

## Marker and *CKX2* gene expression-based selection of high yielding tomato (*Lycopersicon esculentum* Mill.) germplasms

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Tomatoes are an important agricultural crop grown for food, industrial, and pharmaceutical needs. Identification of high-yielding tomato germplasms is crucial to achieving the goal of doubling farmer's income. Our study aimed to select the germplasm with a smaller number of fruits and high weight so that, in a single harvest, maximum yield could be achieved. In the present study, tomato germplasms were evaluated based on agro-morphological traits, molecular markers and Cytokinin Oxidase/Dehydrogenase 2 (*CKX2*) gene expression. Inter simple sequence repeat markers (ISSRs) harbouring multiple allelic variations were used to study the genetic diversity. Among the markers used, UBC 820 exhibited the highest polymorphism, with eight alleles, an amplicon size range of 650–1800 bp and a polymorphic information content (PIC) value of 0.3001. Based on morphological observation and *CKX2* gene expression analysis by qRTPCR, the genotype KS-8105 was found to be the best performer. The mean number of fruits/plants was 79, while the mean weight of fruits/plants was 3.2 kg/plant in the tomato germplasm KS-8105. In future, introgression of desirable traits like weight of fruits/plants may be introgressed from KS-8105 to the elite cultivars with the help of molecular markers.

**Keywords:** Cytokinin Oxidase/Dehydrogenase 2, Genetic diversity, ISSR Marker, Tomato, Yield

Variability among living organisms, *i.e.*, genetic diversity, is a prerequisite for molecular breeding to enhance crop yields<sup>1</sup>. In today's context of climate change and environmental stress, the exploration and use of genetic resources through bioprospecting has become increasingly common. Among the various biodiversity hotspots around the world, India has four hotspots, *viz.*, the Himalayas, the Western Ghats, Indo-Burma and the Sunderbans<sup>2</sup>. These biodiversity-rich areas hold immense potential for mining of the genes and QTLs associated with the quality, yield and stress-tolerant traits. To eradicate malnutrition and hunger, the United Nations' 2nd Sustainable Development Goal (SDG-2) has set some goals to ensure world's food and nutritional security<sup>3</sup>. Tomato

(*Lycopersicon esculentum* Mill.) is an economically significant crop of the family solanaceae that has great potential in this regard. It is a major component of the human diet and a rich source of vitamins A and C as well as antioxidants<sup>4</sup>. With the diploid chromosome ( $2n=2X=24$ ) with a genome size of ~900 Mbp, wild germplasms of tomato are important reservoir for allele mining which can improve cultivated varieties and facilitate the development of resilient, nutrient-rich crops<sup>5</sup>. The broad range of agro-climatic conditions of India makes it an ideal for tomato cultivation with an annual production of 20.34 million metric tons from 812 million hectares during 2021-2022 (National Horticulture Board, 2021-2022). However, the rigorous selection and domestication processes that improved yield of tomatoes have also led to the loss of genetic diversity in cultivated tomatoes, including the loss of wild cultivars carrying agriculturally important genes/QTLs<sup>6</sup>. This presents a

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pressing challenge for plant breeders, which is how to improve the quality and yield of tomatoes, without compromising genetic diversity. One promising solution lies in linking the genes/QTLs with traits and diversity analysis by using molecular markers. Bio-prospecting in a sustainable way requires deep insights into genetic diversity that could be analysed by molecular markers that offer greater precision and efficiency<sup>7</sup>.

The Inter Simple Sequence Repeat (ISSR) markers are particularly advantageous over other molecular markers due to their PCR-based nature, reproducibility, cost-effectiveness, broad genomic coverage and conserved sequence information<sup>8</sup>. ISSR markers have been widely used for molecular mapping, diversity analysis, cultivar classification and evolutionary studies<sup>9</sup>. Cytokinin plays an important role in the fruit development. A study found that when the *CKX2* gene was overexpressed, it led to smaller fruits by limiting cell division during fruit development. High expression of *CKX2* leads to increased cytokinin degradation, which can result in smaller fruits by reducing the thickness of the pericarp<sup>10</sup>. Considering this, the current study has been carried out to analyse the genetic diversity of available tomato germplasm and the selection of the best-performing cultivar in terms of yield. In the present study our hypothesis was (1) Inter Simple Sequence Repeat (ISSR) markers can deeply exploit the allelic variability (2) The variability among individuals based on molecular markers can provide insights into the crossing ability among germplasms (3) Selection of best-performing germplasms in terms of fruit/plant and weight of fruit/plant in tomato based on *CKX2* gene can help identify the most promising candidates for breeding.

