



## Diallel analysis of production traits among domestic, exotic and mutant germplasms of *Lycopersicon*

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**ABSTRACT.** The effects of wild germplasm on tomato fruit shelf life have not yet been completely evaluated. Three different genotypes of *Lycopersicon esculentum* (a cultivated variety, a homozygote for *nor* and a homozygote for *rin*), LA1385 of *L. esculentum* var. *cerasiforme*, LA722 of *L. pimpinellifolium*, and 10 diallel hybrids were assayed. Mean values of fruit shelf life, weight, shape, and mean number of flowers per cluster were analyzed after Griffing (1956, Aust. J. Biology 9: 463-493), method 2, model 1. Both general and specific combining abilities (GCA and SCA) were significant for the four traits. Negative unidirectional dominance was detected for fruit weight and shelf life, while bidirectional dominance was detected for fruit shape and mean number of flowers per cluster. SCA was greater than GCA for shelf life, so non-additive effects predominantly accounted for this trait. In the heterozygous state, *rin* had smaller mean effects than *nor*. Wild accessions were able to prolong shelf life *per se*, and in crosses to the cultivated variety. The cross between the homozygote for *nor* and LA722 yielded the longest shelf life among hybrids.

**Key words:** Tomato, Fruit quality, Plant genetic resources, Fruit shelf life, Plant breeding

## INTRODUCTION

Spontaneous mutations affecting fruit ripening have been identified in cultivated tomatoes (*Lycopersicon esculentum* Mill.). The *nor* (non-ripening) gene, located on chromosome 10, and the *rin* (ripening inhibitor) gene, located on chromosome 5, are two recessive single mutations that extend fruit shelf life and have pleiotropic effects on the synthesis of carotenoid pigments and other processes associated with ripening that ultimately reduce fruit quality (Ng and Tigchelaar, 1977).

Wild species of *Lycopersicon* have been used extensively as sources of resistance and to increase nutritional quality (Rick, 1979; Alpert and Tanksley, 1996; Bernacchi et al., 1998; Frary et al., 2000). Some varieties with increased pericarp firmness have been derived from crosses between *L. esculentum* and *L. pimpinellifolium* (Stevens and Rick, 1986). Recently, Bernacchi et al. (1998) mapped some quantitative trait loci for pericarp firmness in an advanced backcross of *L. pimpinellifolium* and a processing variety of *L. esculentum*. Although pericarp firmness is closely related to fruit shelf life, very little is known about the effect of wild relatives on this latter trait. From an evolutionary viewpoint, under natural conditions the ability of wild species to maintain fruit quality over an extended period of time could be an adaptive strategy to attract herbivores and ensure seed dispersion. Thus, long shelf life values may be found in fruits with exotic germplasm. In fact, Pratta et al. (1996) and Zorzoli et al. (1998) reported that some lines of *L. esculentum* var. *cerasiforme* and *L. pimpinellifolium*, as well as hybrids with normal ripening genotypes of *L. esculentum*, had a longer fruit shelf life than some commercial varieties.

We evaluated the effects of genes from LA1385 of *L. esculentum* var. *cerasiforme* and LA722 of *L. pimpinellifolium* on tomato fruit shelf life, weight, shape and mean number of flowers per cluster and compared them with those of the *nor* and *rin* mutations of *L. esculentum* in both the homozygous and the heterozygous states.

## MATERIAL AND METHODS

### Plant material and growth conditions

Assays were carried out at the "José F. Villarino" field station (Facultad de Ciencias Agrarias UNR, Zavalla, Argentina, 33°S and 61°W). Five homozygous parents were crossed in a nonreciprocal diallel combination (Griffing, 1956). They were the fresh-market variety 'Platense', a homozygous line with the mutant allele *nor* (named 'B') and a homozygous line with the mutant allele *rin* (named 'A') of the cultivated tomato, and the wild accessions LA1385 of *L. esculentum* var. *cerasiforme* and LA722 of *L. pimpinellifolium*. Seeds of the five parents and the 10 nonreciprocal hybrids were sown in seedling trays in a glasshouse in September. Fifteen seedlings per genotype were transplanted in a completely randomized design after a month and grown in a greenhouse from October to March, during the normal crop-growing period in this zone. Twenty fruits per plant from all genotypes were harvested at 45 days post-

anthesis, when fruits of 'Platense' (the reference genotype) had reached the turning stage, i.e., when 10% of their surface had turned red.

