Experimental Agriculture (2025), vol. 61, e8, 1–15
doi:10.1017/S0014479725000079

CAMBRIDGE UNIVERSITY PRESS

RESEARCH ARTICLE

Genetic potential of Brazilian papaya (*Carica papaya* L.) lines and hybrids for improving fruit quality via specific combining ability and heterosis

Daniel Pereira Miranda, Helaine Christine Cancela Ramos, Renato Santa-Catarina, Juliana Saltires Santos, Julio Cesar Fiorio Vettorazzi, Josefa Grasiela Silva Santana, Tathianne Pastana de Sousa Poltronieri and Messias Gonzaga Pereira

Department of Plant Breeding, Universidade Estatual do Norte Fluminense - Darcy Ribeiro (UENF). Av. Alberto Lamego 2000, 28013-602. Campos dos Goytacazes, RJ – Brazil
Corresponding author: Daniel Pereira Miranda; Email: daniel.p.miranda08@gmail.com

(Received 27 September 2024; revised 05 February 2025; accepted 06 March 2025)

Summary
The development of new papaya cultivars with high genetic potential for production, combined with quality traits that meet the demands of emerging markets, facilitates the expansion of the genetic base, reduces production costs, and broadens papaya cultivation. This study continues the largest Brazilian papaya breeding program, a partnership of over 25 years between UENF and Caliman Agrícola S.A. The objective was to evaluate the ability of inbred lines to generate hybrids with market potential in Brazil and for export. A total of 62 hybrids were obtained through *topcross* strategy. The lines were evaluated based on their specific combining ability (SCA), and the hybrids were analyzed through estimates of functional and varietal heterosis (VH) using three widely cultivated commercial varieties in Brazil: 'UENF/CALIMAN 01', 'Tainung 01', and 'UC10'. Promising lines were identified for both hybrid creation and use as commercial varieties, exhibiting desirable traits for domestic and international markets, such as high fruit firmness and elevated soluble solids content (the lines UCLA08-053 and UCLA08-087 with the 'Intermediate' pattern and the lines UCLA08-066, UCLA08-122, and UCLA08-080 with the 'Formosa' pattern). Several hybrids, including H23, H26, H51, and H89 from the 'Intermediate' type and H4, H9, H19, and H68 from the 'Formosa' type, outperformed their parental lines and commercial varieties. These genotypes demonstrated superior SCA and VH compared to commercial controls, highlighting their strong genetic potential for the production market, increasing the shelf life of the fruits during storage and transportation, and allowing them to travel long distances without compromising fruit quality.

Keywords: Formosa; Intermediate; Solo

Introduction

Papaya (*Carica papaya* L.) is widely consumed worldwide. Brazil is the fifth-largest producer (1,138,343 tonnes) and the third-largest exporter (37,852.31 tonnes), holding the second position in export value (US$ 53,044,000) (FAOSTAT, 2023). Most of the papaya production is intended for fresh consumption, but papaya is also used in the food and pharmaceutical industries (Serrano and Cattaneo, 2010) and is considered a rich source of vitamins A and C, folate, thiamine, niacin, riboflavin, iron, potassium, calcium, and fiber (Tuo *et al.,* 2023). Additionally, papaya has gained recognition for biodiesel production through oil extraction from its seeds (Anwar *et al.,* 2019;

Nayak and Vyas, 2019), highlighting the remarkable versatility of this species across various industry sectors.

To broaden cultivar options and meet market demands, Brazil invests in developing cultivars with fruit patterns from the 'Formosa' and 'Solo' groups, as well as 'Intermediate' fruits through crosses between these groups (Marin *et al.,* 2006; Cardoso *et al.,* 2014; Pereira *et al.,* 2019a). Recently, Santana *et al.* (2023) identified 'Intermediate' fruits in inbred F_5 papaya lines derived from the initial cross of two 'Formosa' genotypes. These fruits typically weigh 700–1000 g (Miranda *et al.,* 2021), offering greater variety to consumers and producers. The 'Intermediate' hybrids 'UC14' and 'UC16' are noted for their high quality and yield, outperforming cultivars like Golden and Tainung 01 (Luz *et al.,* 2015; Pereira *et al.,* 2019b). Thus, crossing heterotic groups is a promising strategy for developing hybrids that cater to both consumer and producer needs.

Developing papaya cultivars poses challenges for breeders, requiring them to balance high yield potential, fruit quality, and disease resistance. Breeders must consider consumer preferences, such as fruit weight, size, flavor, pulp thickness, and firmness. According to Miranda *et al.* (2024), identifying genotypes with high averages for this trait can be challenging, as these traits may exhibit negative correlations. To address this, it is important to assign equivalent selection weights to negatively correlated traits, ensuring that genotypes with high values for one trait are not selected at the expense of another equally important trait.

Given these challenges, papaya breeding can involve developing homozygous lines or hybrids by crossing genetically distinct individuals, with the aim of utilizing heterosis effectively. A key objective is to develop superior parental lines that yield strong hybrid combinations (Gramaje, 2020). According to Dantas and Lima (2001), improved papaya lines can be used "*per se*" in production systems or as parents in the production of hybrids. When using inbred lines, cultivation is viable because self-pollination does not lead to a significant loss of vigor in papaya.

In cases where there are many improved lines, an alternative to evaluating their performance is the use of the topcross strategy (Davis, 1927), making it possible to distinguish the lines that can generate new hybrids, using testers that have been proven to generate good progenies, as performed by Barros *et al.* (2017b). To identify the most promising hybrid combinations, the specific combining ability (SCA) between the lines and the tester can be estimated, where the tester serves as an indicator to determine whether the tested lines can produce superior progenies (Borém and Miranda, 2013). SCA is highly related to non-additive causes, such as dominance deviations and epistatic effects (Musembi *et al.,* 2015), enhancing genetic gain through heterosis exploitation via diverse crosses (Teodoro *et al.,* 2017).

To ensure that the new hybrids are suitable for the consumer market, it is necessary to evaluate their potential in relation to the parents and/or their superiority concerning commercial cultivars widely used in agriculture. One way to obtain this information is by estimating functional and varietal heterosis (VH). In papaya, the exploitation of heterosis proved advantageous for morphoagronomic traits and fruit quality in crosses between lines from different heterotic groups (Marin *et al.,* 2006) or within the same group (Cardoso *et al.,* 2014). These crosses in papaya also favored the production of F_1 hybrids resistant to diseases such as phoma and black spot (Vivas *et al.,* 2016; Poltronieri *et al.,* 2019). Thus, this study aims to evaluate the performance of Brazilian papaya lines and hybrids in improving fruit quality, based on SCA and heterosis and to select potential genotypes to be included in the crop-producing market.

Material and methods

Genetic material and experimental conditions

The experimental trial was carried out in the commercial area of Empresa Caliman Agrícola S.A, located in Linhares-ES, Brazil (19°23′28″ S, 40°04′20″ W, and altitude of 33 m). The papaya lines involved in this topcross were developed from the initial crossing between the UC-Sekati and

https://doi.org/10.1017/S0014479725000079 Published online by Cambridge University Press

UC-JS12 (pollen donor), genotypes belonging to the 'Formosa' group, with contrasting agronomic traits; UC-Sekati, known for large fruits, excellent pulp firmness, and moderate soluble solids, and UC-JS12 (pollen donor), which has moderate pulp firmness and high soluble solids content. Both parents belong to the 'Formosa' heterotic group. An F_1 plant obtained from this cross was self-fertilized to give rise to the F_2 population, which contained about 200 hermaphrodite genotypes. From the F_2 generation, the genotypes were conducted until the F_4 generation by the single seed descent (SSD) method. Ninety-seven papaya lines (pollen donors) of the F_4 generation were crossed with the SS-72/12 parent ('Solo' group tester) to obtain the 62 hybrids (Table S1, supplementary material).

The experimental design used was the 13 × 13 lattice square, composed of 97 F_5 lines from the self-fertilization of parental F_4 lines, 62 topcross hybrids and 10 controls ('UC-Sekati', 'UC10', 'UC-JS12', 'Maradol', 'UENF/CALIMAN 01', 'Tainung 01', 'SS-72/12', 'Golden', 'Aliança', and 'Waimanalo'), totaling 169 genotypes. The design consisted of five replications with two plants per plot, spaced 3.6 m between rows and 1.5 m between plants in the row, each plot containing two plants spaced 3.6 m between rows and 1.5 m within rows. Seedlings were transplanted 30 days post-emergence, with four seedlings per pit, and the sexing was performed after three months after planting, after the first flowers appeared, leaving only one hermaphrodite plant per hole for the experiment.

