

Diallel analysis for fruit traits among tomato recombinant inbred lines derived from an interspecific cross *Solanum lycopersicum* x *S. pimpinellifolium*

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Abstract

Five recombinant inbred lines, generated from a single interspecific cross *S. lycopersicum* x *S. pimpinellifolium*, were crossed in a complete diallel combination without reciprocal. Fruit quality traits were analyzed according to Griffing (1956), method 2, model 1 (fixed effects). Significant general and specific combining ability (GCA and SCA) effects were found for all traits. Weight, reflectance percentage, chroma index, firmness, soluble solids content, pH and titratable acidity presented SCA values greater than GCA values, indicating nonadditive effects. Both additive and nonadditive effects were significant in determining diameter and shape. Positive unidirectional dominance was found for shape, shelf life and chroma index, while negative unidirectional dominance was involved in the expression of weight, diameter, height, reflectance percentage and firmness. Bidirectional dominance was found for soluble solids content, pH and titratable acidity. In spite of being a genetic pool generated from a single interspecific cross, high levels of genotypic and phenotypic variability was found among the fifteen genotypes for important agronomic traits. Both additive and nonadditive effects were important in the genetic determination of these traits.

Key words: Plant breeding, diallel analysis, combining ability, *Solanum lycopersicum*, recombinant inbred lines

Introduction

In most of tomato (*Solanum lycopersicum*) breeding programs, emphasis is given to increase yield relegating important traits as fruit quality (size, shape, color, and flavour) and postharvest attributes (firmness and shelf life). Quality is given by organoleptic characteristics, those that can be perceived by all senses (flavour, aroma, colour and texture). The genetic uniformity of the cultivated species is due to the high selection pressure applied to achieve the desired phenotype, decreasing the possibilities of a successful breeding program. In this way, a plateau has been reached that limits the increase of the fruit quality and postharvest characters (Kannenbergh and Falk, 1993).

The interest for the wild species has increased in order to extend the genetic variability, in view of the fact that they present organoleptic characteristics demanded by the international market. By interspecific crossing (hybridization), it is possible to transfer these characteristics to cultivated species and generate a genetic variability owed to the heterotic effect caused by the interactions among divergent genotypes (Rick, 1976). Lecomte *et al.* (2004); Monforte *et al.* (2001); Rousseaux *et al.* (2005) pointed out that wild germplasm contributes to an increase in internal fruit quality but they reduce fruit weight.

Despite the advances of "molecular breeding", classical quantitative genetics remains useful in practical tomato improvement. Thus, estimation of genetic parameters such as heterosis and combining ability gives inferences about the

predominant action of the genes, indicates the appropriate selection strategy to be applied in the breeding program and allows the identification of the best parents. Diallel mating designs provide useful genetic information, such as general combining ability (GCA) and specific combining ability (SCA), to devise appropriate breeding and selection strategies. Griffing method (1956) partitions the genetic variability into additive component (estimated by GCA) and non additive component (estimated by SCA). The diallel analysis helps specifically to choose the most promising segregant populations for selection.

Pratta *et al.* (1996) evaluating postharvest characteristics in cultivated and wild genotypes, selected the wild accession LA722 of *S. pimpinellifolium* as the high postharvest value. This wild species presents fruits with small size and low weight, but with high nutritional quality and, in natural conditions, preserves organoleptic qualities for a larger period of time than the commercial ones. Pratta *et al.* (2003) analyzed productive traits such as fruit weight, diameter, height and shelf life in a diallel design among domestic, exotic and mutant germplasms. They found that the most promising hybrid for breeding all traits simultaneously was the F₁ between the cultivar Caimanta and the accession LA722 of *S. pimpinellifolium*, since it had the largest differences in allele frequencies and the greatest genetic divergence. Based on these results, Rodriguez *et al.* (2006a) carried out a selection for fruit weight and shelf life in a F₂ generation from a cross between the cultivar Caimanta and the accession LA722 obtaining 17 RILs (Recombinant Inbred

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Specimen Copy: Not for sale

Lines). They observed transgressive segregation for shelf life, obtaining superior genotypes with higher values of this trait than the progenitors. Rodríguez *et al.* (2006b) evaluating the 17 RILs have found divergence values of fruit weight and shelf life, also they found divergence of quality traits. It is possible to select high-performing RILs from a particular heterotic cross and, by intercrossing them, to produce a second cycle hybrid (SCH) that perform even better than the original. Crossing the best RILs will ensure that a maximum number of superior SCHs actually be produced (Kearsey and Pooni, 1996). Segregant F₂ populations can be generated from these superior SCHs to begin a new breeding program.

