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Assessment of Population Structure and Association Mapping for Fruit quality Traits using Molecular Markers in Tomato

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ABSTRACT: Tomato (*Solanum lycopersicum* L.) is an important and most widely grown vegetable crop of both tropics and sub tropics of the world. The high demand for tomato makes it a high value crop that can generate much income to farmers. Tomato fruits are an important source of fiber and nutrients in the human diet and a model for the studying fruit development. The combination of large germplasm collections, high-throughput genomic tools, and traits of economic interest provide a framework to apply genome wide association study (GWAS), which is promising genetic method for the dissection of complex traits in this species. The estimation of genetic relatedness among accessions and sub-populations is a prerequisite for the identification of true genome wide associations. The genotyping of accessions using wide genome simple sequence repeats could give correct estimates of genetic relatedness. The genotyping of enough markers also decides the outcome of true causal variants. Here we report the population structure of 264 tomato germplasm using the wide genome distributed simple sequence repeats (SSRs). The capital K value of population is estimated to K=4. The association mapping in structured population resulted in significant marker trait associations for fruit quality traits wise fruit firmness, shelf life, ascorbic acid, lycopene content, total soluble solids and locule number. Associations between SSR alleles and fruit quality traits were obtained using the generalized linear model (GLM) and the population structure matrix Q = 4. A total of 133 SSR alleles (P<0.05) were detected for six fruit quality traits.

Keywords: Germplasm, Simple sequence repeats, Population structure, Genome wide association study, Alleles.

INTRODUCTION

Tomato, as the most important vegetable globally has adapted widely from gardens to open fields to soil less cultivation. Since increased consumption per capita, consumers have become more concerned about the quality of tomato fruits (Hobson, 1988; Bruhn et al., 1991). A strong environmental selection pressure generated tremendous diversity of fruit. The *Solanaceae* family covers nearly 10,000 species with great diversity of fruit types occurring in more than 90 genera (Knapp, 2002). Tomato as model crop differs from other model crops by having fleshy fruit, a sympodial shoot, and compound. These special features make tomato as important model plant system to study desirable traits with special emphasis on fruit anatomy, development and quality (Kimura and Sinha 2008). Along with a short life cycle, high multiplication rate, self-pollination, and ease of mechanical crossing led to the emergence of tomato as model species for fleshy fruits (Gillaspy *et al.*, 1993; Tanksley, 2004; Klee and Giovannoni 2011). These species have undergone breeding schemes for improvement of various quality traits such as shelf life, texture, sugar-acid ratio, pigments and vitamins (Azzi *et al.*, 2015).

However, genetic improvement progress is still limited concerning fruit quality traits due to the complexity of traits. Since polygenes control many quality traits in tomato, the associated genomic regions known as QTLs can be identified by molecular markers through the mapping approach. Molecular mapping helps in tracing the alleles that control targeted traits (Collard *et al.*, 2008). Many fruit quality traits are mapped using bi parental population with the QTL mapping approach (Goldman *et al*., 1995; Chen *et al*., 1999; Causse *et al.*, 2002; Adhikari *et al*., 2020; Prinzenberg *et al*., 2021). However, QTL mapping using bi-parental population suffers from low genetic resolution and low accuracy of high-throughput genotyping mainly due to restricted allelic variation and limited recombination rate (Hall *et*

al., 2010; Xu *et al*., 2012; Zhang *et al.*, 2015). Repeated intercrossing in RIL population over generations helps to overcome the resolution problem, while Multi-parent Advanced Generation Inter-Cross (MAGIC) assists for increasing allelic diversity (Arones *et al*., 2020). These kinds of allelic frequencies and combinations will differ from the natural population and allows only limited view of functional diversity (Korte and Farlow 2013).

