLA08-055, for NMF, FW, YLD and NDF, SS-72/12 × UCLA08-026, for NMF, YLD and NFN; and SS-72/12 × UCLA08-092, for NMF, YLD, NDF and NFN.

Discussion

Estimates of genetic parameters

The experimental coefficient of variation (C_{Ve}) is a parameter that allows the breeder to check experimental precision. The C_{Ve} values found for FFIH (15 %), PH (10 %), SD (11 %), and FW (11 %) traits are considered medium, indicating good experimental precision (Ferreira et al., 2016). Ramos et al. (2014) and Cortes et al. (2018) also found C_{Ve} values below 20 % for PH, FFIH, and SD, agreeing with our results.

In this study, the C_{Ve} values for NMF, NDF and YLD were considered high, agreeing with Ramos et al. (2014), Luz et al. (2015), Barros et al. (2017), and Luz et al. (2018). High C_{Ve} values indicate low experimental precision. The low experimental precision found for NMF, NDF, and YLD may be associated with summer sterility, since sterility (NFN) increases in hotter months of the year, whereas the rates of carpelloid and pentandry (NDF) increase in colder months (Moreira et al., 2019). This opposition between sterility and pentandry and/or carpelloid in these months alters the data on the number of fruits, which results in high data dispersal and high experimental error.

Heritability (h²) values for FFIH, PH, NMF, and FW were higher than 80 %, indicating great chances of achieving genetic gain through simple selection procedures. According to Bi et al. (2015), high h² values indicate the predominance of additive gene action. The traits SD, NDF, NFN, and YLD showed h² values that ranged from 60 % to 68 %. These values are higher than 50 % and are considered high, that is, although those traits evidenced greater environmental influence, the observed heritability values indicate that the selection procedures results in elevated genetic gains. Alternatively, for this case, indirect selection can be performed through correlated responses.

Lattice efficiency ranged from 111 % for FW to 129 % for YLD, suggesting greater environmental control in the experiment and, thus, decreased variations caused by the environment (reduction of phenotypic variance). This means that most variation observed in the treatments evaluated is of genetic origin, leading to an increase in heritability. Barros et al. (2017) evaluated the SCA of 22 papaya lines derived from the sex reversal of the 'Cariflora' genotype using a Lattice design and found efficiency values of 102 % and 107 % for fruit length and fruit diameter, respectively.

Estimates of genetic coefficient of variation (CV_g) allow the breeder to have a perception of the relative volume of the changes that can be obtained through selection in a breeding program, since this parameter is directly proportional to genetic variance. In this study, the highest CV_g values were found for NMF (33), YLD (23), FW (23) and NDF (18), indicating genetic dispersal of the genotype in relation to the overall means of those traits. This parameter allows inferences on the relative dimensions of possible changes in each variable. Cortes et al. (2018) compared conventional and digital phenotyping and found similar CV_g values between the two methodologies. For PH, CV_g was 9 in both approaches; for SD, CV_g ranged from 7 (digital phenotyping) to 8 (manual phenotyping); for NDF, CV_g ranged from 17 to 22 (manual and digital phenotyping); and for YLD, CV_g ranged from 20 to 21 (manual and digital phenotyping).

The PH, NMF, and FW traits showed V_i values higher than a unity (111, 102 and 198 %, respectively). The V_i values equal to or higher than a unity indicate the success chances in selection. Nevertheless, it is possible to achieve good accuracy when the V_i is higher 50 % if a higher number of replicates is adopted. The variation index is thus more adequate than the experimental coefficient of variation (C_{Ve}), since the variation index also takes into account the number of replicates used and the residual variation.

SCA estimates

The SCA estimates are related to non-additive interactions resulting from gene complementation between parents, which allows predicting responses with genetic gain with a heterotic effect. Positive and negative SCA values were observed for all traits evaluated, indicating the existence of dominance deviations, which leads to genes that increase expression of the traits and others that are equally dominant and reduce this expression. Such estimates allow the selection of genotypes with superior related yield traits (Rocha et al., 2019).