Evaluated traits

For fruit quality, eight traits were evaluated. The measurements of the variables were performed from five fruits per plant at the first stage of maturation (Basulto *et al.,* 2009). The evaluations were carried out three times: 210 (October 2017), 300 (January 2018), and 390 (May 2018) days after planting. The traits evaluated were (1) fruit weight (FW), expressed in g and measured with the aid of a Toledo model 9094 digital analytical balance; (2) fruit length (FL) in cm; (3) fruit diameter (FD) in cm; and (4) pulp thickness (PT) in cm. Variables 2, 3, and 4 were analysed using digital images according to Santa-Catarina *et al.* (2018). (5) Fruit firmness (FF) in Newton (N) was determined from three perforations at equidistant points in the equatorial region; (6) pulp firmness (PF) in N was obtained from fruits cut transversally on two equal sides and made three equidistant perforations in the pulp. For fruit and pulp firmness, a Benchtop Digital Penetrometer (*Fruit Pressure Tester*, Italy, Model 53205) with a 3.0 x 0.5 cm adapter (height x diameter) was used; (7) soluble solids content (SSC) in Brix was determined using an Atago N1 portable refractometer; (8) pulp volume percentage (PV%) was obtained from the calculation of ovarian cavity volume (OCV), fruit volume (FV), and pulp volume (PV). The OCV and FV were calculated using measurements of the lengths and diameters of the fruit and the ovarian cavity following the formula: $V_e = \pi(L\ x\ D^2/6)$, in which V_e is the estimated volume, L is the length, and D is the diameter, as described by Santa-Catarina *et al.* (2018), adapted from Koc (2007). The difference between FV and OCV estimated PV. The percentage of pulp volume (PV%) was calculated using the formula: PV% = (PV*100)/FV.

Specific combining ability (SCA)

The SCA estimates were obtained according to the expression presented by Hallauer *et al.* (2010) through the differences between the average of each of the hybrids obtained from a tester (Xe) and the general average of crosses with that tester (Xg), as illustrated below: $SCA_{gTi} = X_{e.Ti} - X_{g.Ti}$. The significance of SCA was tested through a t-test analysis ($t \leq 0.01$ and $t \leq 0.05$): $t = \frac{SCA}{(\sigma_e^2/r)^{1/2}}\ x\ 100$, where SCA = SCA; σ_e^2 = mean square error, and r = repetition number.

https://doi.org/10.1017/S0014479725000079 Published online by Cambridge University Press

Heterosis

Functional heterosis (FH) and VH were estimated using the treatment means, as described by Huang *et al.* (2015) and Gramaje *et al.* (2020): $FH = \frac{(F_1-PL)}{PL}\ x\ 100$, and $VH = \frac{(F_1-CC)}{CC} x\ 100$, where PL = performance of the lines; CC = performance of commercial cultivars. The VH was calculated using commercial cultivars from the 'Formosa' group: VH1 with UENF/CALIMAN 01, VH2 with UC10, and VH3 with Tainung 01.

The significance of heterosis was tested using the t-test (t≤0.01 and t≤0.05):

$$t = \frac{(F_1 -\ CC)\ or\ (F_1 - PL)}{(2\sigma_e^2/r)^{1/2}} x\ 100$$

where σ_e^2= mean square error, and r = number of replications

To enhance the visualization of the results, the estimates of SCA and heterosis were standardized and presented in figures. SCA estimates were visualized in Microsoft Excel, while heterosis estimates were plotted using the 'ggplot2' package in RStudio (version 4.3.1). All estimates with their respective significance levels are attached.

Results

Performance of the lines via SCA

For the evaluated traits, the SCA of some combinations presented positive and negative estimates, with significant effects (Figure 1, and Table S2-S3, supplementary material). Based on SCA, it was possible to separate the hybrids into two groups, mainly based on fruit weight. The 'Intermediate' presented hybrids with fruits weight below 'Formosa' and above 'Solo', with about 746-980 g. The other group, the hybrids, had a patten weight of the 'Formosa' group above 1000 g (data not shown).

For the FW in the 'Intermediate' combinations (Figure 1), the estimates ranged from −187.58 (SS-72/12 x UCLA08-127) to 85.96 (SS-72/12 x UCLA08-113). The FF in the 'Intermediate' group (Figure 1), the combinations of SS-72/12 with UCLA08-088 (6.81), UCLA08-034 (6.38), and UCLA08-060 (6.00) were the ones with the highest positive and significant values (t≤0.05). Estimates for PF in the 'Intermediate' group combinations (Figure 1) ranged from −11.09 (SS-72/12 x UCLA08-111$_{t\leq 0.01}$) to 4.60 (SS3-72/12 x UCLA08-075$_{t\leq 0.05}$). For the SSC (Figure 1), only the combinations with estimates above one showed significance at t≤0.05 (combinations of SS-72/12 with UCLA08-034 and UCLA08-053).

The values for PT of the 'Intermediate' group (Figure 1) ranged from -0.21 (SS-72/12 x UCLA08-069) to 0.16 (SS-72/12 x UCLA08-111), with combinations above 0.13 (combinations of SS-72/12 with UCLA08-111, UCLA08-126, UCLA08-113 and UCLA08-038) were considered significant (t≤0.05). For the FL (Figure 1), estimates ranged from -1.51 (SS-72/12 x UCLA08-021) to 2.15 (SS-72/12 x UCLA08-038), where these two were the only significant combinations (t≤0.05). For FD (Figure 1), only the SS-72/12 x UCLA08-060 (0.61$_{t\leq 0.05}$) presented a significant positive estimate. The PV% of the 'Intermediate' group in the combinations of SS-72/12 with UCLA08-033, UCLA08-001, UCLA08-025, and UCLA08-126 were the higher estimates with values above 3.57$_{t\leq 0.05}$.

In the 'Formosa' combinations, for the FW (Figure 2), the combinations of the SS-72/12 tester with the UCLA08-122, UCLA08-074, and UCLA08-096 lines showed the highest significant SCA estimates (t≤0.05) with the following values 150.54, 147.30, and 128.34, respectively. The estimates for FF (Figure 2) ranged from −6.51 (SS-72/12 x UCLA08-122) to 9.35 (SS-72/12 x UCLA08-026). Positive significant combinations (t≤0.01) reached estimates above 6.95 (combinations of SS-72/12 with UCLA08-026, UCLA08-028, UCLA08-013, and UCLA08-097). To PF, the combinations (Figure 2) presented values between -8.37 (SS-72/12 x UCLA08-084) and 6.94 (SS-72/12 x UCLA08-057), showing statistical significance at ≤0.05 from 4.80 (SS-72/12 x UCLA08-061) and at t≤0.01 from 6.04 (SS-72/12 x UCLA08-080). For the SSC, the combinations

https://doi.org/10.1017/S0014479725000079 Published online by Cambridge University Press

