

WHITE PAPER

Advancements in Tomato Genetics: An Introduction to Molbreeding's GBTS Panel Series

Summary

This white paper presents an overview of the design and purpose of MolBreeding's Tomato Panel Series, which aims to enhance tomato breeding through advanced molecular tools. It discusses the selection of diverse samples, single nucleotide polymorphisms (SNPs), and trait-associated markers. The panels are specifically developed to assist tomato breeders and researchers in deepening their genetic insights, expediting variety development, and reinforcing molecular breeding practices. By leveraging these robust SNP panels, the project seeks to facilitate the creation of superior tomato varieties, addressing contemporary challenges in crop improvement effectively.

Introduction

Tomato (*Solanum lycopersicum*) is one of the world's most valuable horticultural crops, providing essential nutrients and supporting major agricultural economies. Modern tomato breeding faces increasing demands for higher yield, improved fruit quality, and robust resistance to diseases and environmental stress. To meet these challenges, breeders are turning to advanced molecular tools to improve precision and efficiency.

Given the diversity of the wild and cultivated tomato germplasms, and resources published in the academic domain, we have developed three densities of tomato SNP panels for genotyping to meet industrial breeding needs. These panels provide comprehensive genomic coverage for diversity analysis, trait mapping, hybrid purity testing, and marker-assisted selection, enabling researchers and breeders to accelerate the development of superior tomato varieties.

SNP/Marker Discovery and Selection

To capture genome-wide variation across diverse tomato germplasm, we selected single nucleotide polymorphisms (SNPs) from several public resources to represent the major diversity within this crop. These datasets provide a foundation for the selection of the sets that form our tomato panel series:

1. **Tomato Infinium SNP Chip Assay:** This dataset includes **8,740** SNPs derived from transcriptome comparisons of four cultivated tomatoes, one cherry tomato, and one wild tomato (Hamilton et al., 2012; Sim et al., 2012).
2. **Golden Gate SNP Dataset:** A total of **1,337** SNPs are obtained by comparing the transcriptome sequences of Micro-Tom and 19 tomato varieties. These SNPs were subsequently used to genotype 30 modern tomato varieties, two cherry tomato varieties, and eight wild varieties, resulting in the selection of **680** specific SNPs (Hirakawa et al., 2013).
3. **1K_GWAS Panel:** This panel features **1,248** highly polymorphic SNPs identified through resequencing six tomato lines (Shirasawa et al., 2013).

4. **Resequencing-Derived SNPs:** We incorporated **1,552** SNPs from whole-genome resequencing data of 247 samples, comprising 210 cultivated and 37 wild varieties (NCBI SRP150040).
5. **Collaborative Contributions:** **1,710** SNPs and **18** InDel sites and **42694** background marker sites are provided directly by the collaborating Beijing Academy of Agricultural and Forestry Sciences.
6. **SNP Fingerprinting:** A total of **40** SNPs selected from 96 cultivated and wild varieties were utilized to develop variety identification markers (Lin et al., 2014; Zhang et al., 2024).



SNP Filtration

The high-confidence SNPs compiled from public datasets are further validated and filtered through the following steps:

- 1) **Probe Design and Filtering**
 - Probes are designed for all target capture SNPs using the Heinz 1706 reference genome. Each SNP is represented by 2–3 probes to ensure capture efficiency.
 - Design criteria included low sequence homology (<3 for background loci and <5 for trait-specific loci) and a GC content between 30% and 70%.
 - All probes are combined into a preliminary panel.
- 2) **Data Quality and Capture Efficiency Screening**
 - **Genotyping by Target Sequencing (GBTS)** analysis is performed on 136 tomato samples using the preliminary panel.

- Quality control metrics are applied to SNPs as follows:
 - Missing rate < 10%;
 - Uniformity > 25%;
 - On-target rate > 50% at 40× coverage;
 - MAF > 0.05.
 - Highly polymorphic SNPs with an even genomic distribution (≤0.3 Mb gap between adjacent sites) are retained.