Genome wide association studies based on linkage disequilibrium mapping overcome the limitation of classical QTL analysis (Pace *et al*., 2015; Liu *et al*., 2017). Linkage disequilibrium (LD) mapping using variable populations is a better substitute for classical linkage analysis studies. The ancestral polymorphism segregating through the variable panel reveals the correct trait-marker association compared with the polymorphism of the parental lines of the linkage mapping population (de Souza *et al*., 2018). LD mapping relies on the natural patterns of LD in the population investigated (Sauvage *et al.*, 2014). The GWAS unravels the association between genotyped marker and a phenotype of interest across a many individuals. GWAS enables the high-resolution detection of causal candidate genes responsible for phenotypic variation compared to classical QTL analysis (Jin *et al*., 2016; Devate *et al*., 2022). It utilizes polymorphisms broadly and densely distributed throughout the genome including simple sequence repeats and single nucleotide polymorphism (Ogura and Busch 2015). In the present study we performed genome wide association mapping for fruit quality traits (fruit firmness, shelf life, ascorbic acid, lycopene content, total soluble solids and locule number in 260 germplasm using simple sequence repeats .

MATERIALS AND METHODS

Phenotyping. The 264 tomato association mapping panel constituted modern cultivars, exotic collections and advanced breeding lines. The key component of germplasm management prior to utilization in advanced breeding research is harnessing the genetic variability for major traits. The phenotyping and biochemical test methods are explained trait wise in our previous study (Kadam *et al.*, 2022).

Genotyping. DNA was extracted from all genotypes. Leaves of three to four week old seedlings were taken from glasshouse and frozen in liquid nitrogen. The leaf samples were stored at –20°C until further use. Genomic DNA was prepared following the method of Krishna and Jawali (1997), with a few minor modifications. Pure preparations of DNA have 260 nm/ 280 nm OD ratio between 1.7 and 1.8 (Sambrook and Russel, 2001). The stock DNA solutions were diluted to 5 ng/µl of 100 ng/µl working solution for PCR. The amplification reaction of 97 SSR primers was performed in a final volume of 10 µl.

Population structure. The population structure of the 264 accessions was evaluated with 97 SSR markers via STRUCTURE2.3.4 software (Pritchard *et al.*, 2000).

Association mapping. Associations between phenotypes and genotypes were determined using TASSEL. The input phenotype file was arranged which contains number of genotypes, traits and matrix. Intercept joining of each fruit quality trait and input genotype file was done and the associations between phenotype and genotype were analyzed using generalized linear model with significant P value.

RESULTS AND DISCUSSION

Phenotypic variability. The germplasm adapted to natural environments holds a large reservoir of diversity for economically important traits. The foundation of new breeding programs is highly dependent on understanding the plasticity of phenotypes across the location and over the years. Therefore exploration of germplasm to rediscover the hidden traits is fundamental of complex traits improvement (Pham and McConnaughay 2014). Here we previously assessed the variability of fruit firmness, shelf life, ascorbic acid, lycopene content, total soluble solids and locule number and all key findings are published (Kadam *et al.*, 2022). For support the distribution of fruit quality traits throughout the mini core collection is presented in Fig. 1.

Population structure. More than 100 SSR markers were used to analyze the genetic matrix among accessions. 97 markers were found to be informative among all the accessions. The population stratification and significant associations can be achieved by using high polymorphic markers with minor allele frequency (MAF) greater than 5%. The genotyping assay was done on agarose gel electrophoresis using 3% agarose gel. The accuracy of marker trait associations depends on true allele size. In order to minimize false positives, we scored the gels using Syngene gene tool software. This software has automatic lane and peak detection feature. It calculates the allele molecular weight using standard DNA ladder.

The structure analysis was conducted for 260 accessions and 4 commercial checks using 246 alleles amplified from 71 SSR markers. Although 97 markers were informative, we selected 71 SSRs with minor allele frequency 5% for association study to minimize the false positives. According to the Evano method in STRUCTURE v2.3.4. software, the capital K value of the population is estimated to be K=4 (Fig. 2). The entire accessions were split into four main populations. The first group was composed of cluster of 56, the second group was composed of a cluster of 70 accessions followed by 103 accessions in third group and fourth group was composed of 35 accessions. The population structure of accessions is presented in Fig. 3. Understanding the diversity of natural population is of utmost importance for development of cultivars with

trait of interest. Molecular markers distributed across the genome help to unravel the germplasm diversity. The structured population allows researcher to minimize the false positive marker trait associations. The population structure analysis can estimate the genetic relatedness among accessions, sub-populations number and degree of admixture in germplasm. Earlier in the study of Pidigam *et al.* (2021) out of 130 SSR markers, 84 polymorphic markers were used in the analysis of genetic diversity of 48 tomato accessions. The structure clustering grouped the germplasm accessions into 2 sub-populations (k=2) with different levels of admixture. However, K=4 value accounted for genetic diversity study of 55 genotypes which contained different species of *S. pimpinellifolium*, *S. l. cerasiforme*, *S. lycopersicum* and *S. peruvianum.* The group pattern of accessions did not follow the geographical area of origin. The diverse genetic base possibly due to process of introgression of alleles from wild species to cultivated ones and degree of the allele flow among each other species (Vargas *et al.,* 2020).