### Evaluation of traits and statistical analysis

The number of flowers per cluster was evaluated as the average of three clusters per plant at 30 days after transplanting. Fruit traits, weight (in grams), shape (ratio height/diameter), and shelf life (in days), were evaluated after harvesting. Shelf life was measured as the number of days from harvesting until the beginning of visually detected softening of fruits stored at  $25 \pm 3^\circ\text{C}$ .

The normal distribution of the four traits was tested according to Shapiro and Wilk's test (1965). The mean values of fruit shelf life, weight and shape, and flowers per cluster were compared by ANOVA. The diallel crosses were analyzed following Griffing (1956) method 2, model 1:

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

where  $Y_{ij}$  is the mean phenotypic value,  $\mu$  is the general mean,  $g_i$  is the general combining ability (GCA) effect,  $s_{ij}$  is the specific combining ability (SCA) effect and  $e_{ijk}$  is the error term. The mid-parent heterosis (in percent) and degrees of dominance (d/a) were calculated according to Mather and Jinks (1977) for all traits in each cross.

## RESULTS

All traits displayed a normal distribution (Table 1,  $W > 0.90$ , ns). Highly significant differences were detected among genotypes for fruit shelf life, weight and shape, and flowers per cluster. Highly significant effects ( $P < 0.01$ ) were detected for GCA in the four traits (Tables 2 and 3,  $F = 5.89$  for shelf life,  $F = 158.19$  for weight,  $F = 81.99$  for shape and  $F = 16.70$  for flowers per cluster) and for SCA in shelf life ( $F = 4.58$ ), weight ( $F = 16.49$ ) and shape ( $F = 9.14$ ). The SCA effect on flowers per cluster was significant at the 5% level ( $F = 3.05$ ). The mean square effect of GCA was greater than that of SCA for weight (2253.04 vs 1165.44), shape (0.030 vs 0.006) and flowers per cluster (16.46 vs 4.25), but the opposite was found for shelf life (32.30 vs 46.38). Both the mid-parent heterosis and the degrees of dominance were predominantly negative for fruit shelf life and weight, in agreement with the generally positive SCA effects of the parents for these traits. In the cases of fruit shape and flowers per cluster, positive and negative mid-parent heterosis and degrees of dominance were found, following the negative and positive SCA effects of the parents.

## DISCUSSION

Genetic variability was found for four productive traits among a set of tomato parents and their hybrids (Table 1). Both GCA and SCA effects appeared to account for the genetic determination of production traits (Tables 2 and 3). Additive gene action mostly affected fruit weight, shape, and flowers per cluster, since GCA was greater than SCA for these traits (Griffing, 1956). Conversely, nonadditive gene action was more noticeable for shelf life.

