Journal of Animal & Plant Sciences, 33(5): 2023, Page: 1043-1050
ISSN (print): 1018-7081; ISSN (online): 2309-8694
https://doi.org/10.36899/JAPS.2023.5.0697

ANALYSES of *P-Tst-1*, *P-Tst-3* and *P-Tst-6* RETROTRANSPOSONS IN CONVENTIONALLY AND ORGANICALLY PRODUCED TOMATOES

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ABSTRACT

Tomato is one of the best-studied cultivated dicotyledonous plants in molecular studies. Mobile genetic elements constitute large parts of plant genomes. Retrotransposons are mobile genetic elements within the genome and constitute more than 60% of the tomato genome. Transposable elements (TE) or transposons are DNA sequences that can alter their position within a genome, cause mutations and change the genetic identity of the cells and genome size. We aimed to analyze potato specific-*P-Tst-1, P-Tst-3* and *P-Tst-6* retrotransposon movements in tomatoes at different developmental stages (mature seedling, flowering stage and fruiting stage) under different cultural conditions (organic and conventional) by IRAP (Inter-Retrotransposon Amplified Polymorphism) technique. We found polymorphism rates between 1-100% for *P-Tst-1, P-Tst-3* and 0-86% for *P-Tst-6*. When compared to organically produced tomatoes, conventionally produced tomatoes showed high polymorphism. Moreover, polymorphism ratios were different at developmental stages. This is the first report to analyze potato-specific retrotransposon movements in tomatoes grown under different conditions. Obtaining findings are expected to understand the evolutionary relationships between tomato and potato, and even the effects of different growing conditions on tomato genome to increase yield in agriculture.

Key Words: IRAP, Mobile genetic elements, *Solanum lycopersicum*

Published first online June 20, 2023 Published final September 30, 2023

INTRODUCTION

Solanum lycopersicum L. (tomato), belonging to Solanaceae family, is one of the most consumed vegetables. This plant is a perennial herbaceous plant but is regularly grown as an annual crop (Al-Remi *et al.* 2018). Tomato is grown worldwide for local consumption and export purposes in a wide variety of geographical areas in greenhouses or open fields (Knapp 2002; Bergougnoux 2014). Tomatoes are self-pollinated or pollinated by another representative of the same variety to out breed (cross-pollinated) to create hybrid variety which possesses traits of the two families (Samsulrizal and Yusof 2019). In many parts of the world, the vast majority of greenhouse tomatoes are produced using conventional production systems compared to organic systems. Conventional and organic agricultural systems are different regarding soils, pests, fertilizers, insecticides, fungicides and even economic conditions (Mitchell *et al.* 2007; Seçgin *et al.* 2018).

Some sequences in genomes tend to maximize their representation from one generation to the next by replicating themselves at a higher rate than other DNA sequences. These genetic materials named transposons or TEs change their places within the genome (Tufan *et al.* 2020). Different kinds of transposons show distinct mechanisms to increase their copy number. The most common types of transposons are RNA transposons (Class I elements) which transpose a "copy and paste" mechanism with an RNA intermediate, and DNA transposons (Class II elements) which move via "cut and paste" mechanism without an RNA intermediate. In contrast, transposon-like elements (Helitrons) are speculated to transpose via a "rolling circle" strategy (Piégu *et al.* 2015). Most of transposons of any type are non-autonomous elements that lack coding ability and

require the functions encoded by autonomous elements of a similar family (Wicker *et al.* 2007; Todorovska 2007).

TEs can make up most of the genetic information in different genomes (Kidwell 2002; Kaya *et al.* 2013). Even though they can occasionally provide a selective advantage to their host species (Arvas *et al.* 2021), they multiply in large portions to self-perpetuate (Kumar and Bennetzen 1999). The number and distribution of TEs are dramatically variable among closely related species and cover a meaningful proportion of many animal and plant genomes (Kidwell 2002; Vitte and Panaud 2005; Marakli *et al.* 2019). As a result of genome contraction and expansion, the number of transposon families may fall and rise in genomes (Piegu *et al.* 2006; Lisch 2009). The variations in DNA content are a reflection of a constantly shifting balance between selection at host level to regulate transposon activity and at the level of transposons to increase their copy number (Kalendar *et al.* 2021).