Genome wide association analysis. The innovation in genomics has paved the pathway for the dissection of the genetic basis of complex traits. It has lead to the implementation of wide genome mapping principle in multiple crop species where genome sequence is available. GWAS as a powerful approach identifies causal genetic variants for a target phenotype in natural population (Tripodi *et al.,* 2021). GWAS has greater advantage over bi-parental map due to high recombination events which gives better mapping resolution (Linge *at al.,* 2021). Here we conducted GWAS to identity significant preliminarily associations between fruit quality traits and SSR markers.

Associations between SSR alleles and fruit quality traits were obtained on the basis of a genome-wide association analysis (GWAS) approach using the generalized linear model (GLM) and the population structure matrix Q = 4. The generalized linear model (GLM) utilizes principal components as covariates in the GWAS model. A total of 133 SSR alleles (P<0.05) for fruit quality traits were identified (Table 1). There are a total of 19 alleles (P<0.05) for the fruit firmness trait of which top three significant associations (P<0.005) accounting for 9% phenotypic variation. The substantial association numbers were detected for Shelf life with 30 SSR alleles possessing 15% phenotypic variation for most significant associations (P<0.005). For Ascorbic acid, a total of 12 alleles found to be associated but the level of significance was (P<0.05) accounted for 22% phenotypic variation. The optimum association for lycopene content and total soluble solids are 18 and 19 with 6% lycopene phenotypic variation for top 2 significant associations with p value <0.005 and 32% phenotypic variation correspondingly for total soluble solids where no substantial associations were found with p value <0.005. The locule numbers revealed 35 associations among which 14 alleles had significant value (P<0.005) with 50 % phenotypic variation.

The strategy of a genome-wide association (GWA) study has revolutionized the genetic mapping of plants (Nordborg and Weigel 2008). Here genotyping of enough markers throughout the genome is critical to tackle actual true causal variants linked with phenotype. In actual, the marker density required to get most significant associations is defined by genome size of crop. Here we used SSRs to tackle the marker trait associations, but tomato being most omics decoded crop, utilization of high density SNP markers will provide stringent associations with large phenotypic variability (Myles *et al.,* 2009). However, in era of SNP chips, we used the SSR markers to identify associations. Overall resolution of this work is still relatively low comparative to SNP based associations. In present study for ascorbic acid, most significant association was found on chromosome number 5, in addition among all associations for TSS second top significant marker was present on chromosome 7. These findings are in support with Zhang *et al.* (2015). Here most significantly associated marker for ascorbic acid was on chromosome 5 with 8.51 % of the total phenotypic variation. Further the TSS associated markers were mapped on chromosome 2, 6 and 7 with 14.22 % of the total phenotypic variation. A genetic map using RILs is generated to map the QTLs for fruit quality traits. Three QTLs for lycopene content were mapped on chromosome 2, 4, and 6. Our findings had fourth and fifth significant SSRs present on chromosome 6 and 2, indicates consistency with previous study. Whereas seven QTL for TSS were located on chromosomes 1, 2, 3, 5, 7, and 12 (Capel *et al.,* 2015). Our association study for locule numbers revealed that the most significant marker is present on chromosome number 11 as presented in table 28. This association was consistent with an earlier study by Tripodi *et al.* (2021) where SNP based mapping was conducted using 244 tomato accessions to trace the locus controlling the variation of agronomic, fruit quality, and root architecture traits. Further Shirasawa *et al.* (2013); Mata-Nicolas *et al.* (2020) identified SNPs that were significantly associated with locule numbers which also presented on chromosome 11. Further, the effectiveness of Genome-wide association study was explored for identifying the favorable alleles for fruit quality traits using 162 diverse tomato accessions. The traits targeted were fruit weight, fruit width, fruit height, fruit shape index, pericarp thickness, locule number, fruit firmness, and brix. The fruit firmness SNP was localized on chromosome 2,4 and 8 with contributing significant phenotypic variation over the three years (Kim *et al.,* 2021). In our study, the firmness trait association with higher significance reported on same chromosome. These findings support our research stringency, although we used SSR markers.