The present study was carried out using a diallel cross system among five RILs to assess the general and specific combining abilities and discriminate the superior parents and second cycle hybrid combinations as a step in developing a new selection process in the tomato breeding program.

Materials and methods

The experiment was carried out at the field station “José F. Villarino” (Facultad de Ciencias Agrarias-Universidad Nacional Rosario, Zavalla, Argentina, 33°S 61°W).

Plant material: Five RILs (ToUNR1, ToUNR8, ToUNR9, ToUNR15 and ToUNR18) obtained from an interspecific cross between cv. Caimanta of *S. lycopersicum* and the accession LA722 of *S. pimpinellifolium* were selected based on their agronomic performance (Rodríguez *et al.*, 2006a) and crossed in a complete diallel combination without reciprocal crosses (Griffing, 1956). Fifteen seeds of the five parents and from each hybrid H (1x8), H (1x9), H (1x15), H (18x1), H (9x8), H (15x8), H (18x8), H (15x9), H (18x9) and H (18x15) were grown in seedling trays and transplanted to greenhouse in a complete randomised design.

Traits evaluated: A minimum of ten breaker stage tomatoes per plant of the five RILs and the hybrids (fifteen genotypes) were harvested and evaluated for the following traits: weight (W, in g), height (H, in cm), diameter (D, in cm), shape index (S, ratio H/D), shelf life (SL, measured as the number of days elapsed from harvesting to the first symptoms of deterioration in the fruits, stored at 25±3°C, according to Schuelter *et al.*, 2002), firmness (FR, determined with a fruit pressure tester -12.5 N- type Shore A with a tip of 0.10 in a 0–100 scale), soluble solids content (SS, in °Brix, determined with a hand refractometer in the homogenised juice from the pericarp tissue), pH, colour (a/b, determined with a chromameter CR 300 measuring through the chroma index by calculating the a/b ratio, where a and b are the absorbencies at wavelength of 540 and 675 nm, respectively). L, reflectance percentage, indicates darkness or lightness of colour and ranges from black (0) to white (100) and titratable acidity (TA, g of citric acid/100 g of homogenized juice).

Data analysis: The normal distribution was verified according to Shapiro-Wilk test (1965) for all fruit traits. Mean values were compared by one-way ANOVA. The Diallel crosses were analyzed following Griffing (1956) method 2, model 1 (fixed effects):

$$Y_{ijk} = \mu + g_i + g_j + s_{ij} + e_{ijk}$$

Where, Y_{ijk} is the mean phenotypic value, μ is the general mean, g_i y g_j are the GCA effect of each parent, s_{ij} is the SCA effect

of the hybrid and e_{ijk} is the experimental error. The greater the value of the GCA effect the greater the number of genes that increase the trait expression and the greater the number of positive differences between the gene frequency and the average frequency in the diallel parents. SCA value of hybrids is an indicator of the hybrid's divergence relative to the parents. The higher the SCA value of hybrids, the greater the differences between the expected performance of the hybrid assuming additivity and the observed performance due to non additive effects. Similar information is given by the mid-parent heterosis (Hm), which was also calculated for all traits. In respect to SCA in parents, positive values indicate that there is unidirectional dominance of lowest values, while negative values indicates unidirectional dominance of greatest values. If positive and negative SCA values are found among parents for a given traits, then bidirectional dominance is present (Soriano Viana, 2000).

Results

All traits showed a normal distribution, with W values greater than 0.80. Mean values and standard errors of all fruit quality traits in the fifteen genotypes are shown in Table 1. Highly significant differences were detected among genotypes for all traits. An interesting discrepancy was found for the phenotypic mean values of ToUNR1 and ToUNR8. ToUNR1 had high values of height, diameter, weight, shelf life and pH, whereas ToUNR8 ranked towards the low values of the same traits. An opposite situation was found for soluble solids content and titratable acidity, where ToUNR1 had the lowest values and ToUNR8, the higher ones.