3) Further Validation

- The selected SNPs are used to genotype 199 tomato varieties provided by a breeding company.
- Sites showing low detection rates or excessive missing data are removed.
- The final dataset achieved an average SNP detection rate of 99.34%, uniformity of 98.03%, and capture efficiency of 74.84%.

4) Panel Optimization

- Additional high-MAF SNPs that are previously discarded are re-evaluated and reintroduced (<1% of total markers) to enhance genome coverage.

Trait-Associated Marker Identification

This chapter delves into the intricacies of trait-associated marker identification, focusing on the robust process of SNP discovery, selection, and filtration based on the genetic diversity observed in various tomato varieties. Additionally, we have curated a comprehensive collection of publications detailing the identification of genes and quantitative trait loci (QTLs) associated with key traits such as agronomic performance, abiotic stress tolerance, fruit quality (Table 1, Figure1), and biotic resistance (Table 2, Figure 2).

In the following sections, we will present a summary table that outlines public research findings and the genome distribution of these important traits.

Agronomic & Quality Traits

Agronomic traits determine the overall productivity and cultivation efficiency of tomato, encompassing growth habit, plant architecture, flowering and fruit set, yield stability, and

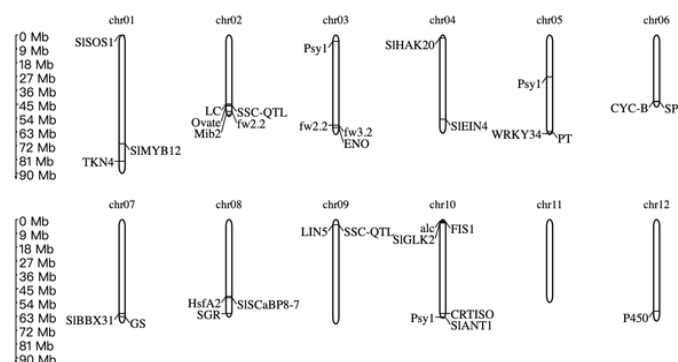


Figure 1. Distribution of functional gene/QTL regions related to on each chromosome

maturity period. Genes regulating these traits modulate the Agronomic traits determine the overall productivity and cultivation efficiency of tomato, encompassing growth habit, plant architecture, flowering and fruit set, yield stability, and maturity period. Genes regulating these traits modulate the balance between vegetative and reproductive growth, directly influencing management practices and adaptability to different production systems.

The **growth habit**, controlled by *SP* (self-pruning), defines determinate versus indeterminate growth, which is critical for field versus greenhouse cultivation (M.-S. Kang et al., 2022). Plant architecture and productivity are further influenced by genes regulating shoot branching. Notably, a wild tomato cytochrome P450 gene enhances lateral fruit-bearing branches,

Trait	Gene	Citation
Sugar content	<i>LIN5</i>	Tieman et al., 2017; Zanor et al., 2009
	<i>SSC-QTL</i>	Ranc et al., 2012
Effective branches number	<i>P450</i>	N. Li et al., 2023
Fruit firmness	<i>FIS1</i>	R. Li et al., 2020
	<i>SIEIN4</i>	Zhang et al., 2024
Fruit flavor	<i>ENO</i>	Yuste-Lisbona et al., 2020
Fruit shape	<i>Ovate</i>	Rodríguez et al., 2011
Fruit shelf-life	<i>alc</i>	Casals et al., 2012
Fruit size	<i>fw2.2, fw3.2</i>	Beauchet et al., 2021
Fruit stripe	<i>GS</i>	G. Liu et al., 2020
Fruit tip morphology	<i>PT</i>	Song et al., 2022
Green shoulder	<i>SIGLK2</i>	Nadakuduti et al., 2014
	<i>TKN4</i>	
Growth habit	<i>SP</i>	M.-S. Kang et al., 2022
Heat stress tolerance	<i>HsfA2</i>	Hu et al., 2020
	<i>Mib2</i>	S. Sun et al., 2024
Locule number	<i>LC</i>	Rodríguez et al., 2011
Pigment content	<i>CRTISO</i>	Isaacson et al., 2002
	<i>CYC-B</i>	Manoharan et al., 2017
	<i>Psy1</i>	S.-I. Kang et al., 2017
	<i>SGR</i>	Manoharan et al., 2017
	<i>SIANT1</i>	Yan et al., 2020
	<i>SIMYB12</i>	S.-I. Kang et al., 2017
Saline-alkaline tolerance	<i>SISCaBP8-7</i>	Liu et al., 2024
Salt tolerance	<i>SIHAK20</i>	Z. Wang, Hong, Zhu, et al., 2020
	<i>SISOS1</i>	Z. Wang, Hong, Li, et al., 2020
Cold tolerance	<i>SIBBX31</i>	Zhu et al., 2023
	<i>WRKY34</i>	Guo et al., 2024