## Materials and methods

### Plant Material and growth condition

Thirty-four determinate tomato genotypes were selected for evaluation based on ten key morphological traits (Suppl. Table 1). The experiment was conducted in the open field of the Department of Vegetable Science, C.S. Azad University of Agriculture and Technology, Kanpur, India, during the Rabi season. The experimental field was prepared with a gentle slope to mitigate the water-logging situation, promote seed germination and encourage healthy seedling growth. The field layout followed a randomized block design (RBD). Traits like days to flowering, plant height (cm), number of branches per plant, number of fruit clusters per plant, fruit length

(cm), fruit width (cm), number of locules per fruit, number of fruits per plant, days to fruit maturity, and weight of fruit/per plant (kg) were all recorded in triplicates. Five subsamples were taken for each replication to prevent sampling bias. A heat map and correlation heat map matrix were generated using MeV software<sup>11</sup> based on the number of fruits per plant and the weight of fruit/per plant (kg) data mean value (Fig. 1A & B).

### DNA Extraction and genotyping by inter simple sequence repeat markers

Fresh, tender leaf samples were collected from all thirty-four tomato genotypes and immediately stored in liquid nitrogen. Genomic DNA was isolated using the CTAB method<sup>12</sup>. Nanodrop (Thermo Scientific, USA) and 0.8% agarose gel electrophoresis were used to analyse the quantity and quality of DNA, respectively. Further PCR reaction conditions were optimized for amplification using twenty-five inter-simple sequence repeats (ISSR) primers. Of these, eighteen primers successfully amplified DNA across all thirty-four tomato genotypes, (Suppl. Table 2). Thermo Cycler (Eppendorf) was used to carry out the PCR reactions with the program that included pre-denaturation (94°C for 5 min), denaturation (35 cycles, 94°C for 30 sec), annealing (55°C for 45 sec), primary extension (72°C for 45 sec), and final extension (72°C for 8 min). The amplified products were separated using a 2.5% agarose gel, and the size of the amplicon was determined using a 100 bp DNA ladder (Fig. 2A).

### Markers scoring and data analysis

The bands from the PCR gel were scored in order to record the genotypic information. The presence of a band was scored as '1' and its absence as '0'. Based on this binary data, alleles were classified as monomorphic, polymorphic, or null. Polymorphic information content (PIC) values were computed using the PIC calculator (<https://www.liverpool.ac.uk/kempsj/pic.html>) (Suppl. Table 2). UPGMA dendrogram and principal component analysis (PCA) were carried out using DARwin6 software<sup>13</sup> (Fig. 2B & C). Furthermore, the genetic structure of 34 tomato germplasms was inferred using the STRUCTURE software<sup>14</sup> (ver. 2.3.3) (Fig. 3).

### Identification of promising tomato germplasm by correlation of dendrogram based on morphological and DNA genotyping data

Based on the UPGMA dendrogram of thirty-four genotypes, along with principal component analysis,