Highly significant GCA and SCA effects were found for all traits (Fig. 1 and 2 and Table 2). GCA effects were greater than SCA effects for height and shelf life. Instead, weight, L, a/b, firmness, soluble solids content, pH, and titratable acidity presented SCA values greater than GCA values. Diameter and shape showed similar values of both combining abilities. ToUNR1 showed positive GCA values for diameter, height, weight, shelf life, and firmness, and ToUNR18 for shape, weight, shelf life, and firmness. Negative or near to zero values were found for these lines in soluble solids content, pH, and titratable acidity. Another line, ToUNR8, presented high GCA values for L, titratable acidity and soluble solids contents, and near to zero values for shape, a/b, and pH.

The SCA values for all traits of each hybrid were verified by the mid-parent heterosis (Table 2). Most hybrids had negative mid-parent heterosis for weight. The exception was H (18x8), which presented a value of 29.80. Positive values of mid-parent heterosis were found for shelf life, and the hybrids H (1x8) and H (15x9) had outstanding values of 23.96 and 29.40, respectively. In general, the mid-parent heterosis was negative for fruit firmness, the values of H (15x9) and H (18x15) being noticeable (-19.58 and -17.86, respectively). For a/b, the remarkable genotype H (15x8) presented a value of 23.01. Finally, most hybrids had negative SCA values for soluble solids content. Exceptions were H (1x8) and H (1x9), for which SCA was 11.32 and 12.71, respectively.

Discussion

The fruit quality traits analysis suggest that in spite of being a genetic pool generated from a single interspecific cross *S.*

Table 1. Mean value and standard error of fruit quality traits in tomato

Genotype	D	H	S	W	SL	L	a/b	FR	SS	pH	TA
ToUNR1	3.55 ± 0.06	2.85 ± 0.09	0.81 ± 0.02	21.66 ± 1.35	24.79 ± 1.18	39.81 ± 1.68	1.04 ± 0.15	54.17 ± 7.06	5.54 ± 0.25	4.96 ± 0.05	0.32 ± 0.02
ToUNR8	1.58 ± 0.06	1.42 ± 0.04	0.90 ± 0.01	2.34 ± 0.21	17.98 ± 0.62	40.42 ± 1.37	1.14 ± 0.11	54.55 ± 4.68	9.30 ± 0.66	4.51 ± 0.09	0.65 ± 0.02
ToUNR9	1.83 ± 0.06	1.63 ± 0.04	0.89 ± 0.01	3.81 ± 0.32	18.70 ± 0.43	37.09 ± 0.40	1.37 ± 0.05	53.39 ± 3.38	7.04 ± 0.18	4.35 ± 0.05	0.79 ± 0.04
ToUNR15	2.84 ± 0.09	2.22 ± 0.07	0.79 ± 0.02	11.59 ± 1.04	14.41 ± 1.49	38.81 ± 1.66	1.12 ± 0.16	54.32 ± 4.52	7.91 ± 0.34	4.61 ± 0.11	0.44 ± 0.03
ToUNR18	2.83 ± 0.06	2.77 ± 0.07	0.97 ± 0.02	13.72 ± 0.72	21.11 ± 1.20	36.54 ± 1.54	1.15 ± 0.10	52.47 ± 4.51	7.69 ± 0.26	4.72 ± 0.07	0.37 ± 0.03
H (1x8)	2.21 ± 0.05	1.90 ± 0.03	0.88 ± 0.01	5.80 ± 0.23	26.51 ± 1.24	35.39 ± 0.94	1.18 ± 0.06	47.15 ± 4.68	8.26 ± 0.24	4.50 ± 0.07	0.59 ± 0.05
H (1x9)	2.17 ± 0.03	2.02 ± 0.02	0.94 ± 0.02	5.81 ± 0.02	24.60 ± 1.27	37.82 ± 1.04	1.19 ± 0.07	55.71 ± 6.88	7.09 ± 0.21	4.65 ± 0.11	0.39 ± 0.05
H (1x15)	2.40 ± 0.07	2.09 ± 0.07	0.89 ± 0.01	7.31 ± 0.05	21.93 ± 1.40	37.96 ± 1.14	1.25 ± 0.09	45.53 ± 7.40	5.49 ± 0.44	4.49 ± 0.09	0.42 ± 0.06
H (18x1)	2.59 ± 0.11	2.59 ± 0.09	1.02 ± 0.02	10.62 ± 0.99	23.08 ± 1.80	37.11 ± 1.00	1.15 ± 0.12	54.85 ± 7.72	6.48 ± 0.34	4.54 ± 0.08	0.44 ± 0.07
H (9x8)	1.8 ± 0.04	1.67 ± 0.07	0.93 ± 0.02	3.36 ± 0.26	18.77 ± 0.93	38.09 ± 1.04	1.27 ± 0.08	48.89 ± 6.27	8.09 ± 0.87	4.42 ± 0.08	0.55 ± 0.08
H (15x8)	1.84 ± 0.04	1.64 ± 0.04	0.89 ± 0.01	3.50 ± 0.22	15.47 ± 0.75	37.46 ± 0.58	1.39 ± 0.07	52.39 ± 5.12	6.89 ± 0.36	4.62 ± 0.11	0.55 ± 0.04
H (18x8)	2.57 ± 0.05	2.47 ± 0.06	0.97 ± 0.02	10.42 ± 0.66	20.58 ± 1.06	36.99 ± 0.68	1.23 ± 0.11	44.87 ± 7.07	7.31 ± 0.27	4.74 ± 0.10	0.33 ± 0.02
H (15x9)	2.36 ± 0.04	2.11 ± 0.03	0.91 ± 0.01	7.37 ± 0.32	21.42 ± 0.84	36.29 ± 0.99	1.24 ± 0.12	43.31 ± 8.33	7.20 ± 0.22	4.50 ± 0.09	0.55 ± 0.04
H (18x9)	1.96 ± 0.05	1.89 ± 0.05	0.98 ± 0.01	4.62 ± 0.31	20.67 ± 0.98	36.86 ± 1.13	1.26 ± 0.10	49.00 ± 7.13	7.23 ± 1.52	4.62 ± 0.08	0.40 ± 0.07
H (18x15)	2.63 ± 0.08	2.41 ± 0.09	0.92 ± 0.03	10.64 ± 0.95	14.68 ± 0.88	37.39 ± 1.27	1.19 ± 0.17	43.86 ± 8.44	7.35 ± 0.53	4.65 ± 0.18	0.46 ± 0.03
F	70.80***	50.17***	14.52***	61.90***	10.78***	37.13***	21.14***	14.35***	28.51***	23.90***	79.11***