Table 1. Key agronomic and quality traits in modern tomato breeding.

a trait largely lost during domestication (N. Li et al., 2023).

Fruit quality and **nutritional traits** underpin consumer preference, marketability, and processing performance. *SUN* and *OVATE* control elongated **fruit shape** whereas *FASCIATED* (*FAS*) and *LOCULE NUMVER* (*LC*) control fruit locule number and flat shape (Rodríguez et al., 2011; Sim et al., 2012). Additionally, the *POINTED TIP* (*PT*) gene encodes a C2H2-type zinc finger transcription factor that regulates fruit tip development (Song et al., 2022).



For **fruit size**, *ENO* modulates *WUSCHEL* expression, with a domestication-selected promoter mutation enhancing enlargement (Yuste-Lisbona et al., 2020), whereas *FW2.2*, a major QTL, negatively regulates cell division via plasma membrane-localized CNR/PLAC8 proteins that may influence organ growth through signaling and cell-to-cell communication (Beauchet et al., 2021).

Fruit firmness and **shelf life**—critical for transport and storage—are governed by *FIS1* and *alc*, which strengthen structural integrity and delay ripening through ethylene pathway modulation (Casals et al., 2012; R. Li et al., 2020). The ethylene receptor *SIEIN4* also contributes, with a SNP (A→G) distinguishing softer (AA) from firmer (GG) genotypes (Zhang et al., 2024).

Flavor quality arises from the balance of sugars, acids, and volatiles during ripening. The cell wall invertase *LIN5* plays a

key role by modulating soluble sugar and total soluble solids content, directly impacting sweetness and fruit size (Ranc et al., 2012; Tieman et al., 2017; Zanor et al., 2009).

Fruit color and **nutritional value** arise from coordinated carotenoid and flavonoid biosynthesis. *CRTISO* converts phytyl diester to all-trans-lycopene, conferring red pigmentation (Isaacson et al., 2002). Mutations in *CYC-B* elevate β -carotene, producing orange fruit, whereas combined allelic variation in *CYC-B* and *SGR* generates novel “orange-brown” phenotypes with retained chlorophyll (Manoharan et al., 2017). *PSY1*, *SGR*, and *SIMYB12* orchestrate the green-to-red transition through chlorophyll degradation and carotenoid accumulation, and *SIANT1* enhances anthocyanin biosynthesis, improving both coloration and antioxidant capacity (S.-I. Kang et al., 2017; Yan et al., 2020).

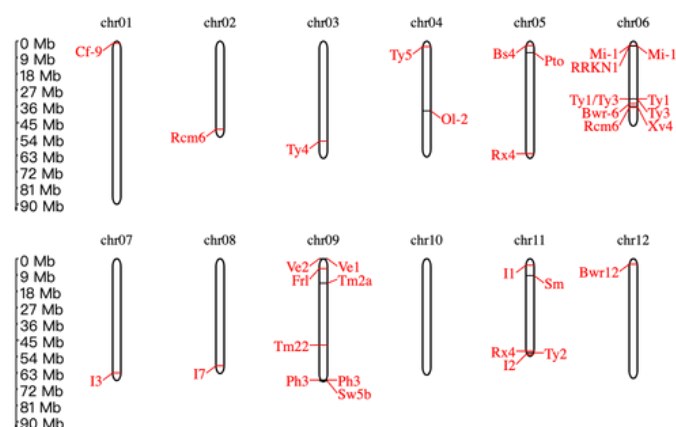


Figure 2 Distribution of functional gene/QTL regions related to agronomic traits and resistance traits on each chromosome