**Table 1.** Mean value  $\pm$  standard error of productive traits in five tomato parents and their hybrids.

Genotype	Fruit weight	Fruit shelf life	Fruit shape	Flowers per cluster
cv 'A'	103.87 $\pm$ 17.51	35.20 $\pm$ 5.35	0.88 $\pm$ 0.03	8.56 $\pm$ 0.34
cv 'Platense'	155.92 $\pm$ 13.57	12.90 $\pm$ 0.82	0.72 $\pm$ 0.03	4.45 $\pm$ 0.33
cv 'B'	55.92 $\pm$ 4.50	25.90 $\pm$ 2.23	0.81 $\pm$ 0.02	5.64 $\pm$ 0.23
LA1385	4.42 $\pm$ 0.21	18.83 $\pm$ 0.73	0.98 $\pm$ 0.02	9.30 $\pm$ 0.34
LA722	0.97 $\pm$ 0.04	18.77 $\pm$ 1.16	0.97 $\pm$ 0.02	15.15 $\pm$ 0.20
F <sub>1</sub> ('A' x 'Platense')	87.88 $\pm$ 3.14	12.00 $\pm$ 0.43	0.83 $\pm$ 0.01	4.86 $\pm$ 0.28
F <sub>1</sub> ('A' x 'B')	85.60 $\pm$ 3.64	17.87 $\pm$ 0.98	0.72 $\pm$ 0.02	7.22 $\pm$ 0.16
F <sub>1</sub> ('A' x LA1385)	33.44 $\pm$ 1.66	12.40 $\pm$ 0.45	0.88 $\pm$ 0.02	5.07 $\pm$ 0.27
F <sub>1</sub> ('A' x LA722)	6.42 $\pm$ 0.43	19.17 $\pm$ 0.68	0.97 $\pm$ 0.01	10.18 $\pm$ 0.26
F <sub>1</sub> ('Platense' x 'B')	94.21 $\pm$ 7.28	17.00 $\pm$ 1.25	0.69 $\pm$ 0.03	6.50 $\pm$ 0.13
F <sub>1</sub> ('Platense' x LA1385)	20.97 $\pm$ 0.96	19.20 $\pm$ 0.87	0.85 $\pm$ 0.04	9.10 $\pm$ 0.24
F <sub>1</sub> ('Platense' x LA722)	7.56 $\pm$ 0.31	16.40 $\pm$ 0.63	0.97 $\pm$ 0.01	9.30 $\pm$ 0.27
F <sub>1</sub> ('B' x LA1385)	21.41 $\pm$ 1.53	15.57 $\pm$ 0.88	0.89 $\pm$ 0.02	9.15 $\pm$ 0.42
F <sub>1</sub> ('B' x LA722)	5.06 $\pm$ 0.29	22.10 $\pm$ 1.07	0.98 $\pm$ 0.01	8.25 $\pm$ 0.23
F <sub>1</sub> (LA1385 x LA722)	2.77 $\pm$ 0.19	15.53 $\pm$ 1.01	1.00 $\pm$ 0.01	8.79 $\pm$ 0.11
F value	56.98*	4.95*	29.96*	6.95*

\*P&lt;0.01

**Table 2.** General (GCA) and specific combining ability (SCA) for production traits in five tomato parents.

Parents	Fruit weight		Fruit shelf life		Fruit shape		Flowers per cluster	
	GCA	SCA	GCA	SCA	GCA	SCA	GCA	SCA
cv 'A'	20.92	16.24	2.90	10.81	-0.015	0.028	-0.59	1.65
cv 'Platense'	35.41	39.33	-3.02	0.35	-0.069	-0.020	-1.42	-0.81
cv 'B'	6.22	-2.28	1.83	3.65	-0.052	0.037	-0.89	-0.69
LA1385	-26.73	12.13	-1.60	3.43	0.048	0.009	0.30	0.60
LA722	-35.83	26.87	-0.11	0.41	0.088	-0.076	2.60	1.85
$\sigma^2$ estimates	9.43	18.21	1.59	1.23	8 x 10 <sup>-5</sup>	1 x 10 <sup>-4</sup>	0.24	0.43
$\sigma^2$ contrasts	23.58	52.04	3.98	2.96	2 x 10 <sup>-4</sup>	6 x 10 <sup>-4</sup>	0.60	1.04

 $\sigma^2$  estimates: variance of the estimates of GCA and SCA of each parent ( $g_i$  and  $s_{ii}$  in Griffing, 1956). $\sigma^2$  contrasts: variance of the contrasts of GCA and SCA among two parents ( $g_i - g_j$  and  $s_{ii} - s_{jj}$  in Griffing, 1956).

The *L. esculentum* parents, 'Platense', 'A' and 'B', and their intravarietal hybrids had the greatest weight values (Table 1). The intervarietal hybrids, i.e., crosses among the *L. esculentum* parents and LA1385 (*L. esculentum* var. *cerasiforme*), produced middle-weight fruits. LA1385 and hybrids among the *L. esculentum* parents and LA722 had low-weight fruits. The latter wild accession and its cross with LA1385 (the hybrid between two exotic parents) had extremely low-weight fruits. Hence, GCA was high and positive for 'Platense', 'A' and 'B', and high and negative for LA1385 and LA722. According to Soriano Viana (2000), such a variation in GCA values indicates strong differences in allele frequencies and genetic divergence among the diallel parents for the trait under study. In this particular case, cultivated and exotic germplasm of *Lycopersicon* differed greatly in fruit weight, as also found in previous

**Table 3.** Specific combining ability (SCA), mid-parent heterosis (MPH) and degree of dominance (d/a) of productive traits in 10 tomato hybrids.