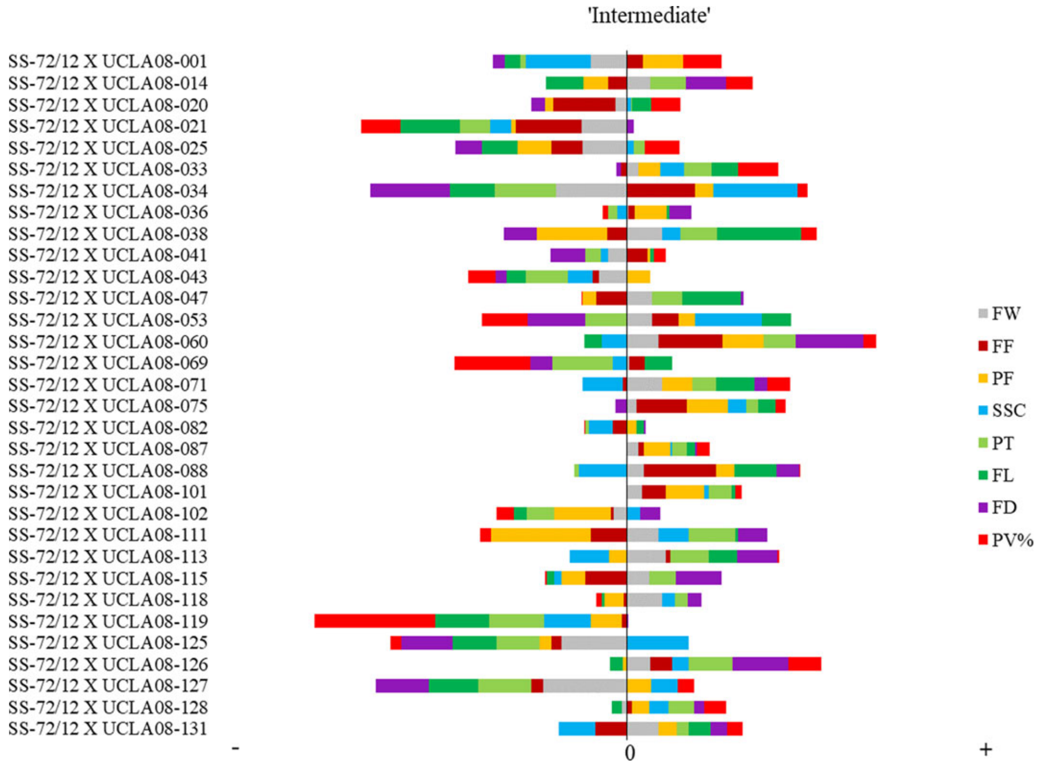

Figure 1. Standardized estimates of the specific combining ability (SCA) considered within the 'Intermediate' patten, for fruit weight (FW $_{(g)}$), fruit firmness (FF $_{(Newtons)}$), pulp (PF $_{(Newtons)}$), soluble solids content (SSC $_{(^{o}Brix)}$), pulp thickness (PT $_{(cm)}$), fruit length (FL $_{(cm)}$), fruit diameter (FD $_{(cm)}$), and pulp volume percentage (PV%). The values to the left (−) and right (+) of point 0 represent the positive and negative SCA estimates, respectively. The higher the bar in each color, the higher the estimated SCA.

of SS-72/12 with UCLA08-114, UCLA08-012 (both with t≤0.01), UCLA08-005, and UCLA08-013 (both with t≤0.05) presented the higher and more significant SCA estimates (0.99-1.47). As for the fruits of the 'Intermediate' group, for the 'Formosa' hybrids, only the combinations with estimates above one showed significance for this same trait (Figure 2).

The best positive combinations of the 'Formosa' group for PT (Figure 2) were the combinations of SS-72/12 with UCLA08-028 ($0.29_{t\leq0.01}$), UCLA08-005 ($0.19_{t\leq0.01}$), UCLA08-091 ($0.16_{t\leq0.05}$), and UCLA08-055 ($0.15_{t\leq0.05}$). The combination SS-72/12 x UCLA08-078 ($1.61_{t\leq0.05}$) was the one that most significantly contributed to the increase in the length of the 'Formosa' fruit (1.61), followed by combination SS-72/12 x UCLA08-028 (1.41). For the trait FD (Figure 2), the combinations of SS-72/12 with UCLA08-122 (0.598) and UCLA08-096 (0.571) presented positive and significant values (t≤0.05) but without major contributions, as well as the hybrids that showed negative values. It was found that for the PV% of the 'Formosa' hybrids (Figure 2), the combinations of SS-72/12 with UCLA08-112, UCLA08-028, UCLA08-057 (all with t≤0.01), and UCLA08-037 (t≤0.05) presented between 4.2 and 7.5, respectively.

Heterosis

Varietal heterosis (VH)

In VH1, the 'Intermediate' hybrids presented for FW, PF, PT, FL, and FD, a greater number of combinations showed negative estimates (Figure 3A, and Table S4, supplementary material)

https://doi.org/10.1017/S0014479725000079 Published online by Cambridge University Press

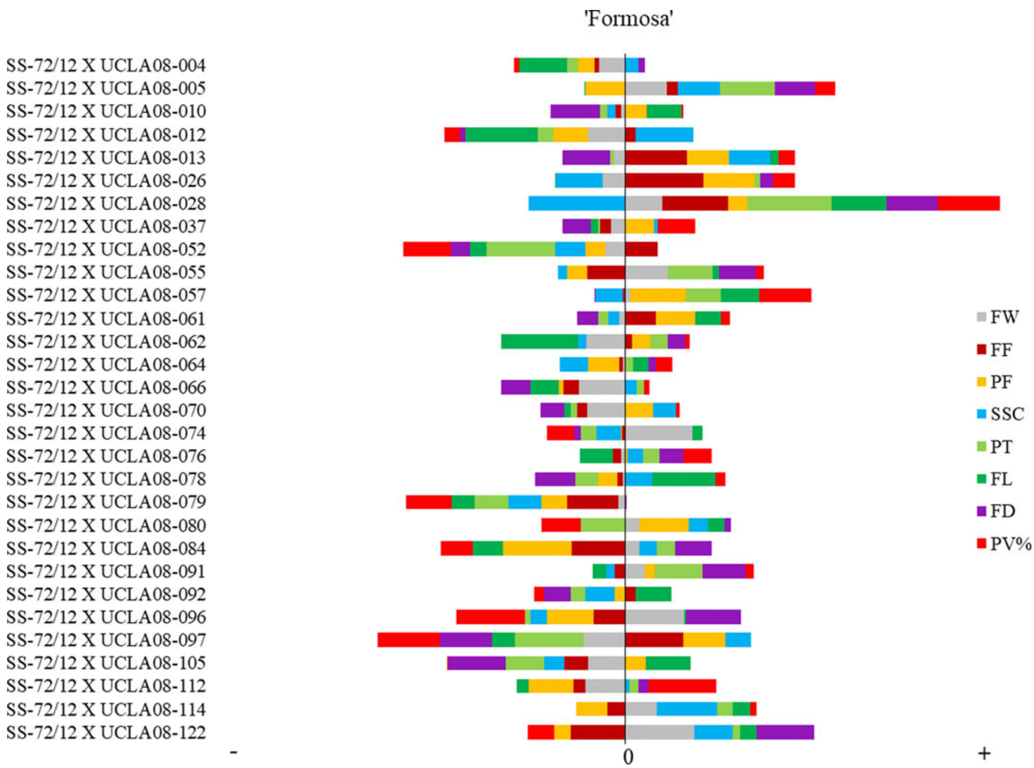

Figure 2. Standardized estimates of the specific combining ability (SCA) considered within the 'Formosa' patten, for fruit weight (FW $_{(g)}$), fruit firmness (FF $_{(Newtons)}$), pulp (PF $_{(Newtons)}$), soluble solids content (SSC $_{(°Brix)}$), pulp thickness (PT $_{(cm)}$), fruit length (FL $_{(cm)}$), fruit diameter (FD $_{(cm)}$), and pulp volume percentage (PV%). The values to the left (−) and right (+) of point 0 represent the positive and negative SCA estimates, respectively. The higher the bar in each color, the higher the estimated SCA.

indicating that the performance in most of the hybrids for these traits was lower than that found for the cultivar UENF/ CALIMAN 01. For VH1 of the 'Formosa' group, most of the hybrids presented lower estimates for FW, PF, and FL than those found in the hybrid 'UENF/CALIMAN 01' (Figure 4A).

In VH1, the 'Intermediate' hybrids for FF, SSC, and PV%, more than 90% of the combinations presented higher estimates to the hybrid 'UENF/CALIMAN 01'. According to the results, the hybrid H89 (SS-72/12 X UCLA08-126) stood out for FF ($6.81_{t\leq0.05}$), SSC ($15.76_{t\leq0.05}$), PT (5.01), FD (1.54), and PV% ($14.03_{t\leq0.01}$) with high positive estimates for these variables. Followed by the H89 hybrid, the hybrids H23 (SS-72/12 X UCLA08-034), H51(SS-72/12 X UCLA08-075), H89 (SS-72/12 X UCLA08-122) showed positive VH at for FF (H23: $10.36_{t\leq0.01}$; H51: $8.93_{t\leq0.01}$; H89: $6.81_{t\leq0.05}$), SSC (H23: $26.49_{t\leq0.01}$; H51: $16.05_{t\leq0.05}$; H89: $15.76_{t\leq0.05}$) and PV% (H23: $10.43_{t\leq0.01}$; H51: $10.44_{t\leq0.01}$; H89: $14.03_{t\leq0.01}$). The other hybrids showed positive and significant VH1 only for two characteristics or less, or even did not show significant values.