Trait	Gene	Citation
Resistance to bacterial canker	<i>Rcm6</i>	Abebe et al., 2022
Resistance to bacterial speck	<i>Pto</i>	W. Sun et al., 2011
Resistance to bacterial spot	<i>Rx4</i>	Sharlach et al., 2013
Resistance to bacterial wilt	<i>Bwr12</i> , <i>Bwr-6</i>	Abebe et al., 2020; Kim et al., 2018
Resistance to Fusarium crown and root rot	<i>Frl</i>	Devran et al., 2018
Resistance to Fusarium wilt	<i>I1</i> , <i>I2</i> , <i>I3</i> , <i>I7</i>	Arens et al., 2010; Catanzariti et al., 2015; Gonzalez-Cendales et al., 2016
Resistance to late blight	<i>Ph3</i>	Jung, 2015
Resistance to leaf mold	<i>Cf-9</i>	Kim et al., 2017
Resistance to leaf spot	<i>Bs4</i>	Schornack et al., 2004
	<i>Xv4</i>	Sharlach et al., 2013
Resistance to powdery mildew	<i>Ol-2</i>	Bai et al., 2008
Resistance to root-knot nematode	<i>Mi-1</i>	Devran et al., 2023
	<i>RRKN1</i>	El-Sappah et al., 2019
Resistance to tobacco mosaic virus	<i>Tm22</i> , <i>Tm2a</i>	Panthee et al., 2013
Resistance to tomato spotted wilt	<i>Sw5b</i>	Tong et al., 2023
Resistance to tomato yellow leaf curl virus	<i>Ty1</i> , <i>Ty1/Ty3</i> , <i>Ty2</i> , <i>Ty3</i> , <i>Ty5</i> , <i>Ty4</i>	Koeda & Kitawaki, 2024; Lee et al., 2021; Y. Wang et al., 2022
Resistance to Verticillium wilt	<i>Ve1</i> , <i>Ve2</i>	Acciarri et al., 2007

Table 2 Key resistance traits in modern tomato breeding.

Chlorophyll retention and **fruit uniformity** also shape appearance and consumer perception. The *TKN4* homeobox gene acts upstream of *SIGLK2* and *SIAPRR2-LIKE* to establish a chloroplast gradient defining the characteristic green shoulder. *MutTKN4* or *SIGLK2* disrupt this pattern, leading to uniform ripening—a hallmark of tomato domestication (Nadakuduti et al., 2014). The *GS* gene alters tomato fruit color via *TAGL1* promoter methylation, with high methylation producing dark green stripes and lower methylation yielding lighter ones (G. Liu et al., 2020).

Abiotic tolerance traits are essential for maintaining yield stability under environmental stresses such as cold, heat and salinity.

Cold tolerance is enhanced by promoters *SIBBX31* and *WRKY34*, which modulate stress-responsive transcriptional networks (Guo et al., 2024; Zhu et al., 2023).

Heat tolerance in tomato is regulated by both developmental and stress-response genes. The *MIB2–SICOL1* module controls inflorescence branching under high temperatures, supporting fruit size and uniformity, while variation in the heat-stress transcription factor *HsfA2* influences rapid stress acclimation through alternative splicing (Hu et al., 2020; S. Sun et al., 2024).

Salt tolerance is largely determined by genes regulating Na^+/K^+ homeostasis and saline–alkaline stress response, with natural variations in *SIHAK20* and *SISOS1* affecting root Na^+/K^+ ratios and domestication-related loss of tolerance, while promoter variation in *SISCaBP8* enhances saline–alkaline tolerance in wild accessions (J. Liu et al., 2024; Z. Wang, Hong, Li, et al., 2020; Z. Wang, Hong, Zhu, et al., 2020).