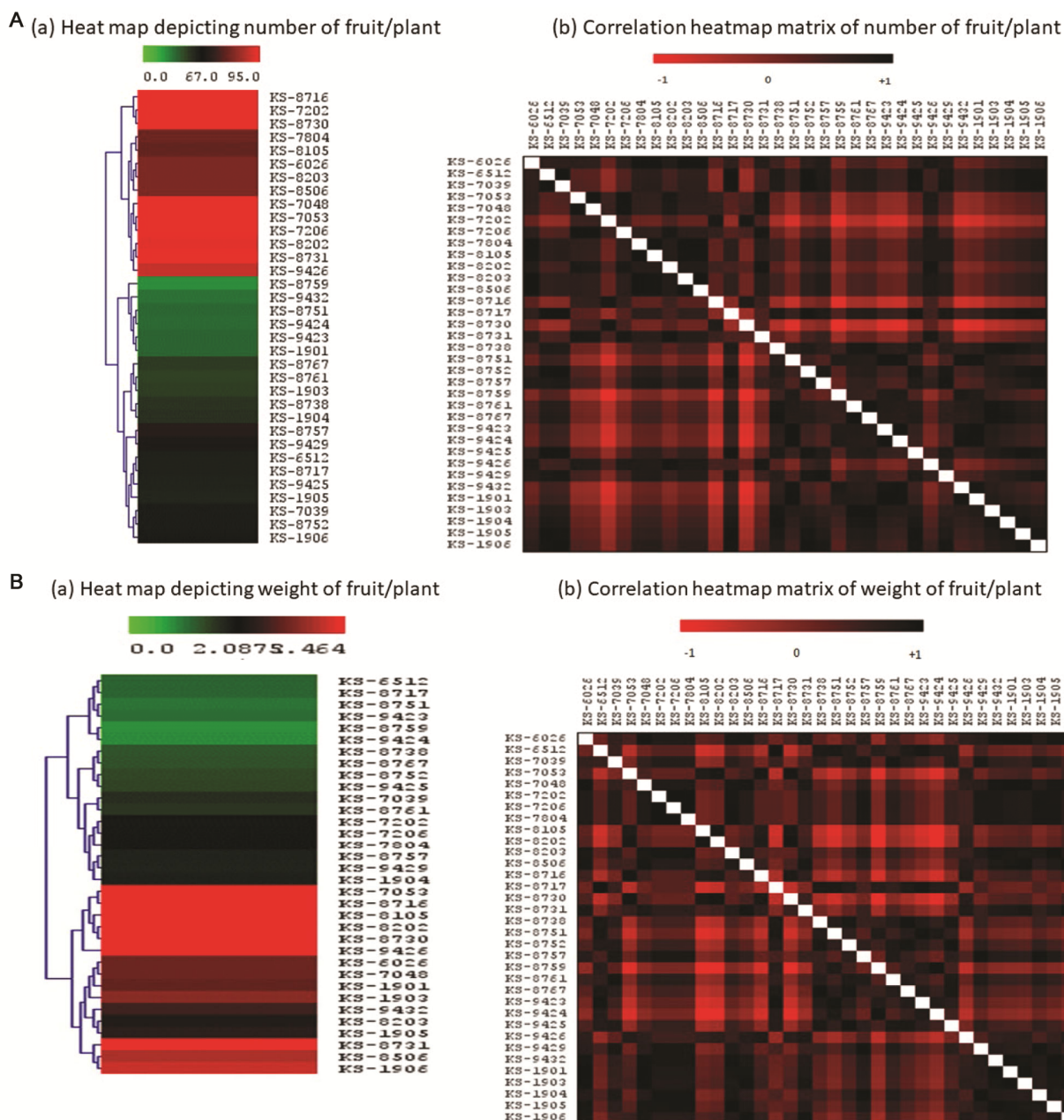


Fig. 1 — Heat map and correlation matrix illustrating the variation and interrelationships among 34 tomato germplasms based on the (A) number; and (B) weight of fruits per plant; a- heat map; b- correlation heatmap matrix

genetic structure and heat map (number of fruits/plant and weight of fruits/plant in kg), a total of eleven promising tomato germplasms were identified using genotype KS-9424 as the reference (Suppl. Table 3). Further differences in each selected trait were analysed using a paired *t*-test and one way ANOVA. Considering the key morphological traits viz. plant height (cm), number of branches per plant, days to flowering, number of fruit clusters per plant, fruit length (cm), fruit width (cm), number of locules

per fruit and days to fruit maturity the genotype KS-8105 was identified as the best one among all eleven genotypes and selected for further study.