For SD, NMF, FW, and YLD, the best hybrid combinations in the SCA study present positive combining abilities, indicating plants that are more vigorous, higher NMF, and higher YLD. For FFIH, PH, NDF, and NFN, however, the best hybrid combinations have negative SCA estimates, that is, estimates that indicate a reduction in both plant height and first-fruit insertion height as well as a smaller number of carpelloid and pentandric fruits and a lower sterility rate.

On the other hand, if the same hybrid combination shows positive SCA for PH and negative SCA for FFIH, it has a greater yield potential due to the larger fruit production segment in the plant. In the present study, hybrid combinations SS-72/12 × UCLA08-020, SS-72/12 × UCLA08-025 (Intermediate) and SS-72/12 × UCLA08-004 (Formosa) showed a higher PH and a lower FFIH.

However, only the SS-72/12 × UCLA08-025 combination showed a higher PH, lower AIFP and elevated YLD. This was one combination selected for the Intermediate group, as it showed SCA estimates for multiple traits favorable to crop breeding. Ide et al. (2009) evaluated combining ability for hybrid selection and found that the cross involving the 'Tailândia' genotype produced plants with low first-fruit insertion heights. The hybrid was high yielding, as its number of fruits per plant was above average.

Stem diameter should be taken into consideration in papaya breeding programs. Plants with a higher SD tend to lodge less, support more fruits and be more productive. The present data corroborate this information, considering that SD and NMF averages of hybrid combinations in this study were higher than in other categories, that is, hybrid combinations are capable of supporting a higher number of fruits and are thus more productive.

As stated by Ide et al. (2009), NMF and FW are directly related to plant productivity and are traits of major importance in terms of YLD, since they are directly linked to production volume. The NMF and YLD traits were higher than all other categories studied. The FW in the hybrid combinations, in turn, was lower in all categories. This is due to the additive effect, since topcross hybrid combinations were originated from a Solo genotype (SS-72/12) with Formosa lines. Daronch et al. (2014) concluded that additive effects were the most important in determining characters in relation to non-additive effects, particularly for quantitative traits, which also allows successful selection in early generations. Based on the information in Figures 2 and 3, we can identify highly productive combinations with an average production much higher than the overall mean of the hybrid combinations from both groups.

Number of fruitless nodes and NDF are traits that express sterility, carpellody and pentandry in papaya. The hybrid combinations should have negative SCA estimates for those traits, as this contributes to reducing sterility, carpellody and pentandry. The hybrids showed an average SCA of 4.79 for NFN, which is lower than 5.06 and 5.19 observed for the lines and controls, respectively. The average SCA for NDF of the hybrid, in turn, was 1.93, which is higher than the 1.62 and 1.83 shown by lines and controls, respectively. Even though the average SCA estimate for NDF in the hybrid was higher, there were hybrid combinations with estimates lower than the averages observed (Figures 2 and 3).

The evaluation of SCA for all traits evaluated suggests that it is possible to select hybrid combinations with promising morph-agronomic traits for papaya breeding. These combinations constitute materials that can meet the demands of the domestic and external markets and that may be available as new papaya cultivars to producers in the future.

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Authors' Contributions

Conceptualization: Pereira, M.G.; Vettorazzi, J.C.F.; Santa-Catarina, R.; Poltronieri, T.P.S.; Ramos, H.C.C.; Cortes, D.F.M. **Data acquisition:** Vettorazzi, J.C.F.; Santa-Catarina, R.; Poltronieri, T.P.S.; Azevedo, A.O.N.; Miranda, D.P.; Santana, J.G.S. **Data analysis:** Vettorazzi, J.C.F.; Santa-Catarina, R.; Poltronieri, T.P.S. **Design of methodology:** Pereira, M.G.; Vettorazzi, J.C.F.; Santa-Catarina, R. **Writing and editing:** Vettorazzi, J.C.F.; Santa-Catarina, R.; Poltronieri, T.P.S.; Pereira, M.G.

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