Integrating these genetic components into breeding programs is critical for developing tomato cultivars resilient to increasingly frequent and extreme environmental conditions.

Resistance Traits

Tomato resistance to pathogens can be categorized as specific (vertical) resistance, where a single R gene recognizes a pathogen effector (*Avr*) gene, and broad-spectrum (horizontal) resistance, which is generally polygenic and independent of individual effectors. Modern breeding combines R-gene pyramiding—stacking multiple complementary resistance genes—with quantitative resistance loci (QTLs), temperature-stable genes, and wild-species alleles to develop cultivars with robust, durable resistance under diverse environmental and pathogen pressures.

Fungal and bacterial diseases are major constraints on tomato production. Race-specific loci such as *I1*, *I2*, *I3*, *I7* confer resistance to *Fusarium oxysporum* races (Arens et al., 2010; Catanzariti et al., 2015; Gonzalez-Cendales et al., 2016), while *Frl* provides broader protection against *Fusarium crown and root rot* (Devran et al., 2018). *Ve1/Ve2* mediate

Verticillium wilt resistance, and *Bwr-6/Bwr-12* control bacterial wilt (Abebe et al., 2020; Acciarri et al., 2007; Kim et al., 2018). Resistance to bacterial speck involves *Pto–AvrPto/AvrPtoB* interactions (W. Sun et al., 2011), and *Rcm6* contributes broad-spectrum resistance to bacterial canker (Abebe et al., 2022). For **bacterial spot**, *Bs4* and *Xv4* (*RXopJ4*) recognize specific *Xanthomonas* effectors (Schornack et al., 2004; Sharlach et al., 2013), while **gray leaf spot** (GLS) resistance in tomato is controlled by one major dominant locus, *Sm* (Yang et al., 2022). *Cf-9* confers race-specific resistance to **leaf mold disease** (Kim et al., 2017). In addition, the natural *ol-2* allele in *S. lycopersicum* var. *cerasiforme* disrupts the *SIMlo1* gene, conferring broad-spectrum, recessive resistance to **powdery mildew** (*Oidium neolyopersici*) (Bai et al., 2008). The *Ph3* locus from *S. pimpinellifolium* (L3708) provides the most effective source of tomato **late blight** resistance, conferring incomplete protection against diverse *Phytophthora infestans* isolates (Jung, 2015).

Viral and nematode resistance is similarly structured. **Tomato yellow leaf curl virus (TYLCV)** resistance could be enhanced by pyramiding *Ty-1/Ty-3*, *Ty-2*, and *Ty-5*, combining complementary defense mechanisms for broad and durable protection (Koeda & Kitawaki, 2024; Lee et al., 2021; Y. Wang et al., 2022).

Resistance to **tomato mosaic virus (ToMV)** is conferred by *Tm-1*, *Tm-2*, *Tm-2²*, and *Tm-2a* (Panthee et al., 2013). Similarly, *Sw5b* confers resistance to **tomato spotted wilt virus (TSWV)** (Tong et al., 2023). **ToBRFV** resistance involves multiple QTLs and gene-specific molecular markers (*TBR11*) facilitating selection also published. For **root-knot nematodes**, *Mi-1.2* provides race-specific resistance, but high soil temperatures can compromise its effectiveness, whereas *RRKN1* confers heat-stable resistance to *RKN*, enabling integration into R-gene pyramiding programs (Devran et al., 2023; El-Sappah et al., 2019).

Collectively, functional genes and QTLs represent a valuable resource for marker-assisted breeding, forming the foundation of trait markers in tomato panels. These trait-specific markers are curated from published studies, emphasizing associations with key agronomic, resistance, and quality traits. While they correspond to validated haplotypes or SNPs that co-segregate with specific traits, their predictive accuracy can be influenced by environmental factors and genetic background—underscoring a persistent challenge in plant breeding.

To enhance the panel's utility, all SNPs within functional genes and their flanking regions (± 7 kb) are annotated, offering additional biological context and potential links to trait variation. Thus, the tomato panel series function not only as a genotyping tool but also as practical resources for trait improvement and selection in tomato breeding programs.