#### RNA isolation and cDNA synthesis

Fresh fruit samples from selected 11 tomato genotypes were collected in triplicate at 0, 5, 10 and 20 days after anthesis and immediately stored in liquid nitrogen. Total RNA was extracted using the Trizol method and treated with RNase-free DNase to remove genomic DNA contamination. The quantity and

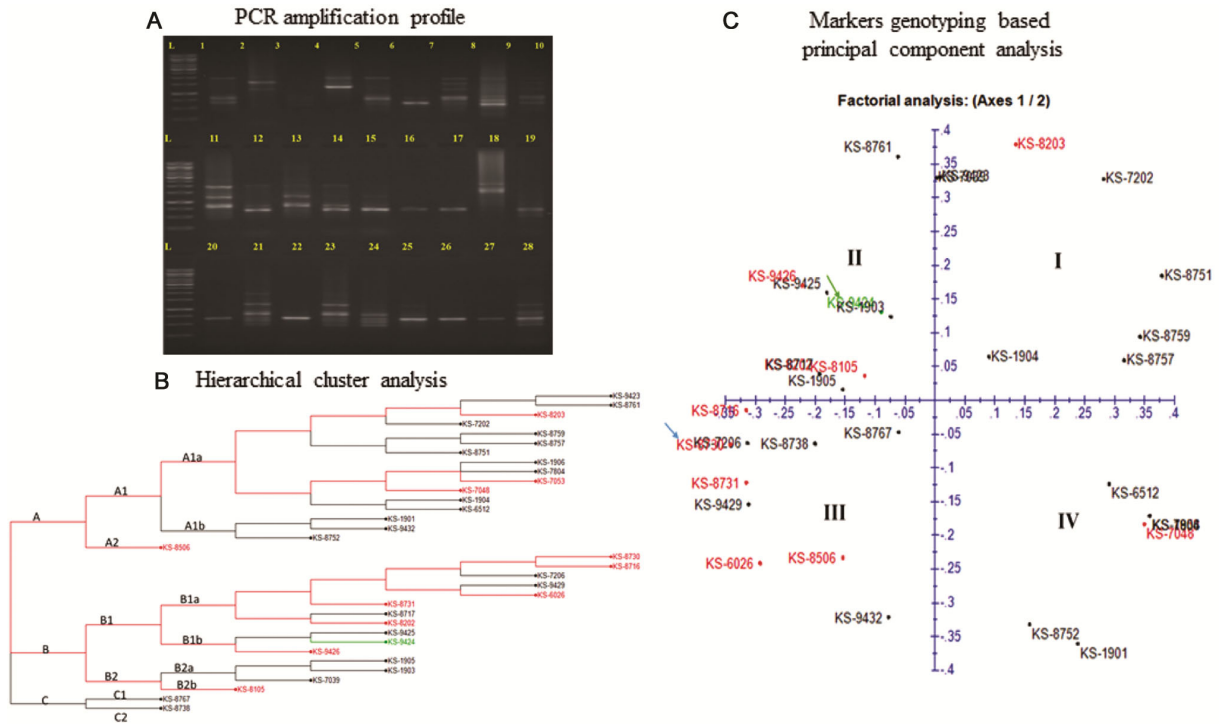


Fig. 2 — Genetic diversity analysis of 34 tomato germplasms using ISSR markers. (A) PCR amplification profile of tomato germplasms using UBC-825 Inter Simple Sequence Repeats (ISSRs) markers along with ladder; (B) UPGMA dendrogram depicting hierarchical clustering of genotypes; and (C) PCA biplot illustrating two-dimensional genetic dispersion based on ISSR polymorphism

