

THE ROLE OF MARKER-ASSISTED SELECTION (MAS) AND GENOTYPING IN THE DEVELOPMENT OF INDETERMINATE, GREENHOUSE-ADAPTED TOMATO HYBRIDS: A REVIEW

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Abstract

Protected cultivation places exceptional demands on the tomato (*Solanum lycopersicum* L.). Indeterminate hybrids grown under glass or plastic are expected to combine continuous, high-truss yield with durable resistance to a battery of soil-borne, foliar and viral pathogens, tolerance of the elevated temperatures and humidity typical of enclosed structures, and the fruit-quality attributes demanded by fresh markets. Assembling so many favourable alleles in a single F1 by phenotypic selection alone is slow, costly and, for several traits, unreliable, because resistance genes are often recessive, race-specific or masked by the environment. Marker-assisted selection (MAS) and modern genotyping have transformed this task by allowing breeders to track resistance and quality alleles directly at the DNA level, independent of growth stage, inoculum pressure or season. This review synthesises the current state of molecular-marker technology relevant to greenhouse tomato hybrid breeding: the transition from RFLP and SSR markers to SCAR, CAPS and, increasingly, single-nucleotide-polymorphism (SNP) systems such as KASP and targeted-sequencing panels; the well-characterised genes and diagnostic markers for the principal greenhouse diseases (TYLCV, TSWV, ToMV, Fusarium and Verticillium wilts, root-knot nematode, late blight and powdery mildew); marker-assisted backcrossing and gene pyramiding for stacking multiple resistances into elite indeterminate parents; and the emergence of genomic selection for polygenic traits such as yield, soluble-solids content and heat tolerance. The relevance of these tools to the

tomato breeding programme of the Andijan Scientific-Experimental Station is considered, together with the practical constraints, and priorities for their adoption in Uzbekistan are proposed.

Keywords: *Solanum lycopersicum*, indeterminate hybrid, greenhouse tomato, marker-assisted selection, SNP genotyping, KASP, gene pyramiding, genomic selection, disease resistance.

Introduction

Tomato is among the most economically important vegetable crops worldwide, and a growing share of its production now takes place under protected cultivation. Greenhouses and plastic tunnels extend the growing season, raise yield per unit area, buffer the crop against weather extremes and give producers access to premium off-season markets. Indeterminate (vine-type) hybrids are the dominant choice for such systems because their continuous growth habit allows repeated harvesting from many trusses over a long cropping cycle, maximising the return on the fixed cost of a heated or ventilated structure. In Uzbekistan, where protected vegetable production has expanded rapidly and government policy has prioritised the modernisation of horticulture, demand for locally adapted greenhouse tomato hybrids that reduce dependence on imported seed is particularly acute.

The protected environment, however, imposes its own selection pressures. The warm, humid and enclosed conditions that favour rapid tomato growth also favour the persistence and spread of pathogens. Whitefly-transmitted tomato yellow leaf curl virus (TYLCV), tomato spotted wilt virus (TSWV), tomato mosaic virus (ToMV), soil-borne *Fusarium* and *Verticillium* wilts, root-knot nematodes, late blight and powdery mildew are recurrent constraints in greenhouse tomato, and the crop as a whole is host to more than a hundred described pathogens. Because chemical control is expensive, environmentally undesirable and often ineffective against viruses and nematodes, genetic resistance built into the hybrid is the most sustainable line of defence. At the same time, greenhouse hybrids must set fruit and maintain quality under the high temperatures that build up inside enclosed structures, a polygenic challenge that conventional selection addresses only slowly.

Conventional phenotypic selection for these traits is constrained in several ways. Many resistance genes act recessively or are effective only against specific pathogen races, so their presence cannot be inferred reliably from field symptoms; resistance and susceptibility can be confounded by escape, by variable inoculum pressure and by the environment; and the evaluation of quantitative traits such as yield, soluble-solids content and heat tolerance requires large, replicated, multi-season trials. Introgressing several such traits into one elite indeterminate parent by phenotype alone can take a decade or more. Marker-assisted selection (MAS) circumvents these limitations by allowing breeders to identify carriers of target alleles directly from DNA, at the seedling stage, in any season, and without exposing plants to the pathogen. This review examines how MAS and contemporary genotyping platforms are applied to the specific problem of breeding indeterminate, greenhouse-adapted tomato hybrids, and considers the prospects for their deployment at the Andijan Scientific-Experimental Station.