Ready-to-Use Tomato GBTS Panels

Building on these background markers and trait genes, MolBreeding compiles these public resources and develops into the following tomato genotyping panels (Table 3).

GenoPlexs Tomato 1K Panel

The 1K panel gives a set of 1,046 core SNPs and 17 InDels, including 170 trait markers across 32 key trait categories. In recent commercial project analyses, the panel demonstrates stable sequencing performance:

- Alignment Rate: 96.08%
- Coverage Uniformity 20%*: 97.56%
- Mean Depth of reads: 403.39
- Target SNP Call Rate: 98.92%

GenoBaits Tomato 5K Panel

The 5K panel includes 4,146 core SNPs, 1,211 mSNPs, and 9 InDels, integrating 112 trait-associated markers across 21 traits to support more detailed genome-wide diversity assessment. The panel shows technical metrics across recent projects:

- Alignment Rate: 97.23%
- Coverage Uniformity 20%*: 97.74%
- Mean Depth of reads: 130.96
- Target SNP Call Rate: 98.20%

GenoBaits Tomato 10K Panel

The 10K tomato panel contains 11,491 SNPs and 35 InDels, offering the high-resolution and broadest trait representation with 474 markers associated with 34 traits for advanced breeding decisions. Full details on 10K panel development are published (Adedze et al., 2025). The following metrics summarize the actual performance of the 10K panel in recent genotyping projects.

- Alignment Rate: 95.05%
- Coverage Uniformity 20%*: 95.21%
- Mean Depth of reads: 50.20
- Target SNP Call Rate: 98.23%

Product Name	Technology	SNP	Indel	Trait	Site Type
GenoPlexs Tomato 1K Panel	GenoPlexs	1,046	17	32	SNP, InDel
GenoBaits Tomato 5K Panel	GenoBaits	5,357	9	21	SNP, InDel
GenoBaits Tomato 10K Panel	GenoBaits	11,491	35	34	SNP, InDel

Reference genome: SL 4.0 (GCA_000188115.5, *Solanum lycopersicum*, Heinz 1706)

Table 3. Genotype by Targeted Sequencing (GBTS) Panels – Ready to Use

***Coverage uniformity 20%** refers to the percentage of SNP loci whose sequencing depth is at least 20% of the average sequencing depth across all SNPs in the panel.

Together, these panels deliver scalable marker densities—supporting genome-wide analysis

