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Molecular tools complementing conventional breeding approaches in vegetable crops: A critical review

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Abstract

Vegetable crops constitute an essential component of global food and nutritional security by providing vital vitamins, minerals, antioxidants and dietary fibre essential for maintaining human health and preventing nutritional deficiencies. With rapid demographic growth, accelerated urbanisation and climate-induced environmental fluctuations, the demand for high-yielding, resilient and nutritionally dense vegetable cultivars have increased substantially. However, vegetable production faces pervasive constraints, including devastating biotic pressures (fungi, bacteria, viruses, insect pests and nematodes) alongside abiotic stresses such as drought, extreme temperatures, salinity and water scarcity. Conventional breeding approaches have laid the cornerstone of vegetable improvement through recurrent selection, hybridisation and wide backcrossing. Nonetheless, empirical reliance on phenotypic evaluation renders conventional selection labour-intensive, time-consuming and prone to environmental noise, particularly for polygenic traits governed by complex genetic architectures and high genotype × environment interactions. The advent of molecular tools has revolutionised vegetable breeding by enabling accurate, genotype-based selection at the DNA level. This review provides a comprehensive critical synthesis of molecular technologies complementing conventional vegetable breeding, spanning diagnostic molecular markers, high-density quantitative trait locus mapping (QTL) mapping, marker-assisted backcrossing and multi-gene pyramiding across solanaceous, cucurbitaceous and cruciferous crops. Furthermore, this review addresses the cutting-edge innovations of the genomic era, including whole-genome resequencing, pangenomics, haplotype-led breeding, speed breeding protocols, doubled haploid technology, multi-omics integration, clustered regularly interspaced short palindromic repeats (CRISPR)-Cas genome editing and artificial intelligence-driven digital phenotyping. Current methodological bottlenecks, epigenetic nuances and synthetic biology avenues are critically evaluated to outline an agile roadmap for climate-resilient and biofortified vegetable development.

Keywords: artificial intelligence; CRISPR-Cas9; doubled haploids; gene pyramiding; genomic selection; high-throughput phenotyping; marker-assisted selection; pan-genomes; speed breeding; vegetable crop improvement

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1. Introduction

Vegetables play an indispensable role in human nutrition by supplying essential micronutrients, vitamins, minerals, antioxidants and dietary bioactive compounds that are deficient in staple cereal-based diets. With the human population projected to surpass nine billion and the arable land base shrinking under urbanisation and climate volatility, vegetable breeding programmes must deliver substantial genetic gains in yield stability, stress resilience and post-harvest quality. Traditional breeding methodologies such as mass selection, pedigree selection, bulk breeding, mutation breeding and wide backcrossing have historically underpinned the commercial development of modern vegetable cultivars (1). However, conventional breeding operates with intrinsic bottlenecks: it relies heavily on phenotypic evaluation, which is confounded by environmental variability, low heritability of quantitative traits, prolonged generation times and pervasive linkage drag during wild introgressions (1, 2).

Economically critical vegetable attributes including total marketable yield, heterosis, drought, thermal tolerance and complex fruit quality parameters are governed by polygenic networks with small-effect quantitative trait loci (QTLs). Phenotypically dissecting such traits across fluctuating open-field environments requires multi-location, multi-year trials that are resource-exhaustive. In this framework, molecular breeding has emerged as a transformative discipline, enabling breeders to decode and exploit allelic variation

directly at the genomic level (2). By coupling genotypic screening with classical hybridisation, molecular tools reduce breeding cycle durations, eliminate environmental confounding and accelerate recurrent parent genome recovery.

While earlier reviews predominantly compiled individual mapping studies in a descriptive, study-by-study format, there is an urgent scientific imperative to critically synthesise overarching paradigms, evaluate comparative efficiencies across vegetable families and delineate knowledge gaps. Crops across the families Solanaceae (tomato, pepper, eggplant), Cucurbitaceae (cucumber, melon, watermelon, pumpkin) and Brassicaceae (cabbage, cauliflower, broccoli) share analogous breeding objectives such as disease resistance gene pyramiding, hybrid vigour exploitation and nutraceutical biofortification yet diverge markedly in genomic architecture, ploidy stability and genetic transformation recalcitrance. Furthermore, the molecular breeding landscape has experienced a paradigm shift as low-density gel-based markers are now superseded by whole-genome resequencing, pangenomics, haplotype-led selection, high-throughput digital phenomics, speed breeding and clustered regularly interspaced short palindromic repeats (CRISPR)-Cas genome editing (3–5). Consequently, this review synthesises the evolutionary progression and comparative utility of molecular tools, details marker-assisted breeding and gene pyramiding, evaluates the breakthroughs of the genomic era and highlights practical limitations and future research priorities for sustainable vegetable improvement.