Hybrids	Fruit weight			Fruit shelf life			Fruit shape			Flowers per cluster		
	SCA	MPH	d/a	SCA	MPH	d/a	SCA	MPH	d/a	SCA	MPH	d/a
F <sub>1</sub> ('A' x 'Platense')	-14.22	-32	-1.61	-6.46	-50	-1.08	0.037	41	0.42	-1.22	-25	-0.80
F <sub>1</sub> ('A' x 'B')	12.69	7	0.24	-5.45	-42	-2.73	-0.093	-15	-3.83	0.60	2	0.08
F <sub>1</sub> ('A' x LA1385)	-6.52	-38	-0.41	-7.49	-54	-1.79	-0.024	-5	-0.80	2.74	-43	-10.36
F <sub>1</sub> ('A' x LA722)	-24.44	-88	-0.84	-2.21	-29	-0.95	0.023	5	0.93	0.07	-14	-0.51
F <sub>1</sub> ('Platense' x 'B')	6.81	-11	-0.23	-0.40	-12	-0.37	-0.068	-10	-1.67	0.71	29	2.47
F <sub>1</sub> ('Platense' x LA1385)	-33.47	-74	-0.78	5.23	21	1.12	-0.002	0	0.03	2.12	32	0.92
F <sub>1</sub> ('Platense' x LA722)	-37.79	-90	-0.91	0.94	4	0.19	0.072	14	0.93	0.02	-5	-0.09
F <sub>1</sub> ('B' x LA1385)	-3.84	-29	-0.34	-3.26	-30	-1.92	0.019	0	-0.04	1.64	23	0.92
F <sub>1</sub> ('B' x LA722)	-11.09	-82	-0.85	1.80	-1	-0.07	0.068	10	1.06	-1.56	-20	-0.45
F <sub>1</sub> (LA1385 x LA722)	19.58	3	0.05	-1.34	-19	-∞	-0.076	2	∞	-2.22	-28	-1.18
σ <sup>2</sup> estimates	62.87	-	-	10.61	-	-	6 x 10 <sup>-4</sup>	-	-	1.60	-	-
σ <sup>2</sup> contrasts I	141.45	-	-	23.88	-	-	1 x 10 <sup>-3</sup>	-	-	3.59	-	-
σ <sup>2</sup> contrasts II	117.88	-	-	19.90	-	-	1 x 10 <sup>-3</sup>	-	-	3.00	-	-

σ<sup>2</sup> estimates: variance of the estimates of SCA of each hybrid (s<sub>ij</sub> in Griffing, 1956).

σ<sup>2</sup> contrasts I: variance of the contrasts of SCA among two hybrids with a common parent (s<sub>ij</sub> - s<sub>jk</sub> in Griffing, 1956).

σ<sup>2</sup> contrasts II: variance of the contrasts of SCA among two hybrids of different parents (s<sub>ij</sub> - s<sub>kl</sub> in Griffing, 1956).

studies by Stevens (1986), Tigchelaar (1986), Weller et al. (1988) and Bernacchi et al. (1998). SCA was high and positive for all parents except for 'B', which was not different from zero. This fact indicated that negative unidirectional dominance is involved in the expression of the trait (Griffing, 1956). In our study, genes from *L. esculentum*, as well as from the wild germplasm, caused a reduction in fruit weight. Values of SCA, mid-parent heterosis and degrees of dominance for hybrids support the above proposition. When there is negative dominance, the lower the SCA values of hybrids, the higher the differences in allele frequencies among the parents and in relation to the average frequencies in the diallel parents (Soriano Viana, 2000). Large differences in allele frequencies were detected among 'Platense' and the other parents, while 'A' and 'B', and LA1385 and LA722, had similar allele frequencies. It is possible that 'Platense' carries many of the different genes increasing fruit weight that have been described within the gene pool of the cultivated tomato (Alpert and Tanksley, 1996; Frary et al., 2000). Parents 'A' and 'B', and certainly the exotic germplasm, would carry the dominant alleles that reduce the values of this trait. These observations indicate that to increase fruit weight, intense unidirectional selection should be applied in segregating populations derived from crosses among 'Platense' and any of the other parents.