*** $P < 0.0001$

lycopersicum × *S. pimpinellifolium* ('Caimanta' × LA722), there exist high levels of genetic variability among the fifteen genotypes. Recombination and/or genomic rearrangements occurring during the selfing for obtaining and stabilizing the lines could be the causes of such a genetic variability. Rodríguez *et al.* (2006b) analyzed 17 RILs (that included the five ones evaluated in this work) and also found high genetic variability, suggesting that these genotypes constitute a new source of variability for use in breeding programs.

High significant values of GCA and SCA indicate that both additive and nonadditive gene actions affect the expression of the traits. Additive gene action was important for determining height and shelf life since GCA effects were greater than SCA effects. Instead, weight, L, a/b, firmness, soluble solids content, pH and titratable acidity presented SCA values greater than GCA values, indicating that nonadditive effects have the greatest contribution in controlling these traits. Garg *et al.* (2008) found the similar genetic control for firmness, pH, and titratable acidity in different tomato genotypes. Dhatt *et al.* (2004) have also reported the importance

of nonadditive effects in the genetic control of fruit firmness. In contrast, Chadha *et al.* (2002), Das *et al.* (1988) and Rodríguez *et al.* (2004) reported additive effects in the expression of fruit weight. These discrepancies could be explained by differences in gene frequencies among the populations studied in each research. In the present one, original experimental lines obtained in a novel breeding program were analyzed whereas in the others, plant material included more divergent germplasm such as mutant and exotic genotypes. Pratta *et al.* (2003) and Zorzoli *et al.* (2000) also found predominance of additive effects in the genetic control of weight and nonadditive effects for shelf life, when analyzing the parents of the single cross from which the RILs were derived. These results agree with the above mentioned authors but not with the present results. Hence differences in genetic frequencies could not be proposed to explain these discrepancies, so that the previously mentioned recombination and/or genomic rearrangements could account for them. Finally, both additive and nonadditive effects were important in determining the expression of diameter and shape.