For VH1 of the 'Formosa' group, most of the hybrids presented lower estimates for FW, PF, and FL than those found in the hybrid 'UENF/CALIMAN 01' (Figure 4A). It is worth noting that the percentage of hybrids with positive VH for FF, SSC, PT, FD and PV% were 96.4% (0.01–13.16), 92.8% (2.41–25.78), 78.6% (0.52–14.82), 64.3% (0.80–7.66), and 89.3% (0.05–17.45), respectively. The hybrid H4 (SS-72/12 X UCLA08-005) stood out with high estimates for FW (1.22), FF ($6.49_{t\leq0.05}$), SSC ($21.07_{t\leq0.01}$), PT ($10.62_{t\leq0.01}$), FD (5.72), and a considerable PV% ($9.67_{t\leq0.05}$). Meanwhile, the hybrid H19 (SS-72/12 X UCLA08-028) also presented a favorable

https://doi.org/10.1017/S0014479725000079 Published online by Cambridge University Press

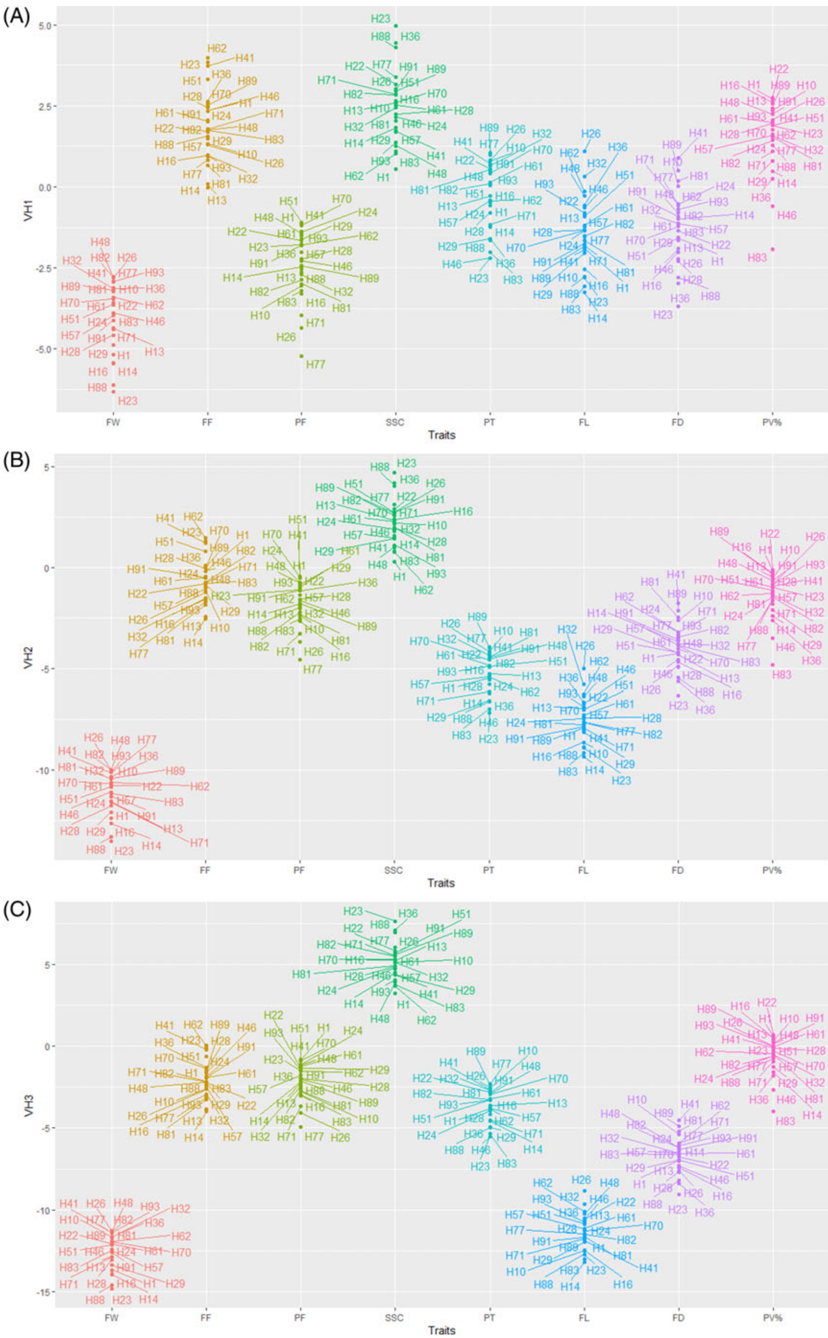

Figure 3. Standardized estimates for the varietal heterosis of the hybrids are considered as 'Intermediate' patten, using the cultivars UENF/CALIMAN 01 (**A**), UC10 (**B**), and Tainung 01 (**C**). Fruit weight (FW $_{(g)}$), fruit firmness (FF $_{(Newtons)}$), pulp firmness (PF $_{(Newtons)}$), soluble solids content (SSC $_{(°Brix)}$), pulp thickness (PT $_{(cm)}$), fruit length (FL $_{(cm)}$), fruit diameter (FD $_{(cm)}$), and pulp volume percentage (PV%).

https://doi.org/10.1017/S0014479725000079 Published online by Cambridge University Press

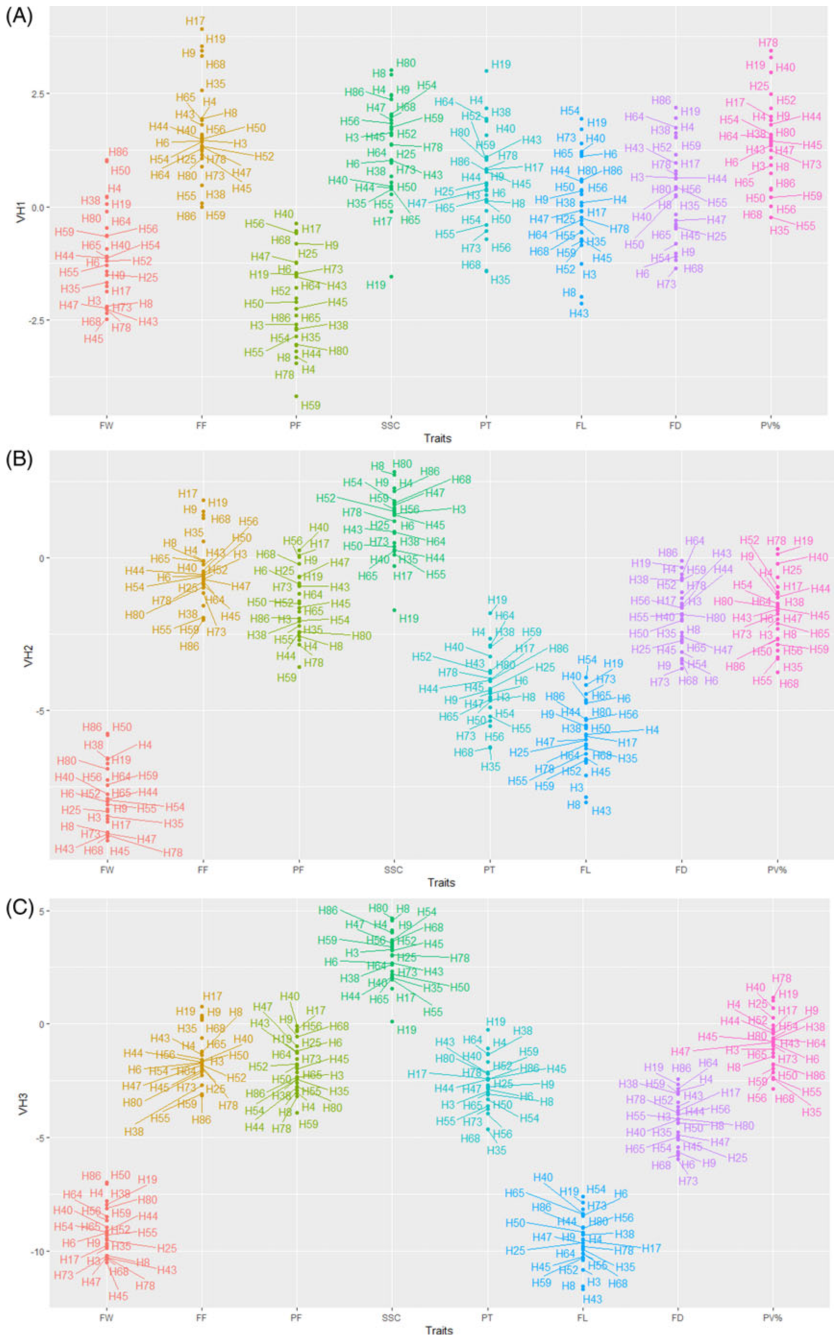

Figure 4. Standardized estimates for the varietal heterosis of the hybrids considered as 'Formosa' patten, using the cultivars UENF/CALIMAN 01 (**A**), UC10 (**B**), and Tainung 01 (**C**). Fruit weight (FW $_{(g)}$), fruit firmness (FF $_{(Newtons)}$), pulp firmness (PF $_{(Newtons)}$), soluble solids content (SSC $_{(°Brix)}$), pulp thickness (PT $_{(cm)}$), fruit length (FL $_{(cm)}$), fruit diameter (FD $_{(cm)}$), and pulp volume percentage (PV%).

estimate for six traits: FW (0.39), FF ($11.91_{t \leq 0.01}$), PT ($14.82_{t \leq 0.01}$), FL (7.94), FD (6.90), and PV% ($16.62_{t \leq 0.01}$).