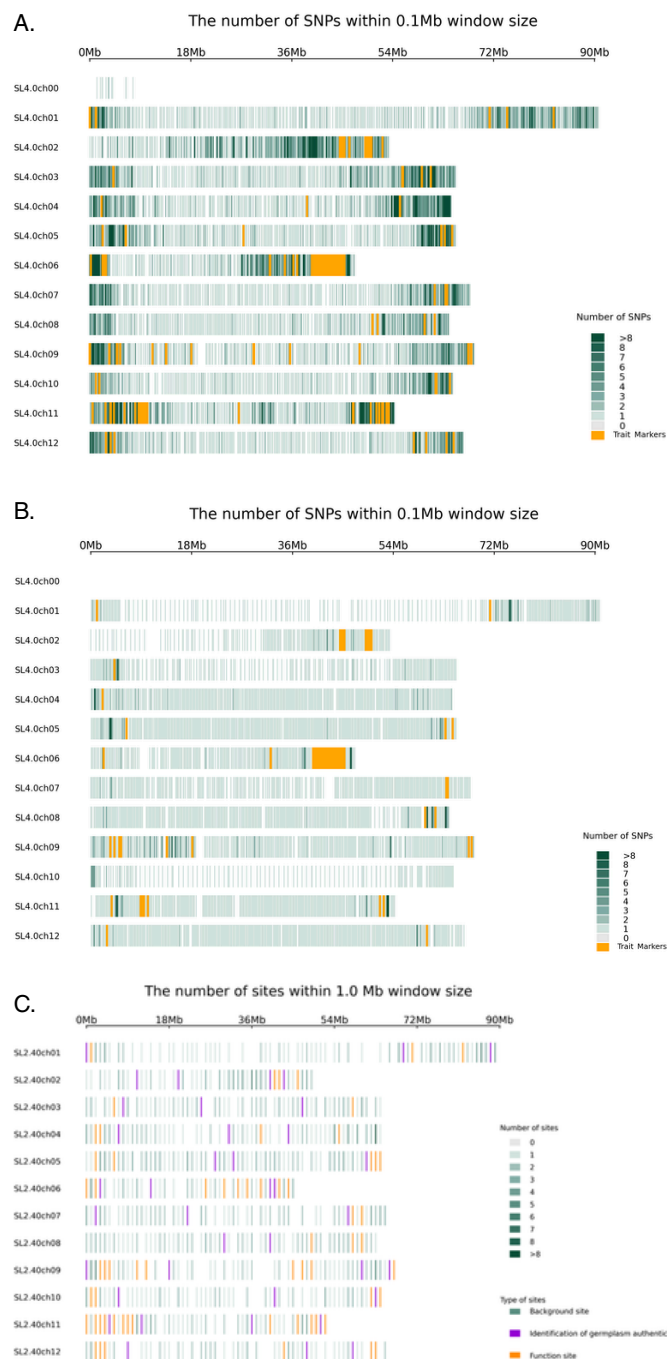


Figure 3. Distribution of Markers in Three Tomato Panels 10K(B), 5K(D), 1K (C). All the SNPs are evenly distributed across the chromosomes.

Validation of GenoBaits 10K Tomato Panel

To validate the GenoBaits Tomato 10K Panel, the corresponding SNP loci are extracted from 71 public whole-genome resequencing (WGS) datasets, including 29 accessions from PRJEB5235 and 42 accessions from PRJNA259308 (Figure 4A). These samples encompass wild relatives, semi-domesticated types, and cultivated tomatoes.

Using the retrieved 10K SNPs, a phylogenetic tree and principal component analysis (PCA) are generated to assess the panel's ability to recover known evolutionary relationships within the tomato lineage.

The 10K marker set demonstrated high discriminatory power:

- The phylogenetic tree clearly reproduces the established separation between the Red-Fruited complex

(*S. lycopersicum*, *S. lycopersicum* var. *cerasiforme*, *S. pimpinellifolium*, *S. cheesmaniae*) and the Green-Fruited complex (*S. habrochaites*, *S. chilense*, *S. peruvianum*) (Figure 4B).

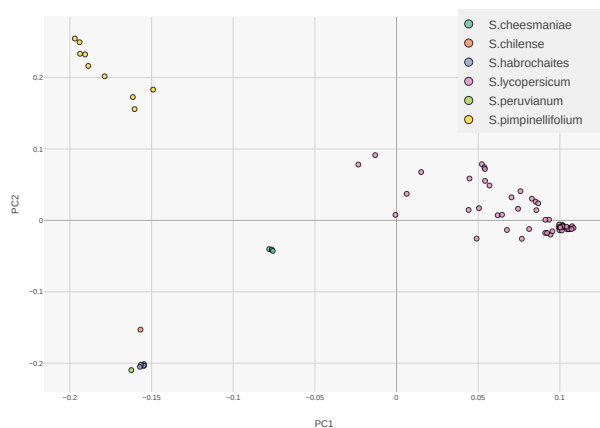
- PCA plot reveals clear, non-overlapping clusters corresponding to these evolutionary groups, demonstrating robust species-level discrimination (Figure 4C).

Overall, these findings confirm that the GenoBaits Tomato 10K Panel provides sufficient genomic resolution to capture evolutionary relationships, and reflect established domestication pathways. This high level of precision makes the 10K panel a powerful solution for germplasm verification, variety authentication, population studies, introgression tracking, and identification of trait-associated genotypes or haplotypes in tomato improvement programs.

A.