Breeding Targets in Indeterminate Greenhouse Tomato

The breeding objective for a modern greenhouse tomato hybrid can be summarised as the simultaneous assembly of four groups of traits into a single, uniform, vigorous F1. First, a suitable plant architecture and physiology: indeterminate growth habit, strong internodes able to support a long cropping cycle, good vigour and, increasingly, tolerance of low light and of the heat that accumulates in closed structures. Second, durable multiple disease and pest resistance, since greenhouse monoculture and continuous cropping intensify pathogen pressure. Third, high and stable marketable yield expressed as fruit number and mean fruit weight sustained across many trusses. Fourth, the fruit-quality profile demanded by the fresh market: shape and size uniformity, firmness and shelf life, colour, soluble-solids content and flavour.

These traits differ fundamentally in their genetic architecture, and this difference dictates the marker strategy. Growth habit is governed largely by the single SELF-PRUNING (SP) locus, whose recessive determinate allele must be excluded to maintain the indeterminate habit. Most of the key disease resistances are controlled by one or a few major genes of large effect, which makes them ideal targets for classical, marker-tagged MAS. Yield, fruit quality and heat tolerance, by contrast, are polygenic, quantitatively inherited and strongly influenced by environment, and are therefore better addressed by quantitative-trait-locus (QTL) mapping and, ultimately, by genomic selection. A practical breeding programme must combine both approaches: single-gene MAS to fix the qualitative resistances, and genome-wide prediction to improve the quantitative background.

From Morphological Markers to High-Throughput SNP Genotyping

The molecular-marker toolkit available to tomato breeders has evolved through several generations, each more informative, more automatable and cheaper per data point than the last. Early restriction-fragment-length-polymorphism (RFLP) and randomly amplified polymorphic DNA (RAPD) markers were laborious and, in the case of RAPD, poorly reproducible. Microsatellite (SSR) markers offered co-dominance and good reproducibility and remain useful for diversity analysis and fingerprinting. For routine MAS, however, the field has largely converged on PCR-based, gene-derived markers and, most recently, on single-nucleotide polymorphisms.

Sequence-based PCR markers: SCAR and CAPS

Sequence-characterised amplified region (SCAR) and cleaved-amplified-polymorphic-sequence (CAPS) markers are the workhorses of practical tomato resistance breeding. Because they are designed from, or tightly linked to, the resistance gene itself, they can be scored on a simple agarose gel and read as the presence or absence of a diagnostic band. Widely used examples include the P6-25 and ACY markers for the Ty-3 TYLCV-resistance allele, the Mi-23 marker for the Mi-1.2 nematode-resistance gene, and gene-based SCAR markers for the Ph-3 late-blight and Sw-5 spotted-wilt loci. Their low equipment requirements make them well suited to breeding stations that do not have access to high-throughput genotyping facilities.

Single-nucleotide polymorphisms and KASP

SNPs are today the marker class of choice for large-scale work because they are extraordinarily abundant across the genome, co-dominant, stable, cheap to score and readily automated. Among the platforms for targeted SNP scoring, Kompetitive Allele-Specific PCR (KASP) has become a global benchmark: it is a fluorescence-based, allele-specific assay that offers low cost, low error rates and high reproducibility, and it is flexible enough for the small-to-medium panels of trait-linked SNPs that a breeding programme actually needs. KASP assays can convert any validated resistance SNP into a rapid, gel-free diagnostic suitable for screening thousands of seedlings. For deeper characterisation, larger fixed arrays and sequencing-based approaches are available.

Arrays, genotyping-by-sequencing and diagnostic panels

At higher throughput, genotyping-by-sequencing (GBS) discovers and scores tens of thousands of SNPs simultaneously and is the standard tool for QTL mapping and for building the marker datasets that genomic selection requires. Fixed SNP arrays, such as the widely used tomato genotyping array of roughly 8,000 SNPs, and newer targeted-sequencing panels have made genome-wide fingerprinting routine. A particularly practical development for breeding is the multiplexed diagnostic panel: a recently described 10K-SNP targeted-sequencing panel for tomato was shown to diagnose nineteen resistance genes covering ten diseases in a single assay, allowing simultaneous screening of an entire resistance portfolio and greatly accelerating backcross breeding and gene pyramiding. Such panels point towards a future in which a single genotyping run replaces dozens of separate marker assays.