For VH2 (Figure 3B, Table S4, supplementary material) of the 'Intermediate' hybrids, estimates were 100% negative for FW, PF, PT, FL, FD, and PV%, while for VH3 (Figure 3C, Table S4, supplementary material), similar results were found, but with 70% of negative estimates for PV%. All hybrids showed positive estimates for SSC in VH2 (1.41-4.63) and VH3 (20.0-47.47), highlighting the hybrids H23 (SS-72/12 X UCLA08-034), H36 (SS-72/12 X UCLA08-053) and H88 (SS-72/12 X UCLA08-125) with significance at t≤0.05 (VH2: 21.11-24.63; VH3: 43.30-47.47) demonstrating great superiority of the hybrids concerning the hybrids 'UC10' and 'Tainung 01', cultivated throughout Brazil.

All the 'Formosa' hybrids presented negative estimates for the FW, PT, FL, FD, and PV% traits, indicating a lower performance than the commercial hybrids 'UC10' and 'Tainung 01'. In VH2, 83.3% and 90.0% of the hybrids showed negative estimates for FF and PF, respectively (Figure 4B, Table S4, supplementary material). In VH3, 100% and 86.6% of the hybrids showed lower PF and FF, respectively when compared to the cultivar Tainung 01 (Figure 4C, Table S4, supplementary material). The hybrid H68 (SS-72/12 x UCLA08-097), compared to cultivar UC10, and the hybrids H9 (SS-72/12 x UCLA08-013) and H68 (SS-72/12 x UCLA08-097), compared to cultivar Tainung 01, present the best performance when the intention is to increase firmness and SSC, presenting for these variables a better performance concerning commercial cultivars.

Functional heterosis (FH)

All hybrids with fruits of the 'Intermediate' (Figure 5A, Table S4, supplementary material) and 'Formosa' (Figure 5B, and Table S4, supplementary material) type evaluated presented for FH concerning FL and PV%, a performance inferior to the lines *per se*, with 100% of the negative estimates. For the 'Intermediate' hybrids, the FH estimates for FW, FF, PF, and FD were negative, and the percentage of hybrids with negative estimates were 86.6%, 53.3%, 83.3%, and 76.6%, respectively (Figure 5A). The hybrids showed a better performance for the SSC than the lines that gave rise to them, with 93.3% of the hybrids with positive estimates (0.85-53.91), except for the hybrids H71 (SS-72/12 X UCLA08-102) and H93 (SS–72/12 X UCLA08-131). For FW, the hybrids 'Intermediate' H88 (SS-72/12 X UCLA08-125), H70 (SS-72/12 X UCLA08-101), H48 (SS-72/12 X UCLA08-071), and H28 (SS-72/ 12 X UCLA08-041) were the ones that presented positive estimates, with superior performance to the parent line, such hybrids also stood out for presenting positive FH for other characteristics related to fruit quality, such as H70 (SS-72/12 X U V CLA08-101), which presented high estimates for FW (19.26), PF (0.33), and FD ($14.71_{t \leq 0.01}$); H88 (SS-72/12 X UCLA08-125), which stood out for FW (30.73), FF (3.93), PT (3.23), and FD ($15.03_{t \leq 0.01}$).

Still, in the 'Intermediate' group, some lines performed better than the hybrids they constitute, the lines UCLA08-075 and UCLA08-119, the ones that stood out the most for this set of characteristics (FW, FF, PT, FL, FD, and PV%). In the case of lines UCLA08-053 and UCLA08-087, the high performance *per se* was related to the characteristics FW, SSC, PT, FL, and PV%, and for FW, FF, PF, PT, FL, FD, and PV%, respectively.

The hybrids of the 'Formosa' group presented positive estimates for the characteristics FW, FF, PF, PT, and FD, with 25.0% (1.81–71.33), 53.8% (0.08–13.46), 17.9% (1.31–6.31), 17.9% (0.51–17.33), and 67.9% (1.10–27.32), respectively (Figure 5B). For SSC, 92.85% of the hybrids showed positive FH (0.26-35.34), indicating that the evaluated hybrids outperformed the parent line, except for the hybrids H19 (SS-72/12 X UCLA08-028) and H73 (SS-72/12 X UCLA08-105), which showed negative functional heterosis. The hybrids H52 (SS-72/12 X UCLA08-076) and H43 (SS-72/12 X UCLA08-062) presented high positive estimates for the FW (H52:$71.33_{t \leq 0.01}$; H43: 6.09), PT (H52:$17.33_{t \leq 0.01}$; H43: $9.24_{t \leq 0.05}$), and FD (H52: $27.32_{t \leq 0.01}$; H43: $15.26_{t \leq 0.01}$) characteristics, being highlighted when the interest is the commercialization of fruits with a higher proportion of pulp. In turn, the hybrid H9 (SS-72/12 X UCLA08-013) concentrated higher

https://doi.org/10.1017/S0014479725000079 Published online by Cambridge University Press

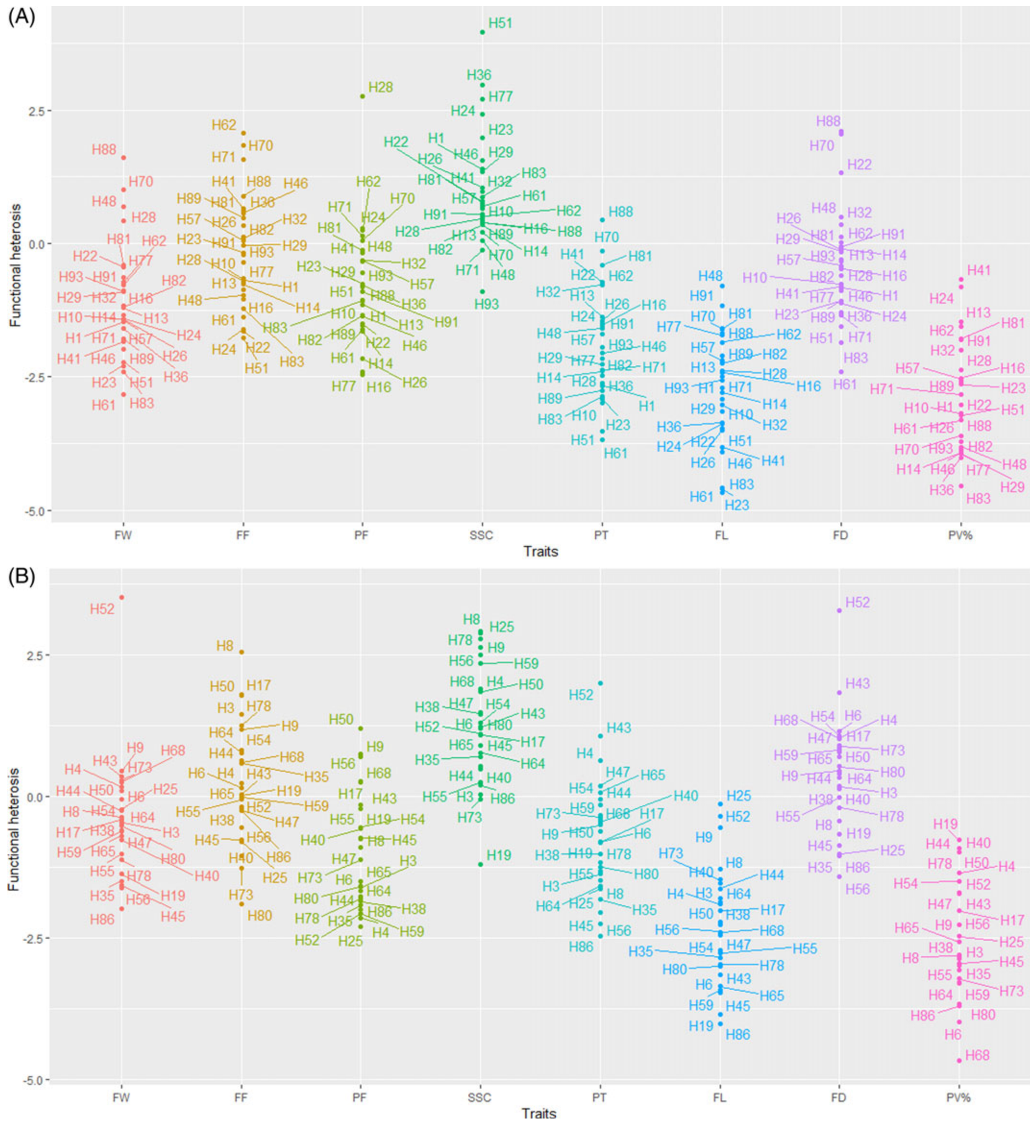

Figure 5. Standardized estimates of the functional heterosis for the hybrids considered as 'Intermediate' (**A**) and 'Formosa' (**B**) pattern, for fruit weight ($FW_{(g)}$), fruit firmness ($FF_{(Newtons)}$), pulp firmness ($PF_{(Newtons)}$), soluble solids content ($SSC_{(°Brix)}$), pulp thickness ($PT_{(cm)}$), fruit length ($FL_{(cm)}$), fruit diameter ($FD_{(cm)}$), and pulp volume percentage.