Molecular markers and their significance in vegetable breeding

Molecular markers are diagnostic nucleotide sequences distributed across the nuclear, mitochondrial or chloroplast genomes that reveal genetic variation among individuals without being altered by environmental fluctuations, developmental stages or epigenetic modulation (6). Molecular markers have transitioned through three successive technological waves: hybridisation-based markers (restriction fragment length polymorphisms (RFLPs)), arbitrary polymerase chain reaction (PCR)-amplified markers such as random amplified polymorphic DNA (RAPD), inter-simple sequence repeat (ISSR) and amplified fragment length polymorphism (AFLP) and sequence-defined co-dominant marker systems such as simple sequence repeats (SSRs), single nucleotide polymorphisms (SNPs) and insertion–deletions (InDels) (2, 6). Table 1 summarises the comparative characteristics, biological properties, operational throughput and specific limitations of the major marker systems deployed in vegetable genetics. Although first-generation markers catalysed early linkage mapping, their severe drawbacks such as radioactive probing in RFLP or PCR non-reproducibility in RAPD precluded high-throughput automation. Second-generation SSRs provided excellent multi-allelic resolution and cross-species transferability, serving as the benchmark for genetic diversity and hybrid purity testing. Today, third-generation SNPs and targeted genotyping-by-sequencing (GBS) dominate vegetable genomics due to their ultra-high genomic density, sequence-level specificity and full compatibility with automated high-throughput fluorescent platforms (e.g., Kompetitive allele-specific PCR (KASP) assays, TaqMan probes and high-density SNP arrays) (1, 7).

Disease and insect pest resistance

In watermelon, three microsatellite markers viz. MCPI_11, BVWS02441 and CYSTSIN linked to powdery mildew resistance were identified on chromosome 2 (8). In cucumber lines S94 (susceptible Northern China open-field type) and S06 (resistant European greenhouse type), four stable QTLs (pm1.1, pm2.1, pm4.1 and pm6.1) were mapped across linkage groups 1, 2, 4 and 6 (9). Tomato leaf curl virus (ToLCV), caused by whitefly-transmitted *Begomovirus*, causes catastrophic losses in the tropical and sub-tropical plains. Six major resistance genes (*Ty-1*, *Ty-2*, *Ty-3*, *Ty-4*, *Ty-5* and *Ty-6*) have been successfully mapped from wild *Solanum* accessions (6). Foreground selection for the Ty-3 gene has been carried out using closely linked co-dominant markers P6-25 and SCAR-1, successfully transferring broad resistance into consumer-preferred cultivars such as Pusa Ruby, Pusa Rohini and Pusa-120 (10). In tomato, previous researchers tagged the powdery mildew resistance gene ol-1 on chromosome 6 using RAPD and sequence-characterised amplified region (SCAR) markers (11). For tomato tospoviruses, the Sw-5b resistance gene confers durable resistance across multiple virus species by recognising a conserved 21-amino-acid viral effector epitope, monitored through specific sequence-tagged markers (12–14). In cucumber, QTLs for cucumber mosaic virus (CMV) have been validated on chromosome 6 using SSR markers (15).

While disease resistance breeding has reached high maturity, molecular breeding for insect-pest resistance has lagged significantly due to polygenic inheritance, complex behavioral defence mechanisms (antixenosis vs. antibiosis) and environmental plasticity. Nevertheless, recent investigations demonstrate major strides. In *Solanum* wild relatives, substantial genetic variation has been characterised for whitefly (*Bemisia tabaci*), two-spotted spider mite (*Tetranychus urticae*) and tomato leafminer (*Tuta absoluta*). The QTL mapping in *Solanum galapagense* S.C.Darwin & Peralta has pinpointed genomic loci regulating type-IV glandular trichome density and the biosynthesis of defensive secondary metabolites, particularly acyl-sugars (16). Concurrently, transcriptomic, proteomic and metabolomic analyses have unraveled multi-gene defence cascades in tomato, pepper and eggplant, linking hormone signaling pathways (jasmonic acid, salicylic acid and ethylene) to herbivore defence (17). The convergence of pan-genomics, genome-wide association study (GWAS) and genomic selection is now overcoming historic bottlenecks, enabling

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accelerated selection for polygenic insect defence loci (18).

Table 1. Comparative characteristics, operational throughput and breeding applications of major molecular marker systems in vegetable crops

Marker system	Inheritance	Abundance and distribution	Reproducibility	Throughput / Automation	Major limitations	Primary breeding applications
RAPD	Dominant	Moderate; random non-coding regions	Low (sensitive to PCR conditions)	Low; manual electrophoresis	Dominance (cannot separate heterozygotes); poor lab reproducibility	Initial germplasm diversity; largely superseded
AFLP	Dominant	High; genome-wide restriction loci	Moderate–High	Moderate; polyacrylamide gels / capillary	Technically laborious multi-step assay; patent enzyme costs	High-density map construction; bulked segregant analysis (BSA)
SSR	Co-dominant	Moderate–High; tandem repetitive motifs	High; locus-specific primers	Moderate; capillary sequencers	Gel/capillary running costs; stutter-band artifacts; discovery cost	Genetic diversity; hybrid purity testing; standard foreground MAS
SNP	Co-dominant	Ultra-High; sequence-wide (every 100–300 bp)	Very High; digital base calling	Ultra-High; automated KASP, arrays, NGS	Bi-allelic nature; requires sequencing for de novo discovery; ascertainment bias	GWAS; Genomic Selection; high-density bin mapping; elite gene tagging
GBS / InDel	Co-dominant	High–Ultra High; sequence-wide structural variants	High; sequence-confirmed	High; automated NGS pipelines	High bioinformatic overhead; missing data imputation required	Fine mapping; pangenome construction; haplotype block dissection