In this study, we determined the potato-specific *P-Tst-1, P-Tst-3* and *P-Tst-6* retrotransposon movements in tomatoes at different developmental stages (mature seedling, flowering, and fruiting stage) grown under different conditions (organic and conventional) by using IRAP technique.

MATERIALS AND METHODS

Plant materials and DNA extraction: *Solanum lycopersicum* L. var. Şencan 9 seeds were provided by Atatürk Horticultural Central Research Institute. During the tomato plant development in a greenhouse, organic fertilizers (cow dung manure and organic NPK-nitrogen, phosphorus and potassium) were provided for organically produced tomatoes. On the other hand, inorganic fertilizers (diammonium phosphate-DAP and ammonium sulphate), insecticides and fungicides were used for conventionally produced tomatoes.

Genomic DNAs (gDNAs) from the youngest leaves of experimental plants were isolated using CTAB method (20). Treatments were named CT, and OT for conventional tomatoes and organic tomatoes, respectively. Each of them was composed of three different plants belonging to three different stages: mature seedling, flowering stage and fruiting stage. Spectrophotometric and electrophoretic analyses were performed to determine the quantity and quality of gDNAs, and then gDNAs were stored at -20˚C until use.

IRAP-PCR

P-Tst-1, P-Tst-3 and *P-Tst-6* retrotransposons' movements in organically and conventionally produced tomatoes were determined by IRAP-PCR marker technique. Primer sequences are indicated in Table 1. For this purpose, 18 samples including six different plants were designated as CT1, CT2, CT3, OT1, OT2 and OT3, with three replications (mature seedling, flowering stage and fruiting stage) used as templates for IRAP-PCR.

P-Tst-1, *P-Tst-3* and *P-Tst-6* IRAP-PCR reactions were carried out using a thermal cycler in a total volume of 25 µL containing 6.5 µL of nuclease-free H_2O, 2 µL of primer (0.8 µM/µL), 4 µL of 20 ng/µL template genomic DNA and 12.5 µL 2X BioMix™ Red Master Mix (BIO-25006). PCR conditions were as follows: initial denaturation at 95°C (3 min), followed by 34 cycles of denaturation at 95°C (30 s), annealing at 40°C for *P-Tst-1*, 46°C for *P-Tst-3* and 48°C for *P-Tst-6* (30 s) and extension at 72°C (1 min). An additional extension at 72°C for 5 min was applied to finish the reaction. IRAP-PCR products and Hyper ladder™ 100 bp (BIO-33056) were resolved by 1% agarose gel electrophoresis at 80 V for 60 min, and then the gels were scanned and photographed on a UV transilluminator.

Polymorphism analysis

Monomorphic and polymorphic bands were determined for each treatment according to band profiles on agarose gels. The similarity ratios among the different samples were calculated using the Jaccard Similarity Coefficient formula (Jaccard, 1908).

Jaccard similarity coefficient (J) = MAB/MB + MA + MAB

MA: Number of bands in treatment A, but not in treatment B

MB: Number of bands in treatment B, but not in treatment A

MAB: Number of bands present in both A and B

RESULTS AND DISCUSSION

IRAP-PCR was performed using gDNAs isolated from organic and conventional tomatoes with 3 replications in different developmental stages. A total of 18 genomic DNA samples were used for templates in IRAP-PCR. PCR products were visualized on 1% agarose gel. The polymorphism rates for *P-Tst-1* were calculated by comparing each individual with others. Only clear bands were included in the count. Accordingly, 83 bands were counted between 800 bp and 2500 bp in Fig. 1. Among total band profiles, 45 bands were observed in conventionally produced tomatoes, and 38 were counted in organically produced ones. In the counted bands 22, 34 and 27 bands were observed at the mature seedling, flowering and fruiting stages, respectively. Polymorphism percentages were calculated among samples by comparing each sample with the other samples, resulting in 0-100% polymorphism (Table 2).

The polymorphism rates for *P-Tst-3* were also calculated by comparing each individual with others. 99 bands (56 for conventionally produced tomatoes and 43 for organically produced ones) between 400 and 2000 bp were counted for polymorphism analyses (Fig. 2).