estimates for a greater number of variables, considering FW, FF, PF, and SSC. (9.13, $6.21_{t\leq 0.05}$, 3.94, $31.78_{t\leq 0.01}$, respectively).

Discussion

SCA reflects non-additive effects such as dominance deviations and/or epistasis, which primarily control genetic variables. Negative SCA estimates may result from unfavorable allelic combinations during recombination, while positive estimates are strong candidates for exploiting heterosis (Reddy *et al.*, 2013). Combinations with high SCA values linked to fruit quality are ideal for selection in breeding programs.

https://doi.org/10.1017/S0014479725000079 Published online by Cambridge University Press

When selecting genotypes for fruit quality, physical and physicochemical characteristics serve as key criteria to differentiate them. These parameters are closely linked to the fruit's market destination and consumer preferences. In this study, two distinct fruit size categories were identified: the 'Formosa' type and the 'Intermediate' type. The evaluated hybrids exhibited phenotypic similarities to commercial cultivars in terms of fruit quality traits, indicating strong potential for commercialization.

Average fruit weight is a critical trait that reflects yield potential in papaya genotype selection (Barros *et al.,* 2017a). Both fruit weight and shape can vary significantly among genotypes, even within the same heterotic group. For instance, 'Formosa' varieties like the hybrids 'UENF/CALIMAN 01' (1200 g), 'Tainung 01' (1500 g), and 'UC10' (1900 g) produce larger fruits, with average weights exceeding 1000 g. On the other hand, the UC14 cultivar (Pereira *et al.,* 2019a) has an average of 800 g, an example of fruit size, a reference for the 'Intermediate' group. The developed combinations resemble the cultivars UENF/CALIMAN 01 (large fruits) and UC14 (small fruits). Notably, SS-72/12 x UCLA08-113 in the 'Intermediate' group, and SS-72/12 crossed with UCLA08-122, UCLA08-074, and UCLA08-096 in the 'Formosa' group, significantly increased fruit size in their respective categories. This morphological similarity may ease market acceptance, as producers can adopt these new genotypes without needing to adjust production practices or incur additional costs for inputs and packaging.

Fruit length, diameter, and thickness vary by market demands. For the 'Intermediate' and 'Formosa' hybrids, no specific combination excelled across all variables. This aligns with Ide *et al.* (2009), who found no combinations with high SCA for all morphological, fruit yield, and quality variables. However, SS-72/12 x UCLA08-038 ('Intermediate') and SS-72/12 x UCLA08-028 ('Formosa') showed desirable estimates for PT and FL.

In papaya, fruit firmness is a critical trait for market success, as firmer fruits are more resilient during handling and transport, providing a clear advantage in trade. Fagundes & Yamanishi (2001) highlighted that fruits with higher firmness are more resistant to damage and enjoy an extended shelf life. In this study, the combinations of SS-72/12 with UCLA08-060 and UCLA08-096 from the 'Intermediate' group and SS-72/12 with UCLA08-026, UCLA08-013, and UCLA08-097 from the 'Formosa' group stood out for exhibiting high firmness. This suggests their suitability for international markets requiring long-distance transportation. Additionally, the combinations of SS-72/12 with UCLA08-001 ('Intermediate') and UCLA08-057 ('Formosa') displayed notable estimates for fruit weight (FW) alongside relatively moderate pulp volume percentage (PV%). This is consistent with the findings of Miranda *et al.* (2024), who observed that fruits with higher weight often have a lower pulp volume percentage. Therefore, these combinations demonstrate strong potential for both industrial processing and consumer markets.

Fresh papaya consumption favors fruits with higher sweetness levels, which can be observed in the combinations of the 'Intermediate' group of SS-72/12 with UCLA08-034 and UCLA08-053 and the group 'Formosa' SS-72/12 with UCLA08-114, UCLA08-012, UCLA08-005, and UCLA08-013. For the soluble solids content, the occurrence of combinations with SCA estimates below zero and with a low amplitude of variation, as observed in this study, is reported by Ide *et al.* (2009), Barros *et al.* (2017b), and Santa-Catarina *et al.* (2019). Thus, greater attention should be paid to the selection of genotypes for this variable, given that it is a trait that directly influences the acceptance and consumption of the fruit.

When analyzing together the SCA estimates for the variables associated with quality in the physical and physicochemical aspects of the fruit, it was not possible to select lines capable of generating superior hybrids for all variables together for the two groups under study. However, in the 'Intermediate' patten, it was possible to select the lines UCLA08-126 for PT and PV%; UCLA08-038 for PT and FL, and UCLA08-060 for FD, FF, and PF. For the lines that generated hybrids with the 'Formosa' pattern, the selection for the most promising combinations when SS-72/12 was crossed with UCLA08-005, which brings together favorable estimates for PT and SSC, and UCLA08-013 for FF and SSC, meeting market requirements for export and consumer.

https://doi.org/10.1017/S0014479725000079 Published online by Cambridge University Press

The evaluation of heterosis is an important parameter when evaluating the performance of a hybrid. In VH, the degree of hybrid vigor is expressed in relation to a commercial cultivar. Thus, it is expected that the hybrids tested for some variables have performance equal or superior to the cultivars of great acceptance in the market. The cultivars UENF Caliman 01, UC10, and Tainung 01, are hybrids widely used in papaya cultivation, especially when desired to obtain fruits in the 'Formosa' pattern. These hybrids belong to the heterotic group 'Formosa' and have phenotypic traits similar to this group.

According to Morais *et al.* (2007), 'UENF/CALIMAN 01' (used as the control for VH1) is characterized by elongated fruits (21.03 cm length, 10.96 cm width), weighing 1.28 kg, and a pulp thickness of 2.74 cm. In this study, most 'Intermediate' hybrids showed negative VH1 estimates for FW, PF, FL, and FD, which is expected since these hybrids typically produce smaller, lighter fruits, intermediate between the 'Formosa' and 'Solo' types. Hybrids from parents with varying fruit sizes often result in fruits with an 'Intermediate' pattern (Pereira *et al.,* 2019b), as observed here, where half of the evaluated hybrids had this intermediate size, especially for FW, FL, and FD, explaining the negative VH1 estimates.

Combinations with positive estimates for VH1 indicate that they perform better than the market cultivar. For the FF, SSC, and PV% of the 'Intermediate' hybrids, many combinations, particularly H23, H26, and H36, displayed positive heterosis, surpassing 'UENF/CALIMAN 01' hybrid, considered promising and with high potential for the consumption of fresh fruit. Besides being superior to the control cultivar, H23 showed a high SCA for the same traits, emphasizing the role of non-additive interactions and the potential of heterosis to enhance fruit quality.

In the 'Formosa' hybrids, most showed negative performance for key traits like FW, FL, and PF, indicating that despite physical similarities, they did not outperform 'UENF/CALIMAN 01' in these traits. On the other hand, H19 added superiority for six variables concerning 'UENF/CALIMAN 01' (FW, FF, PT, FL, FD, and PV%), and H4 excelled in FF, SSC, PT, and PV%, despite not having significantly longer fruits than 'UENF/CALIMAN 01'. Both H19 and H4 also had high SCA estimates, suggesting a high degree of allelic complementation between parental lines. The positive estimates of VH for the quality characteristics of the fruit, which are not associated with the size of the fruit, suggest a potential to select smaller fruits that exhibit superior quality traits compared to 'UENF/CALIMAN 01', expanding market opportunities for patten-sized 'Formosa' fruit.