RAPD: random amplified polymorphic DNA; AFLP: amplified fragment length polymorphism; SSR: simple sequence repeat; SNP: single nucleotide polymorphism; GBS: genotyping-by-sequencing; InDel: insertion–deletion; KASP: Kompetitive Allele-Specific PCR; NGS: next-generation sequencing; GWAS: genome-wide association study; MAS: marker-assisted selection.

Nutritional and quality trait biofortification

Enhancing the nutraceutical density of vegetables represents a core objective of contemporary breeding programs. Vegetables serve as primary sources of dietary carotenoids, anthocyanins, lycopene, vitamins and minerals that combat micronutrient malnutrition (19, 20). Anthocyanin and carotenoid biosyntheses are regulated by complex transcriptional and hormonal networks, including abscisic acid (ABA) and ethylene. In *Brassica* vegetables, candidate genes governing ABA synthesis (such as BoNCED2.1, BoNCED2.2) and ethylene pathways (BoACS11, BoACO4) orchestrate purple curd and leaf pigmentation (19). Marker-assisted introgression of the semi-dominant *Or* gene at ICAR-Indian Agricultural Research Institute, New Delhi, led to the development of India's first biofortified cauliflower cultivar, 'Pusa Beta-Kesari 1', accumulating high beta-carotene levels (8–10 ppm) (21). In *Cucurbita moschata* Duchesne, Earlier researchers developed a high-density SNP linkage map and identified 29 QTLs governing carotenoids, sugars, fruit thickness and fruit diameter with phenotypic variance explained (PVE) values ranging from 9.6 % to 28.6 % (22). Similarly, previous reports mapped major QTLs controlling anthocyanin hyper-accumulation in purple broccoli, identifying key structural transcription factors (BoMYB, BoTT8) for marker-directed selection (23).

Male sterility systems for hybrid seed production

Commercial F_1 hybrid vegetable seed production relies heavily on male sterility systems to eliminate manual emasculation costs and guarantee genetic purity. Genic male sterility (GMS), predominantly monogenic and recessive, segregates into a 1 : 1 fertile-to-sterile ratio upon backcrossing with heterozygous maintainers, necessitating labor-intensive roguing of fertile plants at flowering. The development of tightly linked DNA markers enables early pre-flowering culling of fertile segregants. In tomato, functional positional sterility controlled by ps-2 and ps genes has been successfully tracked using cleaved amplified polymorphic sequence (CAPS) markers C4-30 and C2-21 located on chromosomes 4 and 2, respectively (24). In *Capsicum*, previous researchers employed genotyping-by-sequencing to develop CAPS (HPGMS2, HPGMS3) and derived cleaved amplified polymorphic sequence (dCAPS) (SPGMS1) markers linked within 3.83 cM of the *ms3* gene in hot pepper and co-segregating with the *msw* gene in sweet pepper, respectively (25). In *Brassica napus* L., fine mapping of recessive male sterile genes *Bnms1* and *Bnms3* was achieved using SSR, AFLP and SCAR markers (26).

However, the commercial deployment of male sterility in vegetable breeding continues to face distinct practical challenges. In GMS systems, the recurrent requirement to identify and rogue 50 % fertile segregants in hybrid nursery blocks increases labour

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costs unless ultra-reliable, cost-effective diagnostic markers are deployed at the seedling stage (27, 28). Cytoplasmic male sterility (CMS) and cytoplasmic-genic male sterility (CGMS) avoid 1 : 1 segregation but require functional maintainer (B-line) and fertility restorer (Rf-line) triads. In eggplant, CMS derived from wild *Solanum violaceum* R.Br. and *Solanum grandifolium* C.V.Morton cytoplasm often induces detrimental pleiotropic defects, including floral malformations, reduced nectary development, poor pollinator attraction and female sub-fertility (27–30). Furthermore, environmental sensitivity remains a formidable challenge: elevated temperatures or day-length shifts often trigger partial fertility breakdown in thermosensitive or photoperiod-sensitive genic male sterility (TGMS/PGMS) lines, resulting in unwanted selfing and compromised hybrid seed purity (30–32). Addressing these nucleo-cytoplasmic incompatibilities and environmental instabilities represents an ongoing research priority.

