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Research Paper

Genome-wide expression analysis at three fruit ripening stages for tomato genotypes differing in fruit shelf life

J.H. Pereira da Costa[a,*], G.R. Rodríguez[a], L.A. Picardi[a,b], R. Zorzoli[a,b], G.R. Pratta[a]

[a] Instituto de Investigaciones en Ciencias Agrarias de Rosario IICAR-CONICET-UNR, Zavalla, Santa Fe, Argentina
[b] Consejo de Investigaciones de la Universidad Nacional de Rosario CIUNR, Santa Fe, Argentina

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ABSTRACT

The ripening stage at harvest time determines the tomato fruit quality. After the fruit achieves its maximum size several metabolic changes of typically climacteric fruits are produced. Two cultivated genotypes of *Solanum lycopersicum* (Caimanta and 804627), with normal and altered fruit ripening, respectively and two accession, LA1385 of *S. lycopersicum* var. *cerasiforme* and LA722 of *S. pimpinellifolium*, with genes that prolong fruit shelf life, were tested to: 1) characterize and make a comparatively analysis for the transcriptome at different fruit ripening stages in genotypes that differ in fruit shelf life by cDNA-AFLP; and 2) provide further insight into the relationship between the extreme phenotypic differences for ripening among the genotypes through changes at transcriptomic level. Fruits at the breaker stage (B) were evaluated for fruit weight, firmness and fruit shelf life. The elapsed days between mature green (MG) and breaker stages Days (MG-B) as well as the elapsed days between B and red ripe (RR) stages Days (B-RR) were recorded. Comparison among ripening stages showed a great polymorphism related to the changes in gene expression. For all genotypes the transition from B to RR stages had higher polymorphism than the transition from MG to B. It was observed a great genetic variability for the phenotypic traits in agreement with the changes of gene expression. Moreover, it was observed that the transcriptome expression profiles in the initial and intermediate stages during ripening (MG and B) are more important to characterize genotypes. The wild species which have long shelf life do not show as drastic changes in gene expression as the cultivar with altered ripening that carrythe *nor* gene. These results suggest that the expressed or silenced genes could be involved, in some way, in the determination of the phenotypic traits evaluated in this study.

1. Introduction

The cultivated tomato (*Solanum lycopersicum* L.) is an autogamous species in which the fruit quality plays an important role for both producers and consumers. The ripening stage at harvest time determines the final product quality and the maintenance in good conditions during a period of time (Javanmardi and Kubota, 2006). Fruit ripening is the final step in the fruit development. After the fruit achieves its maximum size several metabolic changes of typically climacteric fruits are produced. Fruit quality traits such as color, aroma, flavor, texture and consistence are defined in this final step of ripening. The accumulation of carotenoid pigments and fruit softening allows to distinguish various ripening stages: mature green, breaker, turning, orange, red firm and red ripe (Rick, 1978; Nuez, 1991; Giovannoni, 2004). Mutants affecting the normal ripening process were detected in *S. lycopersicum* such as *rin* (*ripening inhibitor*), *nor* (*non ripening*), *Nr* (*never ripe*), *alc* (*alcobaca*) (Chalukova and Manuehyan, 1991). These genes block or prolong the fruit ripening so they contribute to extend fruit shelf life. However, these mutants also have undesirable effects on fruit quality due to pleiotropic actions of the genes. Fruits from *S. lycopersicum* var. *cerasiforme* (Dunal) (Spooner et al., 1993) and *S. pimpinellifolium* L. wild species have wide variability for attributes such as flavor, aroma, coloration and texture and they also carrying genes for fruit shelf life (Pratta et al., 1996; Zorzoli et al., 1998). The advantage of the fruit shelf life wild genes is that they have no negative effects on organoleptic fruit quality. A wide range of tomato genotypes such as the standard for ripening Caimanta, variety homozygote for the *nor* allele and some relative wild species have been characterized by our research team at phenotypic, proteomic and genomic levels (Rodríguez et al., 2008; Pereira da Costa et al., 2017). In fact, several polypeptides and genomic regions were associated with fruit traits in segregating populations derived from interespecific crosses (Rodríguez et al., 2010; Pereira da Costa et al., 2013), however a whole gene expression analysis to compare the ripening process among genotypes carrying fruit

* Corresponding author.
E-mail address: jpereira@unr.edu.ar (J.H. Pereira da Costa).