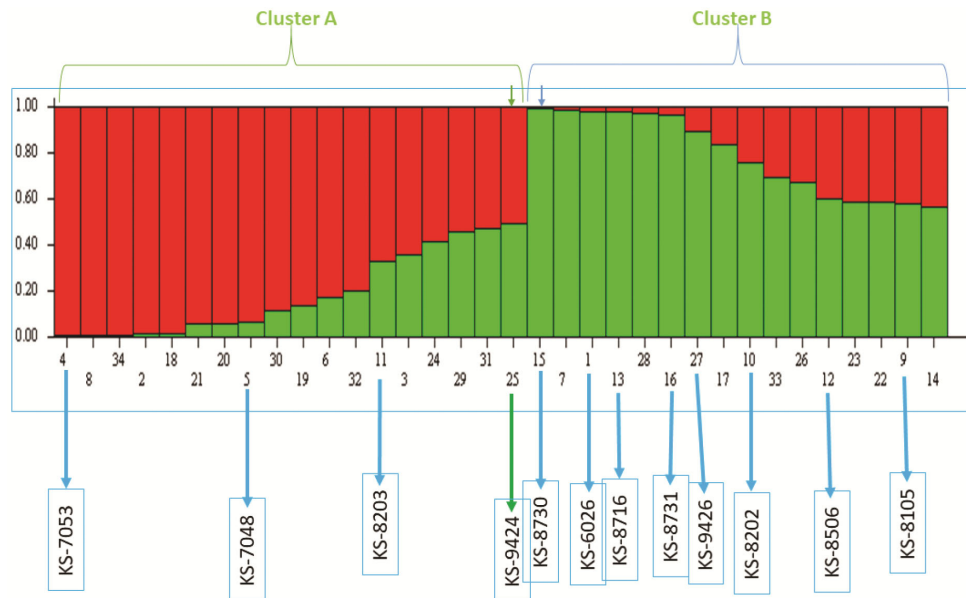


Fig. 3 — Bayesian model based genetic clustering of 34 tomato germplasms

quality of the isolated RNA were assessed by Nanodrop spectrophotometer (Thermo Scientific Nanodrop 2000) and 1.2% denaturing agarose gel electrophoresis, respectively. cDNA synthesis was done using the Thermo Scientific cDNA synthesis kit following manufacturer’s protocol.

**Gene expression analysis using tomato cytokinin oxidase/dehydrogenase-like 2 (*CKX2*) gene**

qRT-PCR primer for the *CKX2* gene was designed from tomato transcripts NM\_001257980.1 using IDT software (Suppl. Table 4). To set up the reaction, 2 µL of template, 0.5 µL primers, 10 µL SYBR green, and

DEPC water were taken with the reaction condition of denaturation at 94°C for 3 min, 35 cycles of 94°C for 30 s, 60 C for 30 s, and 72°C for 30 s. Relative gene expression levels of each sample were calculated using “the comparative Ct method”. Actin was taken as an internal control.

## Results

### Identification and selection of better performing tomato germplasm

#### *Based on morphological data*

In the present study, 34 tomato germplasms were screened for various morphological traits with special emphasis on the number of fruits and weight per plant (Suppl. Table 1). Based on the data from these two morphological traits, a heat map and a correlation heat map matrix were constructed, revealing eleven promising tomato germplasms viz. KS-8716, KS-8730, KS-8105, KS-6026, KS-8203, KS-8506, KS-7048, KS-7053, KS-8202, KS-8731 and KS-9426 (Suppl. Table 3). The number of fruit/plants ranged from 79-130 and the weight of fruit/plant was from 2.12-3.12 kg in selected eleven tomato germplasms (Fig. 1A-B). Based on the pictorial representation of the number of fruits/plant and weight of fruits/plant data collected from 34 tomato germplasms, KS-8105 emerged as the best performing genotype among all.

#### *Based on genotypic data*

Among 25 ISSR markers, the amplified 18 marker's data were analysed to understand the genotypic information of 34 tomato germplasm. The genotypic data were used to construct a UPGMA dendrogram, perform PCA and analyse the population structure. The amplified alleles were 3-9 with band sizes from 200-3000 bp. The PIC value ranged from 0.299 to 0.50 with an average of 0.392 (Suppl. Table 2). Based on genotypic data, the UPGMA dendrogram divided thirty-four germplasms into three main clusters: A, B and C. Among these clusters, the genotypes KS-8203, KS-7053, KS-7048, KS-8506, KS-8730, KS-8716, KS-6026, KS-8731, KS-8202, KS-9426 and KS-8105 were identified as maximum number of fruits/plant and weight of fruit/plant containing germplasms (Suppl. Table 3). The similarity in pattern was observed between the morphological data-based heat map and ISSR marker's genotyping based dendrogram, wherein, among eleven promising germplasms, seven were grouped in cluster B, whereas four were in cluster A. Cluster B was further classified into sub-clusters