Inducing and engineering parthenocarpy

Parthenocarpy is fruit development without pollination or fertilisation, which is exceptionally valuable in greenhouse cultivation and adverse open-field climates where extreme heat or cold impairs viable pollen development. Parthenocarpic fruits are seedless, exhibit firmer pulp textures and command premium commercial value. In tomato, five major parthenocarpic QTLs (pat, pat4.1, pat4.2, pat5.1, pat9.1) have been tagged (31). In muskmelon (*Cucumis melo* L.), two major QTLs (cmpat2.1 and cmpat3.1) were identified on linkage groups 2 and 3 using the fixed parthenocarpic line MP-2 (32). In eggplant, map-based cloning of a spontaneous prickleless and parthenocarpic mutant revealed that the *Pad-1* gene encodes an aminotransferase involved in auxin homeostasis during ovary development (33, 34). Mutational disruption or targeted suppression of *Pad-1* orthologs induces high-frequency parthenocarpy across Solanaceae crops, including tomato and pepper, providing an exciting target for genome editing and marker-assisted selection (34, 35).

Quantitative trait loci mapping and linkage analysis in vegetable crops

Quantitative trait loci (QTL) mapping bridges phenotypic variability and underlying chromosome structure. Utilising segregating populations such as F2, backcross (BC), recombinant inbred lines (RILs) and doubled haploids (DH), linkage maps locate statistical associations between marker genotypes and continuous phenotypic variation (2, 7). In vegetable breeding, QTL mapping has elucidated the genetic architecture of yield, resistance and quality attributes. In cucurbits, high-density saturated linkage maps have unraveled dynamic loci governing fruit elongation, cavity dimensions and organic acid partitioning (9, 36). In tomato, landmark mapping studies successfully localised key domestic genes: the self-pruning gene (*sp*) on chromosome 6 conferring determinate growth, the compound inflorescence gene (*s*) promoting multi-flowering cymes and the jointless-2 (*j-2*) gene on chromosome 12 facilitating stemless mechanical fruit harvesting (37). Furthermore, sequencing-based bin map construction has achieved ultra-high mapping resolution, resolving lycopene and volatile metabolic QTLs into precise candidate gene intervals (1, 38).

Despite its widespread utility, classical bi-parental QTL mapping suffers from fundamental limitations. First, mapping populations sample only a fraction of the allelic diversity existing within the species, capturing solely the alleles that differentiate the two parental lines. Second, mapping resolution is inherently restricted by the finite number of recombination events occurring since cross establishment, resulting in wide confidence intervals spanning 10 or hundreds of candidate genes and exacerbating linkage drag. Third, developing structured recombinant inbred populations requires multiple selfing cycles (6–8 generations), delaying operational gene discovery (7, 39). These bottlenecks have necessitated the transition toward GWAS and multi-parent advanced generation inter-cross (MAGIC) populations.

Marker-assisted selection

Marker-assisted selection (MAS) involves selecting plants possessing favorable alleles based on linked DNA markers rather than direct phenotypic screening (2). The MAS offer tremendous efficiency gains: selection can be conducted at the early seedling stage, destructive bioassays are eliminated, recessive alleles can be tracked in heterozygous individuals without progeny testing and multiple targets can be scored in parallel (2, 39). In vegetable breeding, MAS has been implemented to introgress virus resistance (e.g., Ty-3 in tomato), fungal resistance (e.g., powdery mildew resistance in cucumber using candidate gene-based markers (40, 41)) and abiotic stress tolerance. The MAS is particularly cost-effective for traits that are expensive, destructive or impossible to score reliably in standard nurseries, such as nematode resistance, root architectural depth and specific secondary metabolite contents.

Nevertheless, the operational success of MAS is circumscribed when applied to complex, low-heritability quantitative traits governed by dozens of minor-effect QTLs subject to substantial genotype-by-environment (G × E) interactions. Furthermore, physical recombination between the marker and the target gene during meiosis can lead to false-positive selections unless tightly linked flanking markers or functional, intra-genic diagnostic markers (direct causal polymorphism markers) are utilised (1, 2).

Marker-assisted gene pyramiding

Gene pyramiding involves stacking multiple major genes or complementary QTLs into a single elite genetic background to impart durable, broad-spectrum resistance and prevent pathogen breakdown (42). Monogenic resistance typically breaks down within a few growing seasons due to rapid virulence evolution in fungal, bacterial or viral pathogen races. Phenotypically selecting plants carrying multiple resistance genes is virtually impossible when individual genes confer similar

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phenotypes (epistatic masking). Molecular markers provide the only dependable means to track and confirm the simultaneous presence of multiple resistance alleles in a single plant without pathogen inoculations (42).