The 'Tainung 01' and 'UC10' hybrids have many similarities in traits associated with fruit quality (Luz *et al.,* 2015). This fact explains the similarity in the proportion of 'Intermediate' and 'Formosa' hybrids with negative estimates for the variables analyzed in VH2 and VH3. As was observed in VH1, for VH2 and VH3, the 'Intermediate' hybrids showed an expected response, with many hybrids with negative estimates related to the variables FW, FD, FL, PT, and PF. Nonetheless, 'Intermediate' hybrids H23 and H51, with high VH2 and VH3 for SSC and FF, show promise for meeting domestic market demand, which favors smaller fruits with higher soluble solids and firmness.

'Formosa'-type hybrids showed positive estimates for the FF, PF, and SSC traits in VH2 and VH3, even though this proportion was low for firmness. According to Reis *et al.* (2015), for pulp firmness, the most desirable thing is that the performance of the hybrids is similar to commercial cultivars because excessively firm fruits may be less desirable for fresh consumption. However, for fruit firmness, fruits should present greater firmness with the skin and greater resistance in the transport, storage, and handling of the fruit (Fagundes and Yamanishi, 2001; Morais *et al.,* 2007). In this sense, the hybrids H9 and H68 stand out for presenting high fruit firmness and pulp firmness, similar to the 'UC10' and 'Tainung 01', along with high SCA. As noted by Reis *et al.* (2015), 'Formosa' hybrids are expanding in both domestic and international markets, with growing exports to Europe, Canada, and the U.S. Incorporating new genotypes with desirable traits for these markets could further expand the papaya industry.

https://doi.org/10.1017/S0014479725000079 Published online by Cambridge University Press

From a commercial perspective, a hybrid is advantageous if its performance matches or exceeds that of established commercial cultivars. In papaya, however, there is the possibility of finding lines as good as hybrids due to the species' low inbreeding depression. FH estimation determines whether hybrids or parental lines offer greater commercial potential. Hybrids with negative heterosis effects for specific traits may be less advantageous than directly utilizing parental lines. On the other hand, hybrids with positive heterosis values are ideal for commercial exploitation.

In the case of 'Intermediate' hybrids, some lines exhibited better performance compared to the hybrids they originated from, while certain combinations surpassed the parent lines. Lines such as UCLA08-075, UCLA08-119, UCLA08-053, and UCLA08-087 demonstrated superior performance across multiple fruit quality traits and could be used directly as varieties. While they may not have been strong in combination, these lines excelled in physical fruit characteristics and could be valuable for cultivation. In contrast, 'Formosa' hybrids showed positive FH for traits like PF, FD, and SSC.

Interestingly, the hybrids with the best FH were not necessarily those with the highest VH (VH1, VH2, and VH3). Nonetheless, some lines and hybrids from both the 'Intermediate' and 'Formosa' groups showed superiority in quality traits relevant to the consumer market. These genotypes show promising potential for commercialization, providing an alternative fruit size while maintaining high-quality standards.

Conclusion

The research made it possible to develop genotypes with potential for fruit quality, expanding the crop's genetic base, enabling the increase in the number of cultivars for producers, avoiding the importation of hybrid seeds, and, consequently, reducing the cost of papaya production.

From the VH, it was possible to select hybrids 'Intermediate' patten H23, H26, H51, and H89 and pattern 'Formosa' H4, H9, H19, and H68, superior to commercial hybrids 'UENF/CALIMAN 01', 'UC10', and 'Tainung 01', for at least two characteristics that reflect in the quality of the fruits and good SCA. The FH made it possible to verify that there are lines that can be exploited *per se*, which present characteristics of fruit quality superior to their respective hybrids of the 'Formosa' and 'Solo' pattern. Lines UCLA08-066, UCLA08-122, and UCLA08-080 can be recommended for varietal exploration with the 'Formosa' pattern and lines UCLA08-053 and UCLA08-087 with the 'Intermediate' pattern.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0014479725000079

Data archiving statement. All relevant raw data information; the flowchart for obtaining the hybrid lines; the main environmental factors that acted during the experiment, and the main cultural treatments have been submitted to Mendeley data: Pereira Miranda, Daniel (2020), 'Statistical design', Mendeley Data, V1, doi: 10.17632/hs9c996vkc.1, and Pereira Miranda, Daniel (2024), 'Flowchart and environmental factors during the experiment', Mendeley Data, V1, doi: 10.17632/k78rh5g4gn.1

Acknowledgements. The authors thank the Caliman Agrícola S/A company for financing the experiment. The Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Universidade Estadual do Norte Fluminense – Darcy Ribeiro for providing the scholarships. *This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) - Finance Code 001.*

Author contributions. Data collection was performed by DPM, RSC, JCFV, JGSS, and TPSP. Data analysis was performed by DPM, JCFV, and RSC. The first version of the manuscript was written by DPM and JSS. The acquisition of financing and the resource was carried out by MGP and HCCR. Validation and revision with editing were performed by DPM and JSS.

Competing interests. The authors declare no conflict of interests.

References

Anwar, M., Rasul, M.G. and Ashwath, N. (2019) The synergistic effects of oxygenated additives on papaya biodiesel binary and ternary blends. *Fuel* **256**, 115980. https://doi.org/10.1016/j.fuel.2019.115980.

Barros, F.L. de S., Kuhlcamp, K.T., Arantes, S.D. and Moreira, S.O. (2017a) Productivity and quality of Formosa and Solo papaya over two harvest seasons. *Pesquisa Agropecuária Brasileira* **52**(8), 599–606. https://doi.org/10.1590/s0100-204x2017000800005.

Barros, G.B. de A., Aredes, F.A.S., Ramos, H.C.C., Santa-Catarina, R. and Pereira, M.G. (2017b) Combining ability of recombinant lines of papaya from backcrossing for sexual conversion. *Revista ciência agronômica* **48**, 166–174. https://doi.org/10.5935/1806-6690.20170019.

Basulto, F.S., Duch, E.S., Gil, F.E.Y., Plaza, R.D., Saavedra, A.L. and Santamaría, J.M. (2009) Postharvest ripening and maturity indices for maradol papaya. *Interciencia* **34**(8), 583–588. Available at https://ve.scielo.org/scielo.php?script=sci_arttext&pid=S0378-18442009000800012.

Borém, A., Miranda, G.V. (2013) *Melhoramento de plantas*. Viçosa: UFV, 523 p.

Cardoso, D.L., Da Luz, L.N., Macêdo, C.M.P. de, Gonçalves, L.S.A. and Pereira, M.G. (2014) Heterosis in papaya: inter and intragroup analysis. *Revista Brasileira de Fruticultura* **36**(3), 610–619. https://doi.org/10.1590/0100-2945-279/13.

Dantas, J.L.L. and Lima, J.F. (2001) Seleção e recomendação de variedades de mamoeiro - avaliação de linhagens e híbridos. *Revista Brasileira de Fruticultura* **23**(3), 617–621. https://doi.org/10.1590/S0100-29452001000300035.

Davis, R.L. (1927) Report of the plant breeder. *Agricultural Experiment Station*, 11–14. Available at https://www.cabidigitallibrary.org/doi/full/10.5555/19331100782.

Fagundes, G.R. and Yamanishi, O.K. (2001) Características físicas e químicas de frutos de mamoeiro do grupo 'Solo' comercializados em 4 estabelecimentos de Brasília-Df. *Revista Brasileira de Fruticultura* **23**(3), 541–545. https://doi.org/10.1590/s0100-29452001000300018.

FAOSTAT. Food and Agriculture Organization of the United Nations (2023) Available at http:// http://www.fao.org/faostat/en/.

Gramaje, L.V., Caguiat, J.D., Enriquez, J.O.S, dela Cruz, Q.D., Millas, R.A., Carampatana, J.E. and Tabanao, D.A.A. (2020) Heterosis and combining ability analysis in CMS hybrid rice. *Euphytica* **216**(1), 1–22. https://doi.org/10.1007/s10681-019-2542-y.

Hallauer, A.R., Miranda Filho, J.B., Carena, M.J. (2010) *Quantitative Genetics In Maize Breeding*. New York: Springer, 663 p.

Huang, M., Chen, L.Y. and Chen, Z.Q. (2015) Diallel analysis of combining ability and heterosis for yield and yield components in rice by using positive loci. *Euphytica* **205**(1), 37–50. https://doi.org/10.1007/s10681-015-1381-8.