B1a, B1b, B2a and B2b, wherein seven promising germplasms fall in B1a and B2b. In clusters A and C, most of the germplasms were of inferior type. The reference elite cultivar taken was KS-9424; hence, a few promising germplasms of the cluster A and B (Fig. 2B) can be used for trait introgression into the elite cultivar of tomato. Similarly, the results of Principal Component Analysis (PCA) are similar to genotyping-based UPGMA dendrogram, heat map and correlation heatmap matrix analyses. The selected better-performing eleven tomato germplasms were predominantly clustered in groups II and III, except a few inferior germplasms. In contrast, groups I and IV were mostly dominated by inferior germplasms, with the exceptions of KS-8203 and KS-7048 (Fig. 2C). Notably, the reference genotype KS-9424 was found in PCA group II and cluster B of the UPGMA dendrogram, along with the majority of the selected superior germplasms. With this finding, it is evident that there is less reproductive isolation distance between the reference genotype KS-9424 and the selected promising genotypes.

To further validate the findings, a Bayesian model-based genetic clustering of 34 tomato germplasms was performed. The analysis once again grouped all eleven promising germplasms into group B, while the majority of inferior germplasms into group A (Fig. 3). The consistency across multiple analyses, *i.e.*, genotyping-based UPGMA dendrogram, PCA, heat map and correlation heat map matrix, and Bayesian model-based genetic clustering confirms the robustness and reliability of the ISSR markers used in this study. Therefore, it is evident that the desirable traits could be introgressed from selected germplasms into elite cultivars through marker-assisted selection (MAS).

#### Identification of best tomato genotype containing other desirable traits

Based on the selected two traits, *i.e.*, number of fruits per plant and fruit weight per plant, these 11 germplasms showed highly significant differences ( $P \leq 0.0001$ ) compared to the elite cultivar KS-9424. Among these, the KS-8105 was found to be superior genotype, outperforming all others across several agronomic parameters. The histogram analysis and paired student t test also revealed that KS-8105 was significantly different from KS-9424 ( $*P \leq 0.05$ ;  $**P \leq 0.01$ ) in terms of weight of fruits per plant (kg), number of fruits per plants, plant height (cm), fruit length (cm), and days to maturity. While KS-8105 outperformed KS-9424 in most aspects, it