In tomato, gene pyramiding has successfully integrated multiple *Begomovirus* resistance genes (*Ty-1*, *Ty-2*, *Ty-3*) with late blight resistance genes (*Ph-2*, *Ph-3*), yielding dual-resistant commercial cultivars with durable field performance. In cauliflower, marker-assisted backcrossing was successfully harnessed to pyramid the downy mildew resistance gene *Ppa3* and the black rot resistance gene *Xca1bo* into the elite early-maturity genetic background 'Pusa Meghna' (16, 17). By deploying co-dominant markers for foreground and background selection, recurrent parent genome recovery (> 95 %) was achieved in just three backcross generations, illustrating the power of molecular pyramiding in accelerating commercial cultivar release.

Genetic diversity analysis and germplasm conservation

Assessing genetic diversity within germplasm collections is vital for establishing heterotic pools, identifying novel donor parents and preventing genetic erosion. Molecular markers reveal true phylogenetic relationships unperturbed by environmental fluctuations. In solanaceous vegetables like eggplant, SSR and RAPD fingerprinting have illuminated population structure, cross-compatibility barriers and domestication paths (18, 43). Molecular profiling also underpins DNA fingerprinting for plant variety protection (PVP), distinctness, uniformity and stability (DUS) testing and seed lot hybridity verification, ensuring commercial seed purity across international supply chains.

The genomic era: High-throughput breeding technologies

The convergence of next-generation sequencing, bioinformatics and digital sensors has catalysed a paradigm shift from traditional single-marker assays to comprehensive genomic-scale breeding (Fig. 1). This section critically explores the cutting-edge methodologies defining modern vegetable improvement.

Whole-genome resequencing, pan-genomics and haplotype breeding

The publication of high-quality reference genomes for tomato, pepper, cucumber, melon, watermelon and cabbage provided an unprecedented architectural foundation. However, relying on a single reference genome introduces severe reference bias, as it fails to capture the immense structural variations (SVs), copy number variations (CNVs) and presence-absence variations (PAVs) harboured within wild relatives and traditional landraces. To overcome this, vegetable genomics has rapidly transitioned toward pan-genomics. Recent pan-genome assemblies in tomato and cucumber have revealed that hundreds of disease resistance (NBS-LRR) gene clusters and specialised secondary metabolic genes were lost during domestication bottlenecks. Graph-based pan-genomes capture the complete dispensable and core genome repertoire, allowing breeders to identify and re-introgress valuable wild alleles. Furthermore, haplotype-led breeding is superseding individual SNP markers: by characterising conserved haplotype blocks across target chromosomal segments, breeders can select optimal multi-allelic combinations, avoiding detrimental recombination events and linkage drags (1, 5, 8).

Genome wide association studies and genomic selection

The GWAS circumvents the low allelic diversity and extensive generation requirements of bi-parental QTL mapping by exploiting historical recombination events across diverse natural germplasm panels. Genome wide association studies maps quantitative trait nucleotides (QTNs) with single-base resolution. The GWAS has successfully dissected soluble solids content in *B. napus* shoots (44), insect-deterrent trichome secondary metabolites in wild *Solanum* species (45) and fruit shape, rind thickness and bitterness loci across cucumber and watermelon germplasm collections (36, 46).

For highly complex polygenic traits such as marketable yield, water-use efficiency and shelf-life, genomic selection (GS) offers an indispensable strategy. The GS bypasses the need to identify individual QTLs; instead, it uses genome-wide marker profiles to estimate genomic estimated breeding values (GEBVs) for unphenotyped selection candidates based on models trained on a representative reference population (7). Incorporating parametric (GBLUP) and non-parametric machine learning models (Random Forest, Neural Networks) into GS algorithms enables vegetable breeders to conduct rapid recurrent cycles in off-season nurseries or speed breeding chambers, dramatically elevating annual genetic gain (5).

High throughput digital phenotyping and artificial intelligence

The phenomenal increase in genotyping throughput has shifted the primary breeding bottleneck from genotyping to phenotyping. High-throughput digital phenomics bridges this gap by deploying multi-spectral, hyperspectral, LiDAR and thermal infrared sensors mounted on automated greenhouse gantries, unmanned aerial vehicles (UAVs) and ground phenomobiles. In solanaceous crops, computer vision systems non-destructively measure canopy architecture, photosynthetic capacity, vegetative indices and early-stage disease manifestations long before visible symptoms emerge (5, 47). Artificial intelligence (AI) and deep learning algorithms process multi-dimensional imaging datasets to automate fruit size grading, blossom-end rot scoring and leaf curl symptom severity rating, delivering massive, objective phenotypic data matrices essential for high-accuracy genomic prediction models (5). The major molecular tools validated genes and QTLs, diagnostic markers and their applications in vegetable crops are summarised in Table 2.