Marker-Assisted Selection for Disease Resistance

Disease resistance is the trait class for which MAS delivers its clearest and best-documented benefit in greenhouse tomato, because the major resistances are controlled by identifiable genes for which reliable diagnostic markers exist. Table 1 summarises the principal resistance genes and their associated markers that are relevant to protected cultivation.

Table 1. Major disease-resistance genes and diagnostic molecular markers used in greenhouse tomato breeding.

Disease / pathogen	Resistance gene(s)	Chromosome	Diagnostic marker(s)
Tomato yellow leaf curl virus (TYLCV)	Ty-1 / Ty-3 (allelic), Ty-2, Ty-4, Ty-5, Ty-6	6, 11, 3, 4, 10	P6-25, ACY, Ty1-3, SCAR2 (SCAR/CAPS/InDel)
Tomato spotted wilt virus (TSWV)	Sw-5b	9	Sw-5-2, SW-421, gene-derived SNP/SCAR
Tomato mosaic virus (ToMV)	Tm-2 ²	9	SCN131000, CAPS
Root-knot nematode (<i>Meloidogyne</i> spp.)	Mi-1.2	6	Mi-23, PMi, REX-1 (SCAR)
Fusarium wilt (<i>F. oxysporum</i> f. sp. <i>lycopersici</i>)	I-1, I-2, I-3	11, 11, 7	TAO1 (CAPS), gene-linked SCAR
Verticillium wilt (<i>V. dahliae</i> race 1)	Ve / Ve2	9	Ve-linked SCAR
Late blight (<i>Phytophthora infestans</i>)	Ph-3	9	Ph3-SCAR, Ph3-2, Ph3-3
Powdery mildew (<i>Oidium neolyopersici</i>)	Ol-1	6	SCABO1 (SCAR)
Leaf mould (<i>Passalora fulva</i>)	Cf-9 / Cf-family	1, 6	gene-linked InDel/SCAR

Virus resistance

Viral diseases are the most damaging and the least chemically controllable constraints in greenhouse tomato, and resistance to them is therefore the highest-value target for MAS. TYLCV, a whitefly-transmitted begomovirus, is countered by a series of introgressed loci designated Ty-1 to Ty-6, most of them derived from wild relatives such as *Solanum chilense*, *S. habrochaites* and *S. peruvianum*. Ty-1 and Ty-3 have been shown to be allelic and to encode an RNA-dependent RNA polymerase; Ty-3 in particular is widely deployed in commercial hybrids and is tagged by the well-validated P6-25 marker, complemented by newer gene-based markers such as ACY. Ty-2, on chromosome 11, is tracked by InDel and CAPS markers developed from its candidate gene. Because these resistances confer only partial, quantitative protection individually, MAS is used to pyramid two or more Ty loci for stronger, more durable resistance. TSWV resistance is conferred principally by the dominant Sw-5b gene, for which gene-specific SCAR and SNP markers are available, and ToMV resistance by Tm-2², tracked by CAPS markers. The recessive, race-specific and often symptomless nature of virus resistance makes marker-based selection especially valuable here, since carriers cannot be identified reliably from phenotype alone.

Soil-borne pathogens and nematodes

Greenhouse soils under continuous tomato culture accumulate soil-borne inoculum, making resistance to *Fusarium* wilt, *Verticillium* wilt and root-knot nematode essential. *Fusarium oxysporum* f. sp. *lycopersici* resistance is conferred by the I-series genes (I-1, I-2, I-3), each effective against particular pathogen races, and by CAPS and SCAR markers linked to them; race-3 resistance conferred by I-3 is increasingly important where the pathogen has overcome earlier genes. *Verticillium* wilt race 1 is controlled by the Ve/Ve2 locus, and root-knot nematode by the widely deployed Mi-1.2 gene, for which the Mi-23 SCAR marker is a standard diagnostic. Marker selection is particularly advantageous for these traits because reliable phenotyping requires controlled inoculation and destructive root assessment.