Similarly to *P-Tst-1*, we found 0-100% polymorphism among samples. In the counted bands, 35, 40 and 24 bands were observed at the mature seedling, flowering and fruiting stages, respectively (Table 3).

The other retrotransposon, *P-Tst-6*, also indicated a polymorphic band profile among samples. In analyses, 112 bands (18 monomorphic and 94 polymorphic) were counted between 400 and 2000 bp. In the bands, 61 were observed in conventionally produced tomatoes, and 51 were counted in organically produced ones (Fig. 3). From the total count, 42, 42 and 28 bands were observed at the mature seedling, flowering, and fruiting stages, respectively. There were 0-86% polymorphism rates among samples (Table 4).

P-Tst-1, P-Tst-3 and *P-Tst-6* retrotransposons were discovered as potato retrotransposons (Lightbourn *et al.* 2007; Sharma and Nandineni 2014). Forty-seven Indian varieties of potatoes (*Solanum tuberosum* L.) were assessed using microsatellite and retrotransposon-based marker techniques (Devran *et al.* 2018). Similarly, another study was conducted by using IRAP molecular markers with four *Copia*-type retrotransposons (*ToRL1, Tnt1*, *T265P* and *T135*) to investigate genetic diversity among 10 different commercially important tomato cultivars which have different genotypic and phenotypic characters (Novakova *et al.* 2009). They also studied 20 potato varieties to investigate *P-Tst-1, P-Tst-3* and *P-Tst-6* retrotransposons via IRAP marker technique. They reported that *P-Tst-6* displayed highly polymorphic bands compared to *P-Tst-1* and *P-Tst-3.* The percentages of polymorphic bands were 90, 90 and 100% for *P-Tst-1, P-Tst-3* and *P-Tst-6,* respectively. Concordant with these results, we also found that 0-100%, 0-100% and 0-86% polymorphism ratios of *P-Tst-1, P-Tst-3* and *P-Tst-6,* respectively among conventionally and organically produced tomatoes.

Since tomatoes also shared the same family (*Solanaceae*) with the potato plant, these potato-specific primers such as *P-Tst-1, P-Tst-3* and *P-Tst-6* were used to investigate the presence and movement of retrotransposons organically and conventionally grown tomatoes. According to the results, *P-Tst-1* was highly polymorphic and a 0-100% polymorphism ratio was found among samples. This result indicated the existence of *P-Tst-1* retrotransposon in tomato and potato, and other *Solanaceae* species. Additionally, *P-Tst-1* retrotransposon is active in the tomato genome similar to the potato genome. Moreover, *P-Tst-1* retrotransposon in conventionally produced tomatoes showed higher polymorphism than organically produced tomatoes. This result indicated that applying chemicals to conventional tomatoes increased the activities of *P-Tst-1* in tomato genome. Furthermore, the bands of *P-Tst-1* retrotransposon were also detected with higher numbers at the flowering stage of tomato plants than at the mature seedling and fruiting stage. Similar to *P-Tst-1, P-Tst-3* (0-100%) and *P-Tst-6* (0-86%) were also polymorphic in conventionally and organically produced tomatoes. Furthermore, *P-Tst-3* and *P-Tst-6* retrotransposons had abundant band numbers at the mature seedling and flowering stage of the tomato plant compared to the fruiting stage. Yilmaz *et al.* (2018) studied herbicide effects on rice and reported that herbicide treatment could enhance retrotransposon activity in rice with increasing herbicide concentration. There are numerous reports showing retrotransposition movements in various biotic and abiotic stress conditions like wounding, pathogen attack, and various chemicals such as herbicide, fungicide and insecticide applications (Dimitrov *et al.* 2011, Cakmak *et al.* 2015; Finatto *et al.* 2015; Songstad *et al.* 2017; Yilmaz *et al.* 2018; Nie *et al.* 2019).