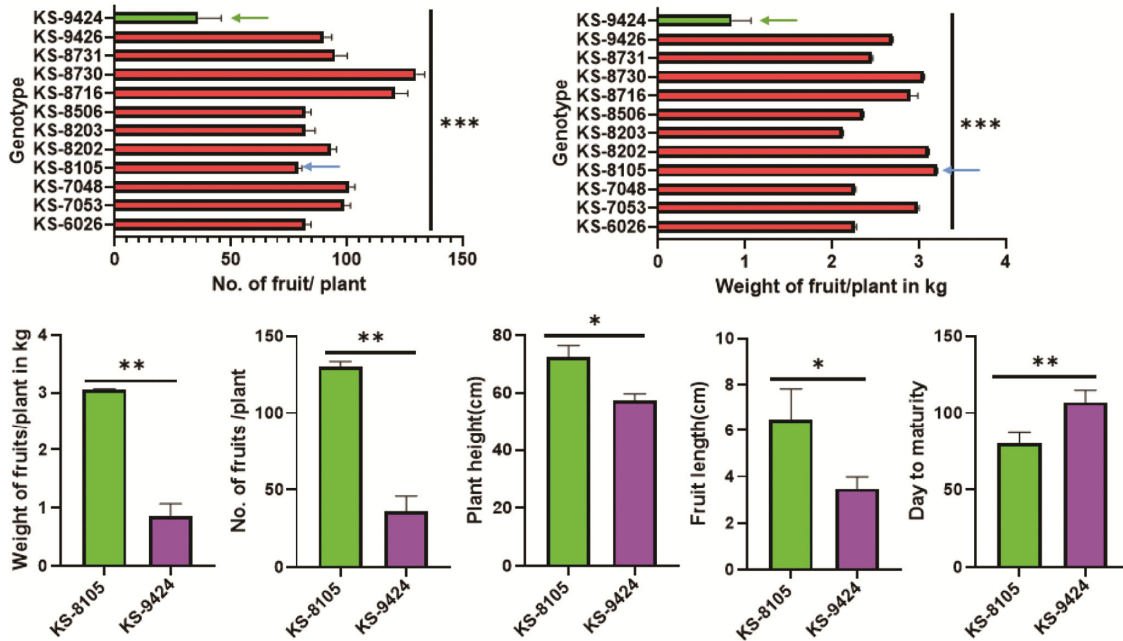


Fig. 4 — Statistical analysis of the selected genotypes for morphological traits (The double ( $P \leq 0.01$ ) and triple ( $P \leq 0.001$ ) asterisks represent the probability levels to reveal significant differences between genotypes)

lagged in only a few specific traits (Fig. 4). Due to its multi-allelic nature, cost-effectiveness, reliability, and no prior sequence information requirement, ISSR markers can be used to introgress the identified traits from KS-8105 to elite tomato cultivars. The genetic mapping, QTL mapping, gene mining and genomic-assisted breeding could be done using selected KS-8105 tomato germplasm.

**Gene expression analysis**

The expression pattern of the *CKX2* gene was analysed across eleven tomato genotypes at four developmental time points: Day 0, Day 5, Day 10, and Day 20 (Fig. 5). The results revealed noticeable variation in *CKX2* activity, reflecting differences in cytokinin regulation across genotypes. To validate the selection of genotypes based on morphological data, *CKX2* gene expression was measured in all 11-tomato germplasm. By Day 5, several genotypes particularly KS-7048, KS-8506 and KS-8203 showed a significant increase in *CKX2* expression. Among them, KS-7048 stood out with the highest fold change (2.12 FC), indicating a rapid and robust response, possibly playing a role in early cytokinin regulation. At Day 10, the expression levels remained relatively high in these genotypes, though a slight decline in intensity was observed compared to Day 5. This suggests a sustained response over time rather than a short-lived spike. By Day 20, expression level in most genotypes

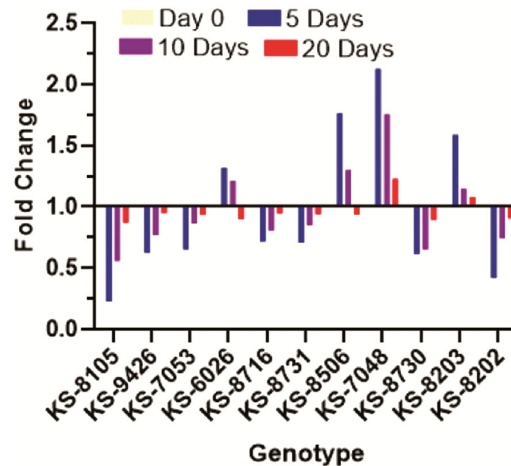


Fig. 5 — Gene expression analysis using qRTPCR with *CKX2* gene primer

had decreased, returning to baseline levels, as seen in KS-8105, KS-8202 and KS-9426, which consistently showed lower expression across all time points. Interestingly, KS-8105 showed a noticeable dip in expression as early as day 5, suggesting that it may naturally maintain a low baseline activity of *CKX2*.

Several tomato genotypes showed down-regulation in the expression of *CKX2* gene. Genotype KS-8105 showed consistently change in *CKX2* fold-change values at Day 5, 10 and 20 by 0.22, 0.55 and 0.87, respectively. This trend may suggest that these plants naturally maintain lower levels of this gene, which

could result in higher levels of cytokinins. The large fruit containing germplasms were KS-8105 and KS-8202 while the smallest fruit containing genotype was KS-7048 (Fig. 5). The *CKX2* gene plays an important role in controlling the levels of cytokinins. Elevated *CKX2* expression enhances cytokinin degradation, which can reduce pericarp thickness and lead to smaller fruit size. On the other hand, when *CKX2* expression is lower, less cytokinin is broken down allowing more of the hormone to stay active in the plant, supporting increased cell division and growth. This can result in larger fruits with thicker walls. Therefore, tomato genotypes with naturally lower *CKX2* expression may be better suited for producing bigger, more robust fruits.