Table 2. Mid-parent heterosis (Hm) and specific combinatory ability (SCA) of fruit quality traits in tomato hybrids

Genotype	D		H		S		W		SL		L		a/b		FR		SS		pH		TA	
	Hm	SCA	Hm	SCA	Hm	SCA	Hm	SCA	Hm	SCA	Hm	SCA	Hm	SCA	Hm	SCA	Hm	SCA	Hm	SCA	Hm	SCA
H (1x8)	-13.80	-0.12	-11.00	-0.14	2.92	-0.01	-51.70	-2.74	23.96	3.40	-11.78	-2.99	8.26	0.02	-13.27	-4.63	11.32	0.94	-4.96	-0.13	21.65	0.11
H (1x9)	-19.30	-0.22	-9.80	-0.08	10.60	0.04	-54.40	-2.87	13.13	0.74	-1.64	0.23	-1.24	-0.02	3.59	3.74	12.71	0.55	-0.11	0.07	-29.73	-0.11
H (1x15)	-24.90	-0.41	-17.50	-0.26	11.25	0.04	-56.00	-4.69	11.90	1.00	-3.43	-0.13	15.74	0.09	-16.07	-5.02	-18.36	-0.92	-6.16	-0.17	10.53	0.00
H (18x1)	-18.80	-0.29	-7.80	-0.07	14.60	0.08	-39.90	-3.06	0.57	-0.54	-2.79	-0.22	5.02	0.02	2.87	3.76	-2.04	-0.07	-6.20	-0.19	27.54	0.09
H (9x8)	5.50	0.11	9.50	0.11	3.91	0.00	9.30	1.10	2.34	-1.03	-1.72	0.38	1.19	-0.01	-9.41	-1.77	-0.98	0.01	-0.22	-0.04	-23.61	-0.07
H (15x8)	-16.70	-0.27	-9.90	-0.17	5.32	0.02	-49.70	-2.06	-4.48	-1.39	-5.44	-0.75	23.01	0.16	-3.76	3.15	-19.93	-1.05	1.32	0.07	0.92	0.01
H (18x8)	16.50	0.39	17.90	0.35	3.74	0.01	29.80	3.20	5.30	1.01	-3.87	-0.47	7.40	0.30	-16.15	-4.91	-13.95	-0.78	2.71	0.12	-35.29	-0.14
H (15x9)	1.10	0.20	9.60	0.24	8.30	0.03	-4.28	1.70	29.40	3.76	-4.37	-1.13	-4.00	-0.04	-19.58	-6.11	-3.68	0.04	0.45	0.01	-10.57	-0.01
H (18x9)	-15.90	-0.27	-14.10	-29.00	5.38	0.01	-47.30	-2.76	3.84	0.31	0.12	0.19	0.00	0.00	-7.43	-0.96	-1.83	-0.08	1.87	0.06	-31.03	-0.09
H (18x15)	-7.20	-0.03	-3.40	-0.02	4.54	0.00	-15.90	-0.06	-17.34	-2.75	-0.76	0.23	4.85	0.00	-17.86	-4.68	-5.77	0.18	-0.32	0.00	13.58	0.06