Retrotransposons belonging to a specific plant could be identified in different species, including plant and human genomes (Vitte and Panaud 2005; Cakmak *et al.* 2017). These mobile elements are important evolutionary drivers with conserved nature in genomes. Moreover, many different situations could affect retrotransposon movements, including epigenetic effects and environmental conditions (Dimitrov *et al.* 2011). Therefore, we used potato-specific retrotransposons in another plant species (tomato) belonging to the same family. Similar to the potato genome, these retrotransposons were mobile in the tomato genome. Moreover, high numbers of bands were observed in conventionally produced tomatoes compared to organically produced ones, which implied that the application of herbicide, fungicide and insecticide could enhance the activities of retrotransposon elements in the tomato genome. This is the first study for conventional and organic tomatoes related to potato-specific retrotransposons' movements. The result could provide a valuable contribution to different epigenetics studies on tomatoes.

Table 1 Primers used in this study.

Primer Names	Sequences (5'→3')	References
P-Tst-1	ATGACTAAATCTGCCTACTCATTCAACA	
P-Tst-3	ACTAAAAATCTGCCTACTCATTCAACA CTC	(Novakova *et al.* 2009)
P-Tst-6	ACTAAATCTGCCTACTCATTCAACACT C	

Table 2. Polymorphism ratios calculated with Jaccard similarity coefficient for *P-Tst-1* retrotransposon

		R1						R2						R3					
		CT1	CT2	CT3	OT1	OT2	OT3	CT1	CT2	CT3	OT1	OT2	OT3	CT1	CT2	CT3	OT1	OT2	OT3
R1	CT1	-																	
	CT2	43	-																
	CT3	86	75	-															
	OT1	29	20	80	-														
	OT2	29	20	80	0	-													
	OT3	100	100	100	100	100	-												
R2	CT1	0	43	86	29	29	100	-											
	CT2	0	43	86	29	29	100	0	-										
	CT3	29	20	80	0	0	100	29	29	-									
	OT1	57	25	67	40	40	100	57	57	40	-								
	OT2	14	33	83	17	17	100	14	14	17	50	-							
	OT3	14	33	83	17	17	100	14	14	17	50	0	-						
R3	CT1	57	83	50	67	67	100	57	57	67	80	50	50	-					
	CT2	14	33	83	17	17	100	14	14	17	50	0	0	50	-				
	CT3	14	33	83	17	17	100	14	14	17	50	0	0	50	0	-			
	OT1	14	33	83	17	17	100	14	14	17	50	0	0	50	0	0	-		
	OT2	43	0	75	20	20	100	43	43	20	25	33	33	83	33	33	33	-	
	OT3	57	25	67	40	40	100	57	57	40	0	50	50	80	50	50	50	25	-‘

Table 3. Polymorphism ratios calculated with Jaccard similarity coefficient for *P-Tst-3* retrotransposon

		R1						R2						R3					
		CT1	CT2	CT3	OT1	OT2	OT3	CT1	CT2	CT3	OT1	OT2	OT3	CT1	CT2	CT3	OT1	OT2	OT3
R1	CT1	-																	
	CT2	29	-																
	CT3	29	0	-															
	OT1	29	0	0	-														
	OT2	29	0	0	0	-													
	OT3	60	71	71	71	71	-												
R2	CT1	29	0	0	0	0	71	-											
	CT2	29	0	0	0	0	71	0	-										
	CT3	29	0	0	0	0	71	0	0	-									
	OT1	29	0	0	0	0	71	0	0	0	-								
	OT2	29	0	0	0	0	71	0	0	0	0	-							

R3	**OT3**	0	29	29	29	29	60	29	29	29	29	29	-						
	CT1	20	43	43	43	43	50	43	43	43	43	43	20	-					
	CT2	17	14	14	14	14	67	14	14	14	14	14	17	33	-				
	CT3	17	14	14	14	14	67	14	14	14	14	14	17	33	0	-			
	OT1	17	14	14	14	14	67	14	14	14	14	14	17	33	0	0	-		
	OT2	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	-	
	OT3	60	71	71	71	71	0	71	71	71	71	71	60	50	67	67	67	100	-‘

Table 4. Polymorphism ratios calculated with Jaccard similarity coefficient for *P-Tst-6* retrotransposon.