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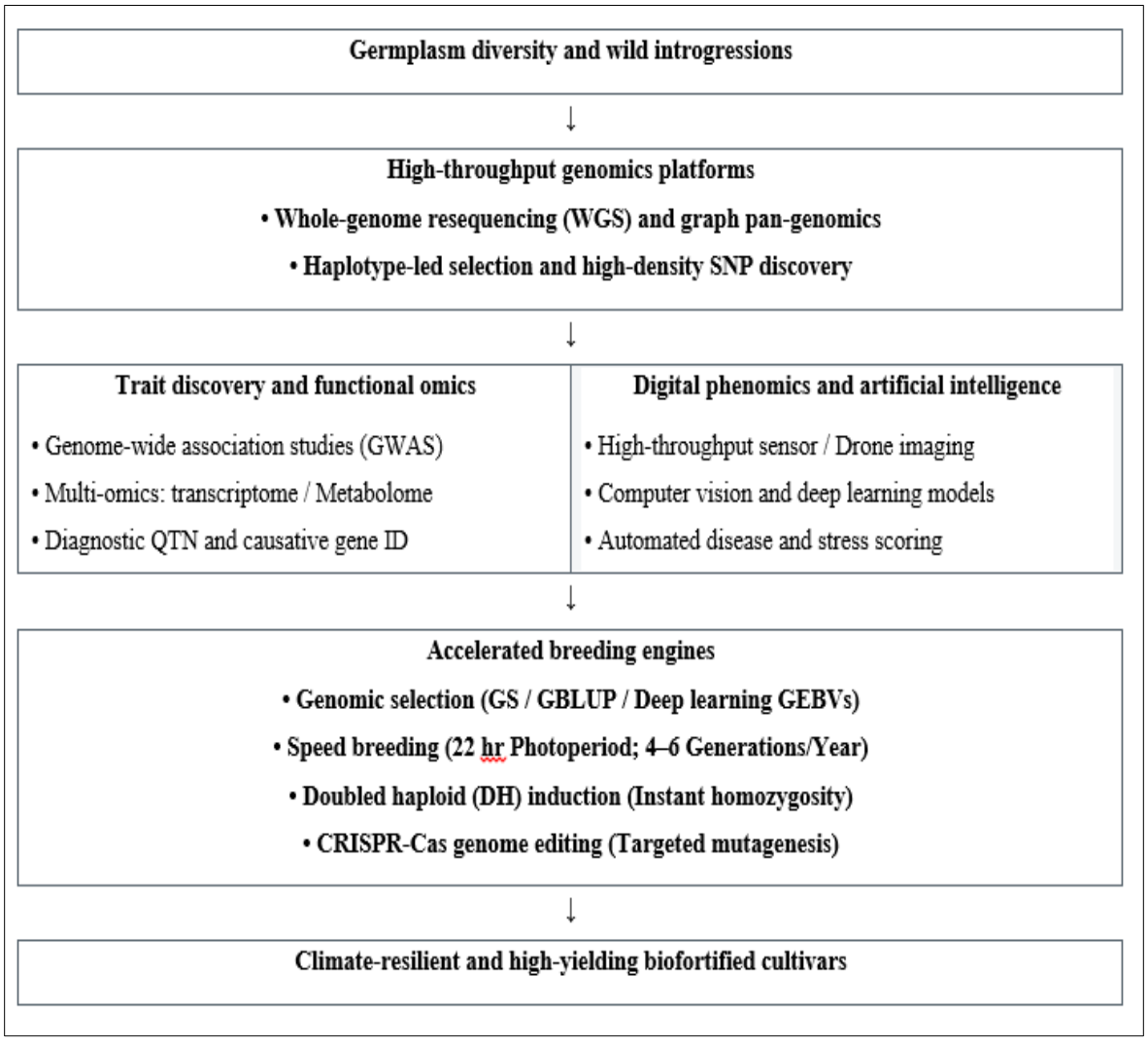


Fig. 1. Integrated pipeline of modern genomic and digital technologies in vegetable breeding.

Accelerating breeding cycles: Doubled haploids and speed breeding

A primary bottleneck in vegetable breeding is the extended timeline (6–8 generations) required to generate homozygous inbred parental lines. Two breakthrough methodologies directly address this challenge: DH technology and speed breeding protocols.

Doubled haploid technology: The DH technology achieves complete, stable homozygosity in a single generation through androgenesis (anther/microspore culture) or in vivo haploid induction mediated by centromere-specific histone H3 (CENH3) engineering or irradiated pollen. The DH lines are extensively utilised in commercial hybrid breeding of *Brassica* crops (cabbage, cauliflower and broccoli) and sweet pepper, drastically compressing breeding cycles and revealing recessive traits for rapid selection. However, recalcitrance to *in vitro* embryogenesis and high genotype-dependency remain operational hurdles in tomato, melon and cucurbits (1, 2).

Speed breeding protocols: Speed breeding accelerates plant development and floral transition by optimising environmental regimes employing continuous 22 hr photoperiods via specialised LED lighting, controlled diurnal temperatures and optimised nutrition. In pepper, tomato and brassicas, speed breeding reduces generation turnover to 60–75 days, permitting 4 to 6 generations per year instead of 1 to 2 in conventional field settings. Integrating speed breeding with marker-assisted selection and genomic prediction allows ultra-rapid parent development and population fixation (5, 47).