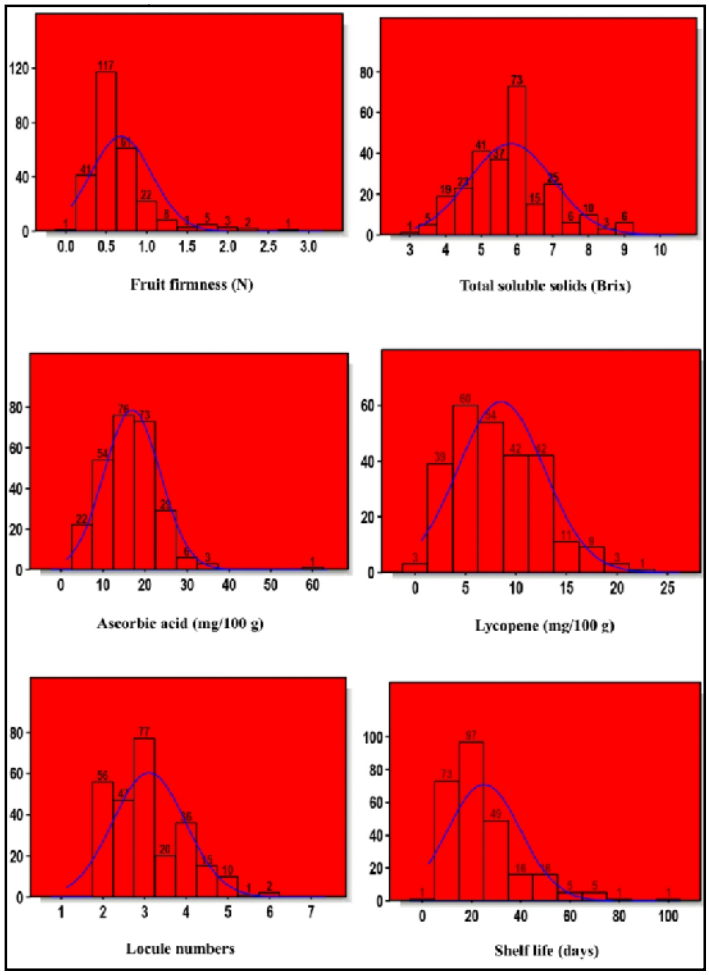

Fig. 1. Distribution of fruit quality traits throughout the mini core collections.

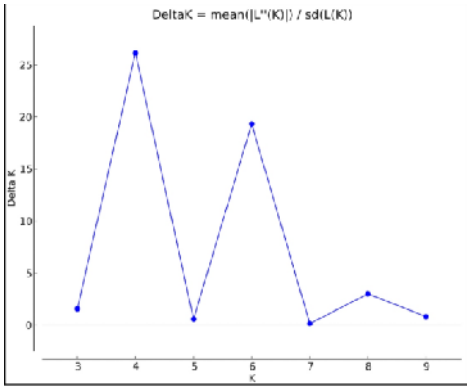

Fig. 2. Optimal K of the population structure of tomato germplasm based on SSR markers.

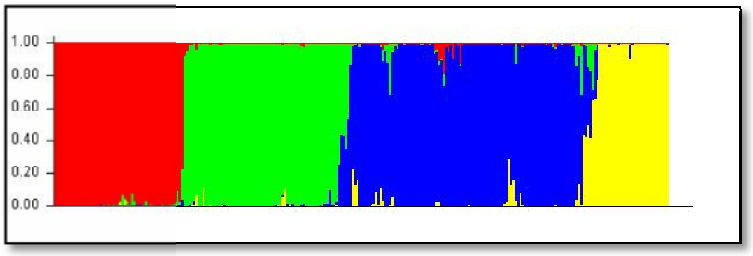

Fig. 3. Population structure of tomato accession.

Table 1: Significant associations for fruit quality traits estimated with GLM.