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Table 1
Restriction enzymes, adapters, pre-amplification primers, selective amplification primers and primer combinations to obtain AFLP-based transcript profiling (cDNA-AFLP) for expression analysis.

Restriction enzymes		*Apo I*	*Mse I*
Adapters	Top Strand	CTCGTAGACTGCGTACC	GACGATGAGTCCTGAG
	Bottom Strand	AATTGGTACGCAGTCTAC	TACTCAGGACTCAT
Pre-amplification primers (0)		CTCGTAGACTGCGTACCAATT	GACGATGAGTCCTGAGTAA
Selective amplification primers (+1)		GACTGCGTACCAATTG (Apo11)	GATGAGTCCTGAGTAAG (Mse37)
		GACTGCGTACCAATTA (Apo12)	GATGAGTCCTGAGTAAT (Mse38)
Combination A	Apo11-Mse37	**Combination C**	Apo11-Mse38
Combination B	Apo12-Mse37	**Combination D**	Apo12-Mse38

Table 2
Mean values and standard error for each genotype and Degree of Genetic Determination (DGD) for each trait. **W**: fruit weight, **Fir**: fruit firmness, **SL**: fruit shelf life, **Days (MG-B)**: days from mature green to breaker stage, **Days (B-RR)**: days from breaker to red ripe stage. **CAI**: Caimanta cultivar of *S. lycopersicum*, **NOR**: accession 804627 of *S. lycopersicum* homozygous for *nor* gene, **LA1385**: accession LA1385 of *S. lycopersicum* var. *cerasiforme* and **LA722**: accession LA722 of *S. pimpinellifolium*. Different letters indicate significant differences. $^{**}p < 0.01$ y $^{***}p < 0.001$.

	W	Fir	SL	Days (MG-B)	Days (B-RR)
CAI	151.62 ± 12.90 ^{c}	50.67 ± 2.02 ^{a}	6.92 ± 0.65 ^{a}	13.81 ± 0.66 ^{b}	5.26 ± 0.42 ^{a}
NOR	80.37 ± 10.38 ^{b}	63.67 ± 7.88 ^{b}	20.67 ± 4.33 ^{c}	16.22 ± 0.73 ^{c}	10.07 ± 0.49 ^{b}
LA1385	3.16 ± 0.26 ^{a}	57.20 ± 2.15 ^{ab}	17.00 ± 1.26 ^{bc}	10.95 ± 0.76 ^{a}	5.36 ± 0.57 ^{a}
LA722	0.83 ± 0.09 ^{a}	61.56 ± 1.83 ^{b}	13.33 ± 1.47 ^{b}	12.54 ± 0.63 ^{ab}	4.93 ± 0.37 ^{a}
F	53.66 ***	5.32 **	15.85 ***	7.25 ***	29.05 ***
DGD	0.88	0.38	0.68	0.13	0.50