Project ID	Species	Fruit Color	Accessions Count
PRJEB5235 (29 accessions)	<i>S. cheesmaniae</i>	Red-fruited	1
	<i>S. chilense</i>	Green-fruited	1
	<i>S. habrochaites</i>	Green-fruited	5
	<i>S. lycopersicum</i>	Red-fruited	21
	<i>S. peruvianum</i>	Green-fruited	1
PRJNA259308 (42 accessions)	<i>S. cheesmaniae</i>	Red-fruited	2
	<i>S. lycopersicum</i>	Red-fruited	31
	<i>S. pimpinellifolium</i>	Red-fruited	9

C.



B.

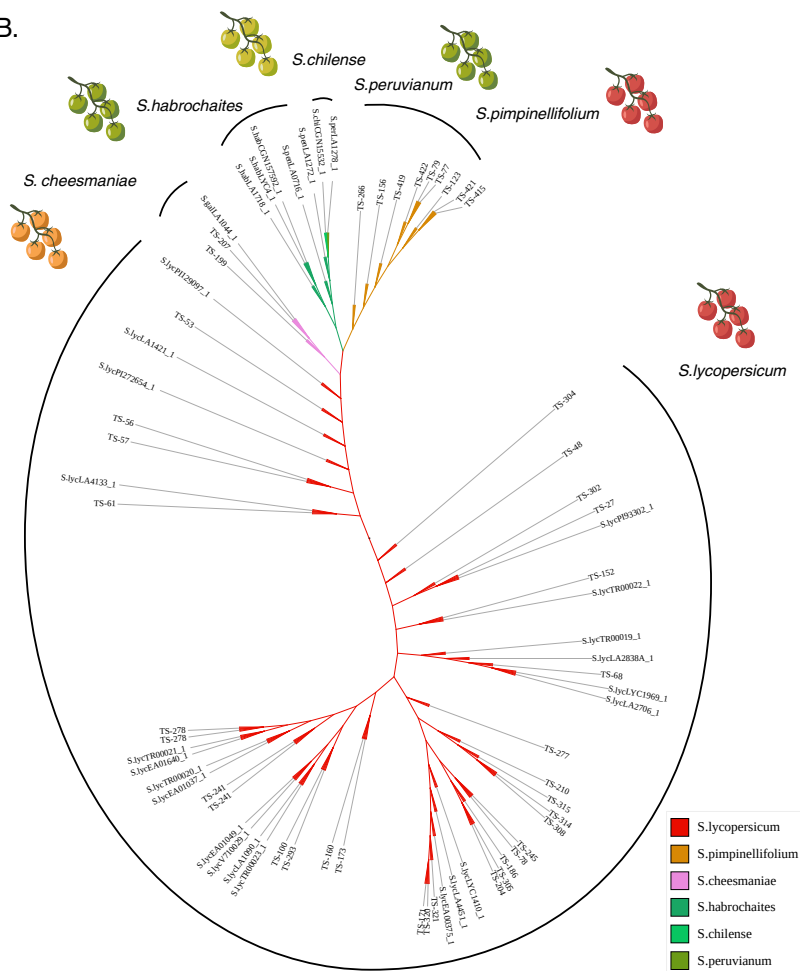


Figure 4. (A) Table of tomato and wild species accessions included in PRJEB5235 and PRJNA259308. (B) Phylogenetic tree based on the GenoBaits 10K marker loci. (C) PCA analysis based on the GenoBaits 10K marker loci.

Conclusion

MolBreeding's Tomato Panels mark a new chapter in precision and efficiency for tomato breeding. With high-quality SNPs, validated assay design, and broad population compatibility, these panels provide a reliable genotyping solution for both research and commercial applications. These panels enable breeders to uncover genetic potential, accelerate variety development, and promote sustainable innovation in tomato improvement worldwide.

Call to Action

We invite tomato researchers, breeders, and industry partners to collaborate with us in applying the Tomato GenoBaits Panels to advance tomato genetics and molecular breeding. Together, we can drive the development of high-yielding, resilient, and high-quality tomato varieties, shaping a more sustainable and innovative future for global tomato cultivation.

Supplementary Table 1

Tomato accessions used for SNP resource development.xlsx

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