Foliar fungal and oomycete diseases

Under the high humidity of enclosed structures, late blight (*Phytophthora infestans*), powdery mildew (*Oidium neolycopersici*) and leaf mould (*Passalora fulva*) can develop rapidly. Late-blight resistance conferred by Ph-3 is selected using gene-based SCAR markers, powdery-mildew resistance via the Ol-1 locus using the SCABO1 marker, and leaf-mould resistance through the Cf gene family. Where markers exist, they allow these resistances to be combined with the virus and soil-borne resistances in a single, coordinated selection scheme.

Fruit Quality, Yield and Heat Tolerance

Beyond disease resistance, greenhouse tomato hybrids must deliver a defined quality and yield profile, and increasingly must set fruit under the elevated temperatures of enclosed structures. These traits are quantitatively inherited and more challenging for classical MAS, but QTL mapping and genome-wide analysis have identified marker-trait associations that can be exploited. Numerous QTLs governing soluble-solids content, fruit weight, fruit shape, firmness and locule number have been mapped, several using inbred backcross lines derived from wild *Solanum pimpinellifolium*, and the corresponding markers can be used to select for improved quality in a segregating



population.

Heat tolerance is especially relevant to protected cultivation in warm climates such as that of the Fergana Valley. Because high temperature impairs pollen viability, fruit set and yield, and because it is controlled by many genes and is difficult to phenotype reliably, it is an attractive target for genomic approaches. Genome-wide association studies in large, transcontinental tomato panels evaluated under greenhouse heat stress have identified SNP markers associated with yield and quality under high temperature, and genomic-prediction models built from such data have achieved useful accuracies — of the order of 0.73 for yield and 0.72 for soluble-solids content under heat stress — demonstrating that genome-based selection can accelerate breeding for thermotolerance. QTL markers validated in these studies provide a practical means of enriching greenhouse breeding populations for heat-tolerant genotypes before field evaluation.

Gene Pyramiding and Marker-Assisted Backcrossing

The commercial value of a greenhouse hybrid depends not on any single resistance but on the durable combination of many favourable alleles in one elite, indeterminate background. Two complementary MAS strategies achieve this. Gene pyramiding uses foreground markers to assemble several resistance genes — for example Ty-3 for TYLCV, Mi-1.2 for nematode and Ph-3 for late blight — into a single line, tracking each allele independently at every generation and identifying the rare individuals that carry all target genes, often in homozygous condition. Because pyramided lines cannot be distinguished from single-gene lines by phenotype when only one pathogen is present, markers are indispensable to this process.

Marker-assisted backcrossing (MABC) is used to move a resistance gene from a donor — frequently a wild relative or a resistant landrace — into an elite recurrent parent while recovering that parent's genome as rapidly as possible. Foreground selection with a tightly linked marker ensures the target gene is retained; recombinant selection with flanking markers minimises the linkage drag of undesirable donor DNA around the gene; and background selection with genome-wide markers accelerates recovery of the recurrent-parent genotype, reducing the number of backcross generations needed. Applied together, foreground, recombinant and background selection can convert an elite indeterminate parent into a resistant, near-isogenic version of itself in far fewer generations than phenotypic backcrossing would require, which is decisive when a hybrid must be brought to market quickly.

Genomic Selection and the Shift to Whole-Genome Breeding

Whereas MAS targets a limited number of markers with known, large effects, genomic selection (GS) uses genome-wide marker data to predict the breeding value of every individual, capturing the many small-effect loci that collectively govern quantitative traits. A training population that has been both genotyped and phenotyped is used to calibrate a prediction model; that model then estimates genomic breeding values for selection candidates from their marker profiles alone, so that superior individuals can be chosen at the seedling stage without full phenotypic evaluation. For traits such as yield, soluble-solids content, earliness and heat tolerance, which are polygenic and expensive to phenotype, GS can shorten the breeding cycle and raise the rate of genetic gain. In tomato, GS has been shown to predict heat-tolerant genotypes and earliness with useful accuracy, and its power grows as marker density, training-population size and phenotyping quality





increase. The combination of a controlled greenhouse environment, single-seed-descent line development, MAS for major-gene resistances and GS for the quantitative background represents the current frontier of tomato breeding and offers a coherent framework within which a national programme can progressively modernise. In practice, most breeding stations will adopt these tools in sequence — first diagnostic MAS for the highest-value resistances, then QTL-based selection for quality, and finally GS as genotyping costs fall and reference datasets accumulate.