Transgenic approaches and advanced genome editing (CRISPR-Cas)

Transgenic approaches have contributed historically to vegetable crop protection most notably the commercial deployment of Bt brinjal expressing Cry1Ac endotoxin for devastating fruit and shoot borer (*Leucinodes orbonalis*) resistance in South Asia. However, extensive regulatory constraints, consumer resistance and high commercialisation costs have constrained wide transgenic deployment across global vegetable production (3, 48).

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Table 2. Key molecular tools, validated genes/QTLs, diagnostic markers and their applications in vegetable crops

Crop	Trait / Breeding target	Gene / QTL / Marker identified	Chromosome / linkage group	Key reference
Tomato	Tomato leaf curl virus resistance	Ty-1, Ty-2, Ty-3, Ty-4, Ty-5, Ty-6 (P6-25, SCAR-1)	Chr 6, 11, 4, 3	(10)
	Powdery mildew resistance	ol-1 (RAPD, SCAR)	Chromosome 6	(11)
	Tospovirus resistance	Sw-5b (Effector epitope markers)	Chromosome 9	(12, 14)
	Functional male sterility	ps, ps-2 (CAPS: C4-30, C2-21)	Chromosomes 2 and 4	(24)
	Parthenocarpic fruit set	pat, pat4.1, pat4.2, pat5.1, pat9.1	Chromosomes 3, 4, 5, 9	(31)
	Fruit shape and architecture	sp, s, j-2 genes; Lycopene QTLs	Chromosomes 6 and 12	(38)
Cucumber	Powdery mildew resistance	pm1.1, pm2.1, pm4.1, pm6.1	LG 1, 2, 4, 6	(9, 39)
	CMV and downy mildew resistance	dm1.1, dm5.1–dm5.3, dm6.1; CMV loci	LG 5 and 6	(15)
	Fruit size, shape, SLAF-seq	FS2.1, FS2.2, SLAF QTLs	LG 2 and 3	(37)
Watermelon	Powdery mildew resistance	MCPI_11, BVWS02441, CYSTSIN	Chromosome 2	(8)
	Fusarium wilt race 2 resistance	GBS-SNP linked QTLs	LG 1 and 9	(36)
Pumpkin	Nutritional quality and fruit traits	29 GBS/SLAF SNPs (carotenoids, TSS)	Multiple linkage Groups	(22, 44)
Melon	Parthenocarpy and SNP bin map	cmpat2.1, cmpat3.1; GBS SNP bin map	LG 2 and 3; Genome-wide	(32, 46)
Pepper	Male sterility (GMS)	ms3 (HPGMS2, HPGMS3), msw (SPGMS1)	LG 1 and 5	(25)
Cauliflower	Beta-carotene biofortification	*Or* gene (Co-dominant PCR)	Undesignated linkage	(21)
	Black rot and downy mildew	Pyramided Xca1bo + Ppa3	Multiple introgressions	(41)
Broccoli	Anthocyanin accumulation	BoMYB, BoTT8 candidate loci	Multiple Linkage Groups	(23)
Eggplant	Parthenocarpy and prickleless	Pad-1 locus; 0.5-kb InDel marker	Conserved Solanaceae locus	(33, 34)

QTL: quantitative trait locus; Chr: chromosome; SCAR: sequence-characterised amplified region; RAPD: random amplified polymorphic DNA; CAPS: cleaved amplified polymorphic sequence; CMV: cucumber mosaic virus; LG: linkage group; SLAF: specific-locus amplified fragment sequencing; GBS: genotyping-by-sequencing; SNP: single nucleotide polymorphism; TSS: total soluble solids; GMS: genic male sterility; HPGMS: hypoxia-induced genic male sterility; SPGMS: sporophytic genic male sterility; InDel: insertion–deletion; PCR: polymerase chain reaction.

CRISPR-Cas genome editing: The emergence of clustered regularly interspaced short palindromic repeats (CRISPR)-associated Cas endonucleases has revolutionised vegetable genetics by facilitating targeted, site-specific nucleotide mutagenesis without integrating foreign DNA into commercial lines (3). In tomato, knockout of the SlDMR6-1 gene conferred broad-spectrum resistance to bacterial speck (*Pseudomonas syringae*) and downy mildew without fitness penalties. Knocking out mildew resistance locus O (*MLO*) genes similarly induced durable powdery mildew resistance in cucumber and tomato (3, 4). Furthermore, editing the promoter elements of architectural genes (such as *SP5G* and *CLV3*) successfully *de novo* domesticated wild tomato relatives, converting sprawling indeterminate wild accessions into compact, early-maturing, highly productive plants suited for vertical indoor farms in just two generations. Beyond single knockouts, multiplex editing, base editing (converting C -> T or A-> G without double-strand breaks) and prime editing permit simultaneous tuning of fruit firmness, shelf-life, pedicel jointlessness and viral resistance (3, 5).