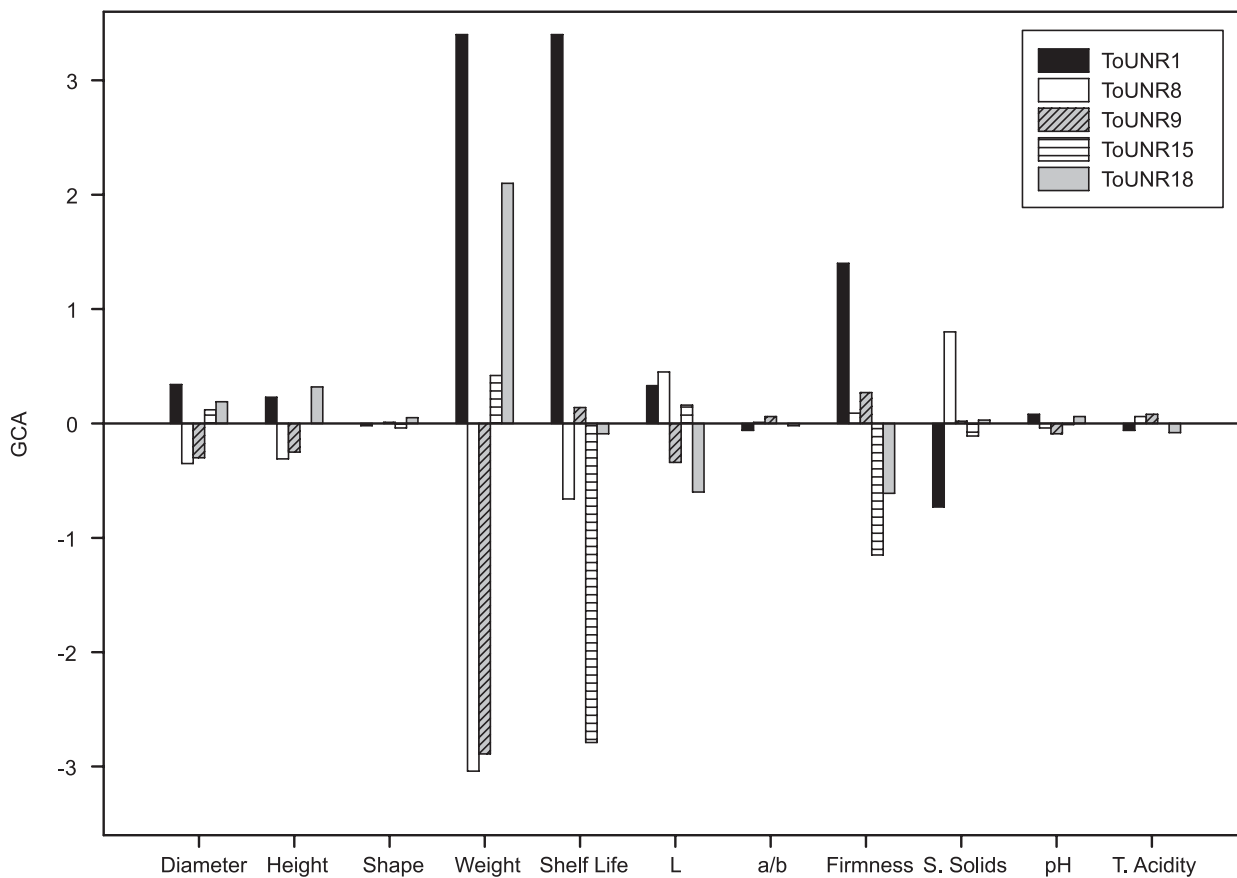


Fig. 1. General combinatory ability (GCA) of fruit quality traits in parents

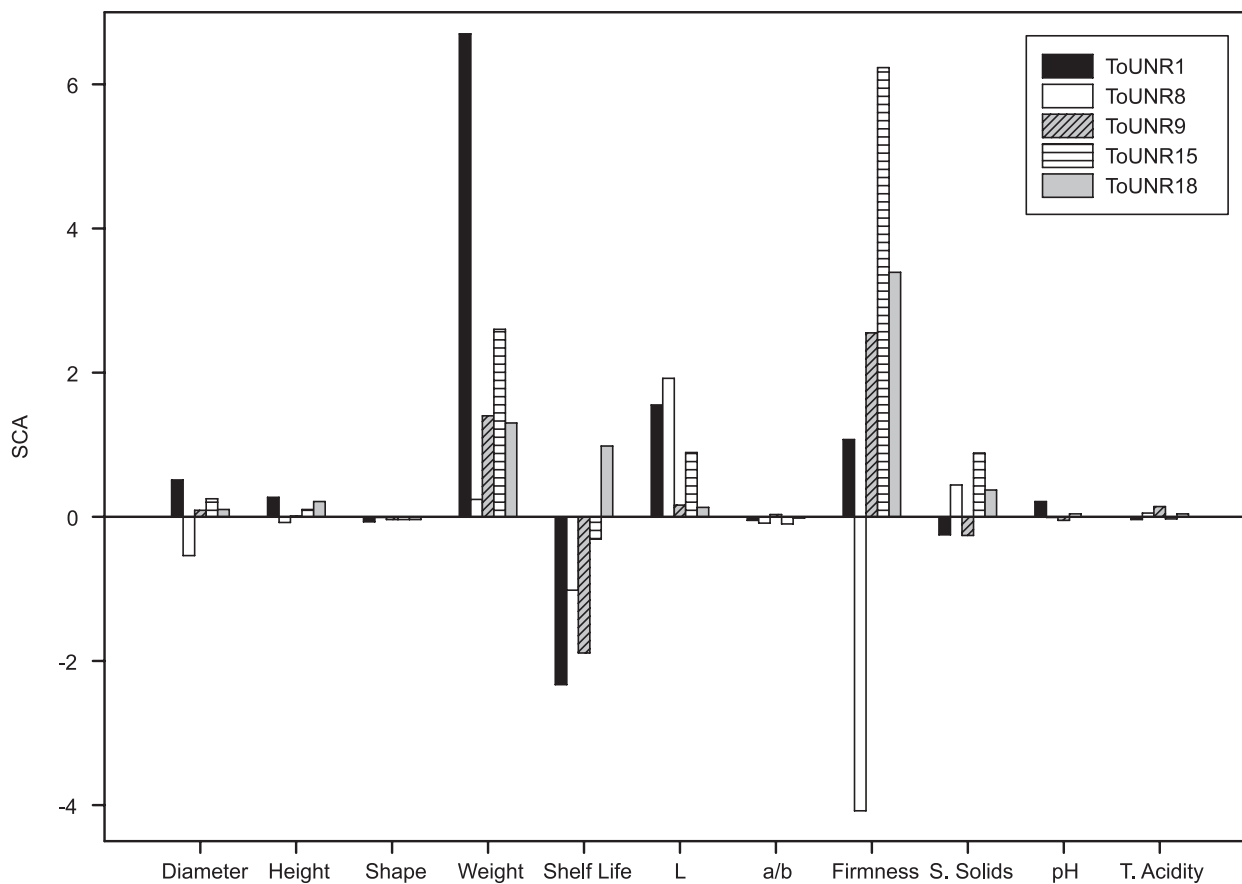


Fig. 2. Specific combinatory ability (SCA) of fruit quality traits in parents

Most parents had negative SCA values for shape, shelf life and a/b (Fig. 2), indicating that unidirectional dominance of the highest values was involved in the expression of these traits (Griffing, 1956). Instead, most parents had positive SCA values for weight, diameter, height, L and firmness, corresponding to dominance effects of the lowest values. These results partially agree with Pratta *et al.* (2003), who found negative unidirectional dominance for both weight and shelf life. Again, variations in gene frequency and chromosomal recombination or genomic rearrangements could explain these differences. Finally, parents presented both positives and negatives SCA values for soluble solids content, pH and titratable acidity. This fact indicated that bidirectional dominance is involved in the expression of these traits, *i.e.*, for a given trait, the highest values were dominant in some crosses but recessive in others.

One of the advantages of the diallel analysis in breeding programs is to allow choosing the best combinations of promissory parents to generate segregant populations for continuing the traits improvement. In this research, the positive GCA values presented by ToUNR1, ToUNR18 and ToUNR8 would indicate that the three lines are potential parents to improve agronomically important traits such as weight, shelf life, colour, soluble solids content and firmness. On the other hand, the hybrid H (15x9) presented high SCA values for weight and shelf life, traits that were the targets of the selection practiced in the interspecific cross 'Caimanta' x LA722 to obtain the RILs used as parents in this experiment. Therefore, H (15x9) is an interesting second cycle hybrid to generate a segregant population for continuing the improvement of both traits. On the other hand, the SCA values of H (1x8) indicate that it is an promising genotypic combination for improving shelf life, soluble solids content, pH and titratable acidity. Also interesting, was that both parental lines had extreme phenotypic mean values for these agronomically important traits. It is a well known fact that crossing phenotypically divergent materials is of importance for broadening the genetic variability. H (1x8) appears as another promissory second cycle hybrid to generate a basal segregant population for beginning a new breeding program.

In conclusion, though the five recombinant lines were generated from an original single interspecific cross, high level of phenotypic and genotypic variability was found among them in important agronomic traits. Both additive and nonadditive effects were important to the genetic determination of these traits. Recombinant lines ToUNR1, ToUNR8 and ToUNR18 are promissory parents, while H (15x9) and H (1x8) are suitable second cycle hybrids, to develop new basal populations for continuing the breeding program.

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