Trait	Locus	Chromosome	P-value	R^2
Firmness	BF_Chr_02_378_5	2	0.003	0.032
	SSR_13826	7	0.004	0.03
	BF_Chr_08_556_3	8	0.007	0.028
	BF_Chr_06_561_2	6	0.01	0.025
	BF_Chr_08_296_3	8	0.01	0.025
	LEat18_2	3	0.012	0.024
	BF_Chr_06_561_1	6	0.027	0.018
	BF_Chr_12_685_1	12	0.029	0.018
	BF_Chr_12_685_2	12	0.029	0.018
	SSR_13826_4	7	0.029	0.018
	BF_Chr_02_1972_4	2	0.031	0.018
	BF_Chr_08_556_1	8	0.032	0.017
	T0302_3	11	0.032	0.017
	BF_Chr_10_2788_3	10	0.037	0.016
	TGS0244_2	12	0.037	0.016
	SSR_14881_5	10	0.04	0.016
	LEaat1_2	9	0.046	0.015
	P6_25_3	6	0.053	0.014
	TGS0209_1	1	0.059	0.013
Shelf life	TGS0209_1	1	1.91E-04	0.050
	BF_Chr_12_685_1	12	0.001	0.038
	BF_Chr_12_685_2	12	0.001	0.038
	BF_Chr_04_2958_4	4	0.004	0.03
	BF_Chr_04_5597_1	4	0.006	0.028
	BF_Chr_04_5597_2	4	0.006	0.028
	TGS0209_4	1	0.009	0.025
	SSR_12362_5	6	0.009	0.025
	BF_Chr_03_3095_2	3	0.01	0.024
	SSR_13826_3	7	0.011	0.024
	BF_Chr_11_648_3	11	0.016	0.021
	BF_Chr_06_561_2	6	0.018	0.02
	T0302_4	11	0.019	0.02
	BF_Chr_04_4346_3	4	0.059	0.013
	TGS0209_2	1	0.059	0.013
	TES0344_2	11	0.02	0.02
	BF_Chr_08_2155_2	8	0.028	0.018
	LEaat1_3	9	0.028	0.018
	BF_Chr_05_1575_3	5	0.031	0.017
	TGS0318_3	12	0.032	0.017
	BF_Chr_08_556_3	8	0.036	0.016
Shelf life	TGS0244_2	12	0.046	0.015
	BF_Chr_11_1139_5	11	0.047	0.015
	SSR_13826_4	7	0.049	0.014
	LEaat7_2	5	0.053	0.014
	SSR_14881_5	10	0.054	0.014
	BF_Chr_10_3389_1	10	0.055	0.014
	BF_Chr_10_3389_2	10	0.055	0.014
	BF_Chr_04_4346_6	4	0.055	0.014
	CD2_2	12	0.057	0.013
Ascorbic Acid	BF_Chr_05_1101_2	5	0.002	0.034
	BF_Chr_11_648_4	11	0.017	0.021
	TG178_6	6	0.02	0.02
	BF_Chr_02_1972_6	2	0.022	0.019
	SSR241_2	7	0.024	0.019
	SSR45_3	7	0.028	0.018
	CD2_2	12	0.036	0.016
	BF_Chr_05_1101_1	5	0.038	0.016
	BF_Chr_02_378_7	2	0.043	0.015
	T0302_2	11	0.049	0.014
	BF_Chr_05_1575_3	5	0.052	0.014
	BF_Chr_02_1972_2	2	0.058	0.013
Lycopene	BF_Chr_12_616_2	12	0.002	0.037
	TES0344_3	11	0.007	0.027
	BF_Chr_11_648_3	11	0.014	0.023
	TG178_1	6	0.032	0.017
	BF_Chr_02_378_1	2	0.033	0.017