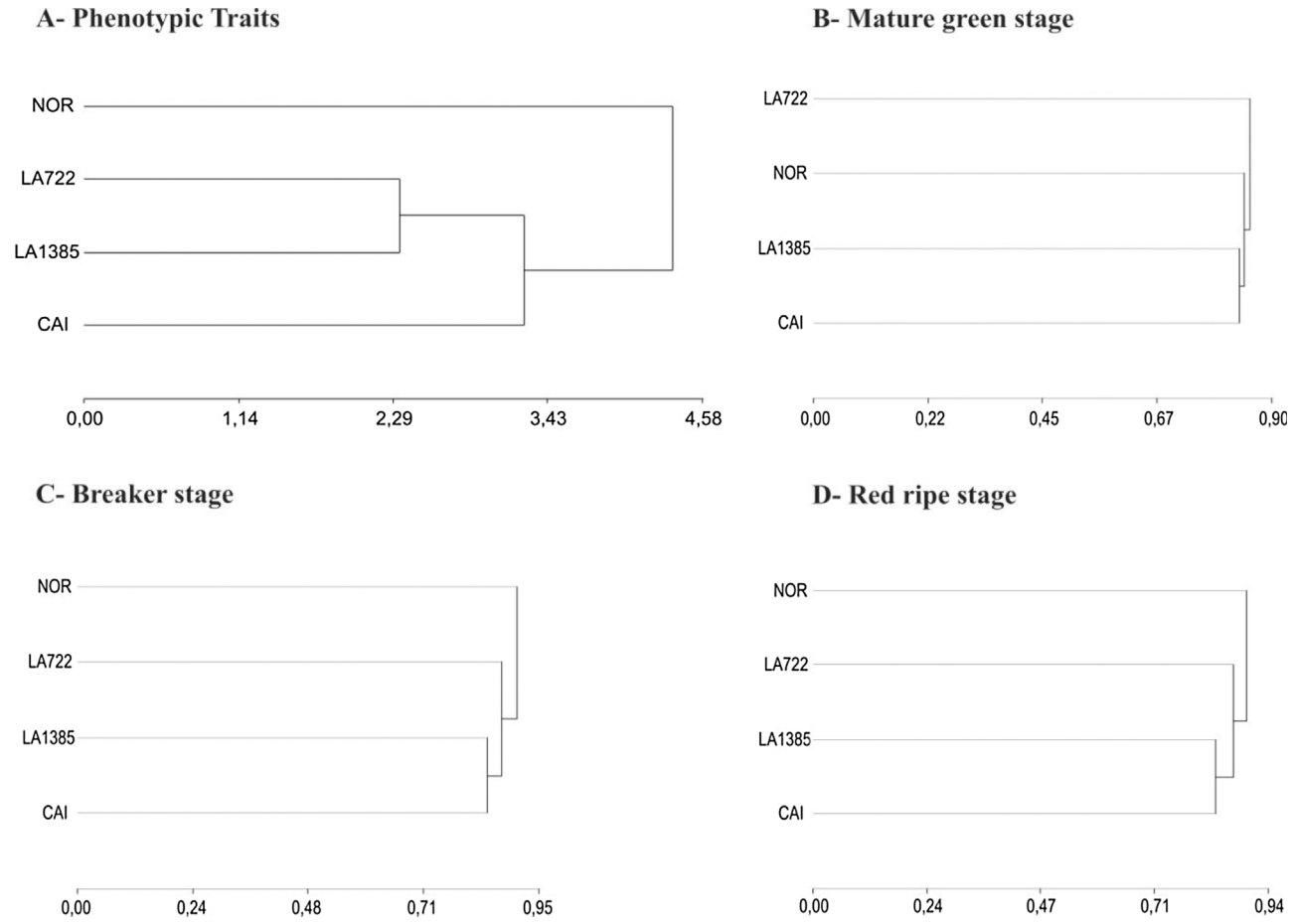

Fig. 1. Analysis of cluster among genotypes from phenotypic traits (*A*) and gene expression profiles at three ripening stages: mature green (*B*), breaker (*C*) and red ripe (*D*). **CAI**: Caimanta cultivar of *S. lycopersicum*, **LA722**: accession LA722 of *S. pimpinellifolium,* **LA1385**: accession LA1385 of *S. lycopersicum* var. *cerasiforme* and **NOR**: accession of *S. lycopersicum* homozygous for *nor* gene.