		R1						**R2**						**R3**					
		CT1	**CT2**	**CT3**	**OT1**	**OT2**	**OT3**	**CT1**	**CT2**	**CT3**	**OT1**	**OT2**	**OT3**	**CT1**	**CT2**	**CT3**	**OT1**	**OT2**	**OT3**
R1	**CT1**	-																	
	CT2	0	-																
	CT3	0	0	-															
	OT1	0	0	0	-														
	OT2	0	0	0	0	-													
	OT3	0	0	0	0	0	-												
R2	**CT1**	0	0	0	0	0	0	-											
	CT2	0	0	0	0	0	0	0	-										
	CT3	0	0	0	0	0	0	0	0	-									
	OT1	0	0	0	0	0	0	0	0	0	-								
	OT2	0	0	0	0	0	0	0	0	0	0	-							
	OT3	0	0	0	0	0	0	0	0	0	0	0	-						
R3	**CT1**	29	29	29	29	29	29	29	29	29	29	29	29	-					
	CT2	0	0	0	0	0	0	0	0	0	0	0	0	29	-				
	CT3	0	0	0	0	0	0	0	0	0	0	0	0	29	0	-			
	OT1	14	14	14	14	14	14	14	14	14	14	14	14	17	14	14	-		
	OT2	71	71	71	71	71	71	71	71	71	71	71	71	60	71	71	67	-	
	OT3	86	86	86	86	86	86	86	86	86	86	86	86	80	86	86	83	50	-

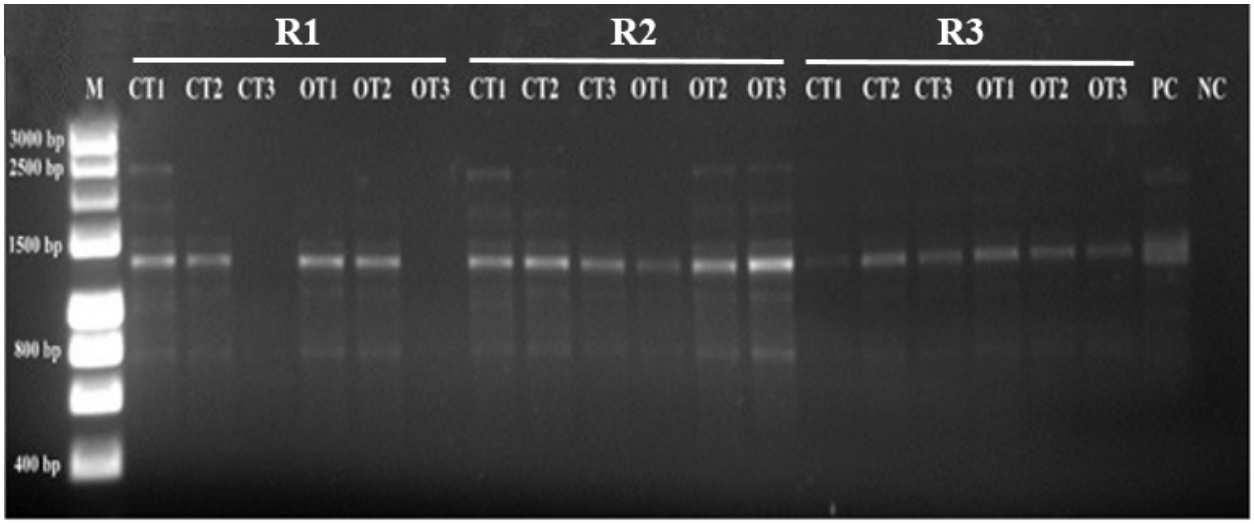

Fig. 1 IRAP-PCR results of *P-Tst-1* retrotransposon. M: marker; CT: conventional tomatoes replication; OT: organic tomatoes replication; PC: positive control (from Potato); NC: negative control (without gDNA); R1: replication one (mature seedling); R2: replication two (flowering stage); R3: replication three (fruiting stage).