The 'A' and 'B' parents had the highest shelf life values, followed by the  $F_1$  ('B' x LA722). 'Platense', the  $F_1$  ('A' x 'Platense'), and the  $F_1$  ('A' x LA1385) had the lowest shelf life values, while the exotic parents and the other hybrids ranked intermediately. Differences in allele frequencies and genetic divergence among parents were also detected for this trait, as was evident from their GCA and SCA values (Soriano Viana, 2000). Compared to the mutant for ripening genotypes, 'A' was the most divergent parent, and its mean effects were smaller than those of 'B'. Similar results were reported by Tigchelaar et al. (1978) and Stevens and Rick (1986). Genes carried by both LA1385 and LA722 were able to prolong shelf life *per se*, in both the homozygous and the heterozygous state. Preliminary observations of Pratta et al. (1996) and Zorzoli et al. (1998) on gene action were confirmed in our study; LA722 appeared to have greater effects than LA1385 on prolonging shelf life. However, unidirectional negative dominance was also detected for this trait, since SCA values for parents were positive. When analyzing each particular cross, this fact could be explained by the strong recessive effects of the *nor* and *rin* mutations, since the putative genes from the exotic germplasm were completely or partially dominant over those of the standard ripening 'Platense'. However, the  $F_1$  (LA1385 x LA722) had a relatively high and negative SCA, suggesting that considerable differences in allele frequencies exist between these two exotic parents. In fact, LA1385 and LA722 perform divergently in crosses to 'A' and 'B', and even to 'Platense', as shown in Table 1. Also, it was evident that 'A' was very different from the other parents, and 'B' and LA722 had similar effects, and consequently similar allele frequencies, for shelf life. Hence, although the  $F_1$  between these two parents was superior to the other hybrids, probably just a small amount of genetic variability would be obtained from this cross. Considering that GCA effects were smaller than SCA effects, applying unidirectional selection will have little effect on changing the mean shelf life value of any segregating populations. Instead interpopulational breeding should be made, by deriving new inbred lines from crosses among divergent parents such as 'Platense' and LA722, or 'A' and LA1385.

The other two production traits, fruit shape and mean number of flowers per cluster, were greatly modified by the exotic germplasm. LA1385 and LA722 had round fruits and several flowers per cluster. Differences in allele frequencies and genetic divergence were also

detected for these traits, but bidirectional dominance (either positive or negative, according to the parents involved) was observed (Soriano Viana, 2000). Also, although GCA effects were larger than SCA for both shape and flowers per cluster, additive effects were more important for shape among the diallel parents. This fact might be explained by the predominant overdominant gene action affecting flowers per cluster, thus reducing the contribution of the additive component. Genotypes having large values for this trait could compensate the field yield (measured in kg of fruit per unit of crop area) by increasing the number of potentially harvested fruits per plant. This is especially important in those situations where a reduction in individual fruit weight is provoked, as was the case here. On the other hand, a correlation among soluble solid content and round shape has been reported by some researchers (Stevens, 1986 and Tigchelaar, 1986). Breeding for shape and flowers per cluster is possible among this set of genotypes, though crossing strategies should be different. For fruit shape, an intrapopulation strategy should be applied in crosses between 'Platense' and LA722, while an interpopulation strategy including these two parents plus 'A' and LA1385 would be more suitable for flowers per cluster.

In the search for an appropriate genotype for breeding all traits simultaneously, the  $F_1$  ('Platense' x LA722) appears to be the most promising hybrid, since its parents had the largest differences in allele frequencies and the greatest genetic divergence.

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