	SSR_4562	3	0.034	0.017
	BF_Chr_08_556_3	8	0.036	0.017
	BF_Chr_11_219_3	11	0.037	0.017
	BF_Chr_08_556_2	8	0.043	0.016
	BF_Chr_12_616_1	12	0.043	0.016
	BF_Chr_08_5299_3	8	0.044	0.015
	TGS0289_1	1	0.045	0.015
	TGS0289_2	1	0.045	0.015
	BF_Chr_11_1139_7	11	0.047	0.015
	BF_Chr_05_290_1	5	0.055	0.014
	BF_Chr_05_290_2	5	0.055	0.014
	BF_Chr_11_1139_3	11	0.056	0.014
	PM3F/R_5	6	0.057	0.014
Locule Numbers	BF_Chr_11_1139_4	11	1.59E-04	0.05186
	BF_CHO3_4	7	9.16E-04	0.04022
	BF_Chr_05_1101_4	5	9.23E-04	0.04017
	LEaat1_3	9	0.001	0.04
	BF_Chr_02_1972_5	2	0.001	0.037
	TGS0244_1	12	0.001	0.037
	BF_Chr_12_616_2	12	0.002	0.036
	TGS0244_2	12	0.002	0.036
	BW4_3	10	0.002	0.036
	BF_Chr_01_431_1	1	0.003	0.032
	BF_Chr_01_431_2	1	0.003	0.032
	BF_Chr_12_542_1	12	0.005	0.029
	BF_Chr_05_1575_4	5	0.005	0.029
	BF_Chr_12_616_1	12	0.005	0.029
	BF_Chr_10_2788_4	10	0.006	0.027
	BF_Chr_08_556_1	8	0.009	0.025
	BF_Chr_08_556_2	8	0.01	0.024
	BF_Chr_10_3817_3	10	0.011	0.024
	CD2_2	12	0.011	0.024
	BF_Chr_04_2960_1	4	0.012	0.023
	PM3F/R_5	6	0.016	0.022
	BF_Chr_10_2788_6	10	0.019	0.02
	BF_Chr_08_2155_3	8	0.021	0.02
	LEat18_5	3	0.023	0.019
	BF_Chr_12_542_3	12	0.023	0.019
	BF_Chr_02_4592_1	2	0.024	0.019
	BF_Chr_02_4592_2	2	0.024	0.019
	BF_Chr_03_1330_2	3	0.029	0.018
	BF_Chr_05_1101_5	5	0.029	0.018
	BW4_1	10	0.037	0.016
	CD2_1	12	0.042	0.015
	LEaat1_2	9	0.048	0.015
	BF_Chr_10_2788_3	10	0.05	0.014
	BF_Chr_02_378_4	2	0.051	0.014
	BF_Chr_03_1330_1	3	0.055	0.014
TSS	LEat18_6	3	0.009	0.026
	SSR45_3	7	0.012	0.024
	BF_Chr_04_2958_1	4	0.013	0.023
	BW4_1	10	0.017	0.021
	SSR_12362_1	6	0.019	0.021
	BF_Chr_08_296_3	8	0.022	0.02
	SSR_12362_7	6	0.027	0.018
	BF_Chr_08_5349_1	8	0.03	0.018
	BF_Chr_03_4812_1	3	0.034	0.017
	BF_Chr_03_4812_2	3	0.034	0.017
	BF_Chr_08_5349_2	8	0.037	0.016
	BF_Chr_08_2155_1	8	0.039	0.016
	LEaat1_3	9	0.044	0.015
	BF_Chr_09_5023_1	9	0.046	0.015
	BF_Chr_09_5023_2	9	0.046	0.015
	BF_Chr_05_1575_5	5	0.048	0.015
	LEat18_5	3	0.048	0.015
	SSR241_1	7	0.052	0.014
	BF_Chr_02_378_7	2	0.057	0.014

CONCLUSION

A study on Genome Wide Association Study for fruit quality traits in Tomato (*Solanum lycopersicum* L.)" was undertaken to investigate variation in tomato association mapping panel. 264 genotypes were analyzed during kharif and rabi season for fruit quality traits *viz;* fruit firmness, shelf life, total soluble solids, lycopene content, ascorbic acid and locule numbers. The present findings established of superior structured population which was useful for identifying significant marker trait associations. The results explain the profound variability for fruit quality traits in germplasm. The significant associations will pave the path for hybrid breeding for fruit quality improvement using the marker assisted selection thereby accelerating the breeding program.

FUTURE SCOPE

The genetic architecture of germplasm will help generate heterogeneous groups, thereby assisting in breeding program design for the specific segment breeding. The identified markers associated with fruit quality traits could serve as source of trait introgression in elite lines through marker assisted backcross breeding. The line development program for target fruit quality traits could be accelerated using the marker assisted selection.

Conflict of Interest: None.

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