### Discussion

To increase production and satisfy future food demands, the selection of high-yielding tomato germplasms is essential<sup>3</sup>. In this study, 34 different tomato germplasms were evaluated for key yield-related traits, including fruit weight and fruit number per plant. Based on heat map and correlation analysis, eleven germplasms were identified, with KS-8105 emerging as the best-performing genotype based on the observed traits. Some researchers have also emphasized the importance of fruit number and weight per plant as major selection criteria in tomato breeding<sup>15</sup>. The genotypic data derived from 18 ISSR markers were used to analyse the genetic diversity among the selected genotypes. The average PIC value (0.392) suggested the efficacy and reliability of the ISSR markers for genetic diversity analysis<sup>16-17</sup>. The UPGMA dendrogram grouped the germplasms into various clusters based on the genetic dissimilarity<sup>18</sup>. Similarly, the PCA biplot also divided these germplasms into different clusters with superior genotypes KS-8105, KS-8202, KS-9426 and KS-8730 falling into groups II and III suggesting better parental lines for breeding. STRUCTURE analysis, focused on the selected eleven germplasms revealed clear distinctness among their genetic makeup. The similarity in clustering pattern of tomato germplasms across UPGMA, PCA and STRUCTURE reinforces the reliability of ISSR markers as a tool for molecular breeding and crop improvement<sup>19</sup>. These findings open the door for targeted trait introgression into elite lines like KS-9424, potentially accelerating the development of improved, high-yielding tomato cultivars.

Expression profiling of *CKX2* gene in the selected eleven germplasms provided insights into its role in

cytokinin metabolism and fruit development. The analysis revealed distinct genotype-specific and time-dependent expression patterns. The *CKX2* gene plays an important role in controlling the levels of cytokinins. High expression of *CKX2* leads to increased cytokinin degradation, which can result in smaller fruits by reducing the thickness of the pericarp<sup>10</sup>. In contrast, lower *CKX2* expression allows for cytokinin accumulation, promoting cell proliferation and production of larger, thicker-walled fruits. Therefore, tomato genotypes with naturally lower *CKX2* expression levels may be adapted to yielding larger, more durable fruits. In our study, based on the *CKX2* down-regulating genotypes, few promising tomato germplasms such as KS-8105 and KS-8202 were identified with the larger fruit size. This observation aligns with findings from other species, particularly *Oryza sativa* and *rabidopsis thaliana*, where reduced CKX expression related with increased cytokinin activity and improved yield attributes<sup>20-21</sup>. Conversely, genotypes like KS-7048, KS-8506 and KS-8203 showed a noticeable up-regulation in *CKX2* expression at day 5, indicating increased cytokinin degradation during the early stages of fruit development. These results complement previous research showing that *CKX2* plays a crucial role in controlling fruit size by degrading active cytokinins, that in turn slows cell division and developmental processes<sup>22-23</sup>. When the gene expression data were correlated with morphological traits like fruit number and fruit weight per plant, the germplasms could be clearly categorized into large, medium, and small-fruited groups. This comprehensive approach of connecting gene expression data with field traits highlights the potential of molecular markers like *CKX2* as valuable tools in tomato breeding programs aimed at improving fruit yield and quality<sup>24</sup>.

### Conclusion

With the study carried out on tomato germplasm based on morphological traits, *CKX2* gene expression and ISSR marker data analysis, we identified KS-8105 as a superior tomato germplasm characterized by fewer but larger fruits and overall higher yield. The finding suggests the importance of integrating morphological traits evaluation with molecular tools for effective selection of high-performing genotypes in tomato breeding programs.

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### Conflict of interest

All authors declare no conflict of interest.

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