Prospects for Application at the Andijan Scientific-Experimental Station

The Andijan Scientific-Experimental Station, part of the Research Institute of Vegetable, Melon Crops and Potato, conducts vegetable-crop breeding in the Fergana Valley, a region with a strong and expanding protected-cultivation sector and a warm continental climate in which both heat stress and the major greenhouse pathogens are relevant. A staged adoption of the tools reviewed here would strengthen the station's capacity to develop locally adapted indeterminate hybrids and reduce dependence on imported seed.

A pragmatic sequence of priorities might be as follows:

- Establish gel-based SCAR/CAPS marker screening for the highest-value resistances first — Ty-3 (P6-25/ACY) for TYLCV, Mi-1.2 (Mi-23) for root-knot nematode and Sw-5 for TSWV — since these require only standard PCR and electrophoresis and address the most damaging greenhouse constraints.
- Assemble a working germplasm panel of local and introduced lines, characterise it with these markers, and identify resistant donors and elite indeterminate recurrent parents for MABC.
- Introduce marker-assisted backcrossing with foreground and, where feasible, background selection to move validated resistances into adapted elite parents while retaining the SP indeterminate habit.
- Progress to gene pyramiding, combining virus, soil-borne and foliar resistances into single parental lines to build durable, multi-resistant hybrids.
- As resources permit, access KASP or targeted-sequencing services — through national or international collaboration — to convert to higher-throughput SNP screening and, ultimately, to build training populations for genomic prediction of heat tolerance and fruit quality under greenhouse conditions.

Such a programme would allow the station to combine the resistance and quality alleles required for competitive greenhouse hybrids far more efficiently than phenotypic selection alone, and to tailor those hybrids to the specific pathogen spectrum and thermal environment of Uzbek protected cultivation.

Challenges and Limitations

The benefits of MAS and genotyping are real but not automatic, and several constraints must be managed. Markers are only as reliable as their linkage to the causal gene: loosely linked markers can be separated from the target by recombination, so gene-based or very tightly linked markers should be preferred and validated in local germplasm before routine use. The initial investment in laboratory infrastructure, reagents and trained personnel is significant, and per-sample genotyping costs, though falling, remain a real consideration for stations with limited budgets. Resistance conferred by single major genes can be overcome by evolving pathogen races, which argues for

pyramiding several genes and for continued phenotypic monitoring rather than reliance on markers alone. Genomic selection additionally demands substantial, high-quality training data and analytical capacity, and its accuracy depends on the genetic relationship between training and breeding populations. Finally, MAS complements rather than replaces field evaluation: markers guide and accelerate selection, but final yield, quality and adaptation must still be confirmed phenotypically under the target greenhouse conditions.

Conclusion

Breeding indeterminate tomato hybrids for greenhouse cultivation requires the simultaneous assembly of durable multiple disease resistance, high sustained yield, market fruit quality and tolerance of the heat and humidity of protected structures — a combination that phenotypic selection alone achieves only slowly and imperfectly. Marker-assisted selection and modern genotyping resolve much of this difficulty. For the major, single-gene resistances that dominate greenhouse breeding — the Ty loci, Sw-5, Tm-2², Mi-1.2, the I-series, Ve, Ph-3 and Ol-1 — diagnostic SCAR, CAPS and SNP markers allow direct, phenotype-independent selection and, through marker-assisted backcrossing and gene pyramiding, the efficient stacking of many resistances into elite indeterminate parents. For the polygenic traits of yield, quality and heat tolerance, QTL-based selection and genomic prediction extend the same DNA-based logic to the quantitative background. A staged adoption of these tools, beginning with gel-based marker screening for the highest-value resistances and progressing towards SNP genotyping and genomic selection, offers breeding programmes such as that of the Andijan Scientific-Experimental Station a realistic path to developing competitive, locally adapted greenhouse tomato hybrids and to reducing national dependence on imported seed.

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