Epigenetics and synthetic biology for novel trait engineering

Epigenetics: Epigenetic regulation encompassing DNA methylation, histone modification and non-coding RNA pathways represent an essential layer of phenotypic diversity independent of DNA sequence alteration. In vegetable crops, epigenetic remodelling orchestrates thermal adaptation, floral timing and fruit ripening. For example, the non-ripening (Cnr) phenotype in tomato is driven by hypermethylation in the promoter of an *SBP-box* gene. Selecting and stabilising stress-induced epi-alleles ('epigenetic memory') offers an untapped non-transgenic approach to breed climate-smart vegetables with enhanced drought and heat plasticity (49).

Synthetic biology and multi-omics: Synthetic biology applies engineering principles to design and construct novel biological circuits, refactored metabolic pathways and artificial genetic switches. In vegetable systems synthetic biology is pursued to reconstruct specialised health-promoting metabolites, introduce synthetic carbon-fixation bypasses to boost photosynthetic efficiency and engineer smart plant biosensors capable of emitting diagnostic fluorescence upon pathogen infection or nutrient deficiency. Coupling

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synthetic biology with multi-omics integration (genomics, transcriptomics, proteomics and metabolomics) allows systemic deciphering of metabolic fluxes establishing a direct link from DNA polymorphism to commercial organoleptic quality (1, 5, 47).

Limitations, knowledge gaps and future research priorities

Despite the remarkable technological breakthroughs achieved in molecular vegetable breeding, several technical, physiological and socioeconomic constraints must be addressed to ensure equitable impact:

1. High capital costs and infrastructural disparities: Next-generation sequencing platforms, high-throughput phenomics facilities and advanced bioinformatics pipelines require substantial capital investments. Public breeding institutions and regional seed enterprises in developing countries often lack access to these resources, maintaining a technological divide between industrialised and emerging economies (1, 2). Developing cost-effective, low-plex targeted genotyping platforms (e.g., KASP or targeted GBS panels) is essential to democratise molecular tools.

2. Polygenic inheritance and G × E interactions: Marketable yield, abiotic stress resilience and post-harvest culinary qualities are governed by hundreds of minor-effect loci exhibiting substantial epistatic (G × G) and environmental (G × E) interactions. Marker predictive power established in one genetic background or environment frequently collapses when deployed across divergent field conditions, requiring robust multi-environment validation models (7).

3. Transformation recalcitrance *in vitro* systems: While genome editing is routine in model tomato accessions, many elite commercial lines of pepper, watermelon, melon, cabbage and *Alliums* remain highly recalcitrant to *in vitro* tissue culture regeneration. Developing genotype independent transformation technologies such as developmental regulator gene overexpression (Wuschel2, Baby boom) or nanoparticle-mediated delivery of ribonucleoproteins (RNPs)-represents an urgent research priority (3, 4).

4. Regulatory frameworks and international harmonisation: Regulatory disparities regarding SDN-1 and SDN-2 genome-edited crops across different global jurisdictions create severe non-tariff trade barriers. Clear, harmonised, science-based policies distinguishing non-transgenic gene-edited crops from genetically modified organisms (GMOs) are imperative to encourage private and public investment in commercial vegetable enhancement (3, 5).

4. Conclusion

Molecular breeding has revolutionised vegetable crop improvement, transitioning selection methodologies from empirical phenotypic selection to precise, sequence-driven genetic enhancement. The integration of diagnostic molecular markers, saturated linkage maps and marker-assisted gene pyramiding has resolved long-standing breeding challenges in biotic resistance, male sterility exploitation and nutraceutical biofortification across solanaceous, cucurbitaceous and cruciferous crops. Moreover, the convergence of genomic selection, pan-genomics, doubled haploid technology, speed breeding and clustered regularly interspaced short palindromic repeats (CRISPR)-Cas genome editing provides an agile, multidisciplinary framework to engineer high-yielding, climate-resilient cultivars. Overcoming persistent bottlenecks specifically tissue culture recalcitrance, phenomics throughput and infrastructural access in resource-limited breeding programmes must remain a global research priority. Ultimately, the synergistic integration of classical breeding expertise, molecular genomics and artificial intelligence (AI)-powered digital technologies will serve as an indispensable cornerstone for sustaining global food security, climate resilience and nutritional wellbeing under accelerating environmental challenges.

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Authors' contributions

AC, DS and RS conceptualised and designed the study. RK^1 and RK^2 developed methodology. AC prepared and wrote the original manuscript draft. NG, AS, S^1, S^2 and PS contributed to writing, reviewing and editing the manuscript. All authors have read and approved the final manuscript [RK^1 stands for Rajeev Kumar and RK^2 stands for Reena Kumari; S^1 stands for Srishti and S^2 stands for Shivani].

Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT to improve language polishing, grammar correction, sentence structure and enhancement of readability. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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