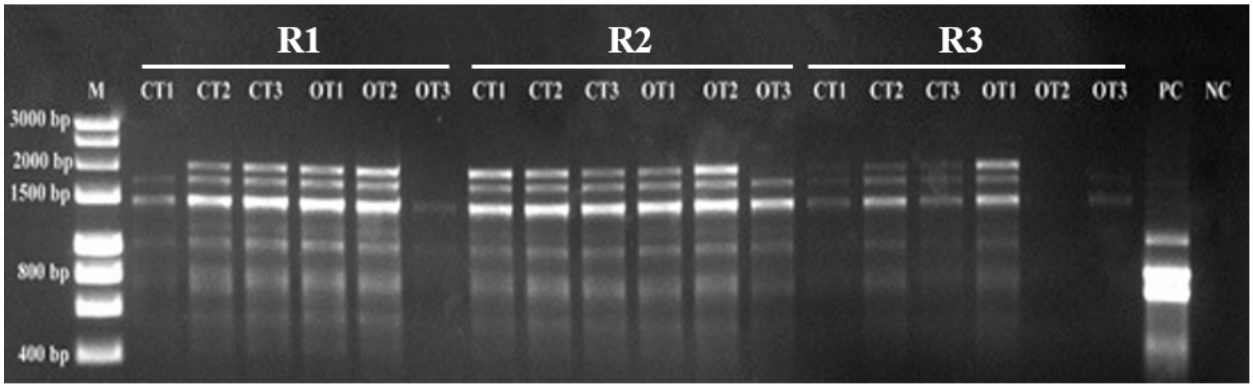

Fig. 2 IRAP-PCR results of *P-Tst-3* retrotransposon. M: marker; CT: conventional tomatoes replication; OT: organic tomatoes replication; PC: positive control (from Potato); NC: negative control (without gDNA); R1: replication one (mature seedling); R2: replication two (flowering stage); R3: replication three (fruiting stage).

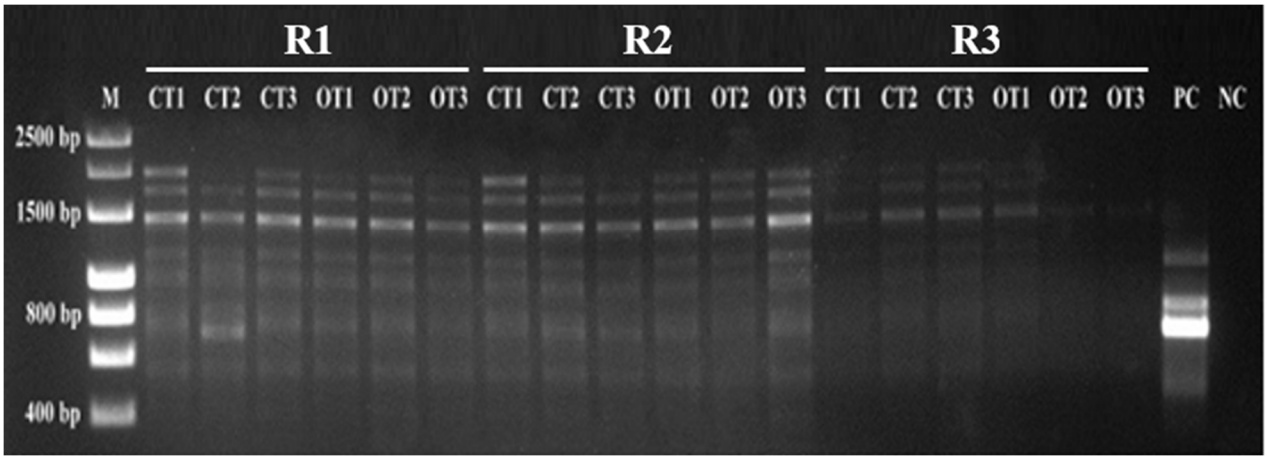

Fig. 3 IRAP-PCR results of *P-Tst-6* retrotransposon. M: marker; CT: conventional tomatoes replication; OT: organic tomatoes replication; PC: positive control (from Potato); NC: negative control (without gDNA); R1: replication one (mature seedling); R2: replication two (flowering stage); R3: replication three (fruiting stage).

Acknowledgments: This study was funded by the Scientific Research Projects Coordination Unit of Ondokuz Mayis University (Project no. PYO.ZRT.1904.18.019).

This paper contained data from the Master thesis of the first author.

Author contributions: EK Haji, YE Arvas and MM Abed performed the majority of the experiments and data analysis. S. Marakli contributed to the activation experiment and data analysis. Y. Kaya designed the experiments and analysed the data. S Marakli, Y Kaya and EK Haji wrote the manuscript. All authors read and approved the final version of the manuscript.

Conflict of interest The authors declare no conflict of interest.

Human and animal rights The study does not include human and animal experiments.

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