Ide, C.D., Pereira, M.G., Viana, A.P. and Pereira, T.N.S. (2009) Use of testers for combining ability and selection of papapya hybrids. *Cropp Breeding and Applied Biotechnology* **9**(1), 60–66. https://doi.org/10.12702/1984-7033.v09n01a09.

Koc, A.B. (2007) Determination of watermelon volume using ellipsoid approximation and image processing. *Postharvest Biology and Technology* **45**(3), 366–371. https://doi.org/10.1016/j.postharvbio.2007.03.010.

Luz, L.N. da, Pereira, M.G., Barros, F.R., Barros, G.D.B. and Ferreguetti, G.A. (2015) Novos híbridos de mamoeiro avaliados nas condições de cultivo tradicional e no semiárido brasileiro. *Revista Brasileira de Fruticultura* **37**(1), 159–171. https://doi.org/10.1590/0100-2945-069/14.

Marin, S.L.D., Pereira, M.G., Do Amaral, A.T., Martelleto, L.A.P. and Ide, C.D. (2006) Heterosis in papaya hybrids from partial diallel of 'Solo' and 'Formosa' parents. *Crop Breeding and Applied Biotechnology* **6**(1), 24–29. https://doi.org/10.12702/1984-7033.v06n01a04.

Miranda, D.P., Ramos, H.C.C., Santa-Catarina, R., Vettorazzi, J.C.F., Santana, J.G.S., Poltronieri, T.P. de S., Pirovani, A.A.V., Azevedo, A.O.N., Duarte, R.P., Rodrigues, A.S., Bohry, D. and Pereira, M.G. (2021) Topcross hybrids in papaya (Carica papaya L.): evaluation of the potential for increasing fruit quality in new cultivars. *Archives of Agronomy and Soil Science* **68**(11), 1473–1486. https://doi.org/10.1080/03650340.2021.1905799.

Miranda, D.P., Ramos, H.C.C., Santa-Catarina, R., Vettorazzi, J.C.F., Santana, J.G.S., Poltronieri, T.P. de S., Pirovani, A.A.V., Duarte, R.P., Rodrigues, A.S., Bohry, D., Santos, J.S., Azevedo, A.O.N. and Pereira, M.G. (2024) Association between traits related to fruit quality in papaya (Carica papaya L.) hybrids and their implications for selection. *Agronomy Journal* **116**(1), 83–93. https://doi.org/10.1002/agj2.21493.

Morais, P.L.D. de, Silva, G.G. da, Menezes, J.B., Maia, F.E.N., Dantas, D.J. and Sales Júnior, R. (2007) Pós-colheita de mamão híbrido UENF/CALIMAN 01 cultivado no Rio Grande do Norte. *Revista Brasileira de Fruticultura* **29**(3), 666–670. https://doi.org/10.1590/S0100-29452007000300046.

Musembi, K.B., Githiri, S.M., Yencho, G.C. and Sibiya, J. (2015) Combining ability and heterosis for yield and drought tolerance traits under managed drought stress in sweetpotato. *Euphytica* **201**(3), 423–440. https://doi.org/10.1007/s10681-014-1230-1.

Nayak, M.G. and Vyas, A.P. (2019) Optimization of microwave-assisted biodiesel production from Papaya oil using response surface methodology. *Renewable Energy* **138**, 18–28. https://doi.org/10.1016/j.renene.2019.01.054.

Pereira, M.G., Da Luz, L.N., Santa-Catarina, R., Ramos, H.C.C., Pereira, T. N.S., De Brito, G.B., Ferregueti, G.A., Cortes, D.F.M., Vettorazzi, J.C.F., Azevedo, A.O.N., Silveira, S.F., De Oliveira, J.G. and Viana, A.P. (2019a) 'UC14': a new papaya cultivar with intermediate fruit size CULTIVAR RELEASE. *Crop Breeding and Applied Biotechnology* **19**, 226–229. https://doi.org/10.1590/1984.

Pereira, M.G., Poltronieri, T.P. de S., Santana, T.N.P., Ramos, H.C.C., Santa-Catarina, R., Vettorazzi, J.C.F., Arêdes, F.A.S., Boechat, M.S.B., Venâncio, T.M., Azevedo, A.O.N., Cortes, D.F.M., Moreira, N.F., Bohry, D., da Silveira, S.F., Vivas, M. and Ferreguetti, G.A. (2019b) Twenty-Two-Year Papaya Breeding Program: From Breeding Strategy Establishment To Cultivar Development. 1(2), 9–27. https://doi.org/10.35418/2526-4117/v1n2a2.

Poltronieri, T.P. de S., da Silveira, S.F., Vivas, M., Santa-Catarina, R., Azevedo, A.O.N., Cortes, D.F.M and Pereira, M.G. (2019) Identification of papaya hybrids resistant to Stagonosporopsis caricae by heterosis: a possible reality? *Euphytica* **215**(2), 1–8. https://doi.org/10.1007/s10681-019-2348-y.

Reddy, M.T., Babu, K.H., Ganesh, M., Begum, H., Dilipbabu, J., Subbarama, R. and Reddy K. (2013) Gene action and combining ability of yield and its components for late kharif season in okra (Abelmoschus esculentus (L.) Moench). *Chilean Journal of Agricultural Research* **73**, 9–16. http://dx.doi.org/10.4067/S0718-58392013000100002.

Reis, R.C., Viana, E. de S., Jesus, J.L., Dantas, J.L.L. and Lucena, R.S. (2015) Caracterização físico-química de frutos de novos híbridos e linhagens de mamoeiro. *Pesquisa Agropecuária Brasileira* **50**(3), 210–217. https://doi.org/10.1590/S0100-204X2015000300004.

Santa-Catarina, R., Cortes, D.F.M., Vettorazzi, J.C.F., Poltronieri, T.P. de S., Barros, G.B. de A., Arêdes, F.A.S., Azevedo, A.O.N., Ramos, H.C.C. and Pereira, M.G. (2019) Combining ability for fruit yield and quality in papaya recombinant inbred lines from the sexual conversion backcrossing. *Euphytica* **215**(10), 154. https://doi.org/10.1007/s10681-019-2485-3.

Santa-Catarina, R., Cortes, D.F.M., Vettorazzi, J.C.F., Ramos, H.C.C., Ferreguetti, G.A. and Pereira, M.G. (2018) Image-based phenotyping of morpho-agronomic traits in papaya fruits (*Carica papaya* L. THB var.). *Australian Journal of Crop Science* **12**(11), 1750–1756. https://doi.org/10.21475/ajcs.18.12.11.p1437.

Santana, J.G.S., Ramos, H.C.C., Santa-Catarina, R., Vettorazzi, J.C.F., Miranda, D.P., Pirovani, A.A.V., Poltronieri, T.P. de S., Duarte, R.P. and Pereira, M.G. (2023) Exploring genetic diversity in inbred papaya lines for fruit quality in advanced stage of improvement. *Scientific Reports* **13**(1), 13431. https://doi.org/10.1038/s41598-023-40613-8.

Serrano, L.A.L. and Cattaneo, L.F. (2010) O cultivo do mamoeiro no Brasil. *Revista Brasileira de Fruticultura* **32**(3), 657. https://doi.org/10.1590/S0100-29452010000300001.

Teodoro, P.E., Rodrigues, E.V., Peixoto, L.D.A., Laviola, B.G. and Bhering, L.L. (2017) Diallel analysis in agronomic traits of Jatropha. *Crop Breeding and Applied Biotechnology* **17**(3), 259–265. http://dx.doi.org/10.1590/1984-70332017v17n3a39.

Tuo, D., Ma, C., Yan, P., Kong, H., Zhou, P., Guo, A., Zhao, H. and Shen, W. (2023) Genetic transformation and gene delivery strategies in *Carica papaya* L. *Tropical Plants* **2**(1), 5. https://doi.org/10.48130/TP-2023-0005.

Vivas, M., Ramos, H.C.C., Santos, P.H.D., Silveira, S.F., Pereira, T.N.S., do Amaral, A.T. and Pereira, M.G. (2016) Heterosis and genetic diversity for selection of papaya hybrids for resistance to black spot and phoma spot. *Tropical Plant Pathology* **41**(6), 380–389. https://doi.org/10.1007/s40858-016-0109-1.

Cite this article: Miranda DP, Ramos HCC, Santa-Catarina R, Santos JS, Vettorazzi JCF, Santana JGS, Poltronieri TP, and Pereira MG. Genetic potential of Brazilian papaya (*Carica papaya* L.) lines and hybrids for improving fruit quality via specific combining ability and heterosis. *Experimental Agriculture*. https://doi.org/10.1017/S0014479725000079