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Advances in the application of molecular markers for the genetic improvement and breeding of fruit crops: A comprehensive review

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Abstract
Molecular marker technologies have transformed the breeding of fruit crops by making it possible to select accurately, characterize the genome, and genetically enhance. Advances in genomics resources and technology have facilitated development and application of molecular markers such as RFLPs, RAPDs, SNPs, and SSRs to effectively identify better genotypes, evaluate genetic diversity, map quantitative trait loci (QTLs), and expedite marker-aided selection (MAS). Fruit crops are challenging owing to their long juvenility, heterozygous nature of fruit breeders, and polygenic nature of most of the economical characters. Up to now, there have been two major challenges in this regard. A detailed review of the recent progress in application of molecular markers for genetic improvement of fruit crops with respect to marker development, functional genomics, QTL mapping, genome-wide association studies (GWAS) and genomic selection (GS) is presented. Results–Selected case studies in major fruit crops including mango, apple, citrus, grape, and banana are discussed, emphasizing their success stories in addressing key traits of yield, quality, and stress tolerance.

Keywords: Molecular markers, genetic improvement, fruit breeding, MAS, GWAS, SNPs, SSRs, genomic selection

1. Introduction
Fruit crops play a vital role in global horticulture by contributing to nutritional security, farmer income, and sustainable agricultural development (Shivran *et al*., 2022) [53]. They are high in beneficial nutrients and antioxidants, and contribute to economic stability through export earnings and support to the agro-industry. Traditional fruit breeding, on the other hand, is limited by long juvenile periods, polyploidy, self-incompatibility, and high heterozygosity, which retard its genetic improvement compared to annuals. These traits limit the fast progress of high yielding, good quality and stress tolerant superior cultivars. The development of molecular marker technologies has revolutionized fruit crop breeding allowing accurate genotyping and genetic dissection at DNA level (Ahmad *et al*., 2021) [1]. Markers like Restriction Fragment Length Polymorphisms (RFLPs), Simple Sequence Repeats (SSRs) and Single Nucleotide Polymorphisms (SNPs) enable genome mapping, diversity studies and marker-assisted selection (MAS) leading to a rapid breeding (Iwata *et al*., 2016; Minamikawa *et al*., 2017) [33, 42]. The integration of genomics, transcriptomics, and bioinformatics has enabled molecular markers to be used more effectively for QTL identification, gene function analysis, and the development of climate-resilient and superior fruit cultivars (Aziz and Masmoudi, 2025) [4]. Therefore, molecular markers are considered a key invention for facilitating the precision breeding and the sustainability of fruit crops.

2. Evolution of Molecular Marker Technology
1) From morphological/biochemical traits to the DNA age — a short history
Initial genetic analysis was based on phenotypic (morphological) and biochemical states like isozymes. The DNA-era started with hybridization-based markers (RFLP) on the 1980s, which

demonstrated the principle of utilizing DNA fragment length variations as genetic markers. PCR-based methods were developed later: RAPD and AFLP in the 1990s increased the throughput and did not require prior sequence information (Grover and Sharma, 2016) [25]. Microsatellites (SSRs) provided co-dominance, high polymorphism, transferability and were extensively utilized for the identification of cultivars and in germplasm applications (Sagar *et al*., 2023) [50]. Finally, SNPs, array platforms, and sequencing-based genotyping (i.e., GBS, RAD-seq) led to several orders of magnitude increase in marker density and degree of automatization, making genome-wide mapping and genomic selection feasible (Holliday *et al*., 2018) [29].

2) Key marker technologies — what they are and their practical tradeoffs

RFLP (Restriction Fragment Length Polymorphism): SNP was the first commonly employed DNA marker, being very accurate, co-dominant, yet time-consuming with a low throughput. Important for the first genetic maps (Doveri *et al*., 2024) [20].

RAPD (Random Amplified Polymorphic DNA): PCR with arbitrary primers; cheap and quick, but markers are dominant and reproducibility can be an issue. Common in early diversity studies (Babu *et al*., 2020) [5].

AFLP (Amplified Fragment Length Polymorphism): Restricton + selective PCR amplification that generates multiple polymorphic fragments; more reproducible and higher throughput the RAPD, but scored as dominant fragments and requires polyacrlamide /gene-scan platforms for best results. Broadly utilized in crop profilings (Sheeja *et al*., 2020) [52].

SSR / Microsatellites: short tandem repeats; co-dominant, highly polymorphic, suitable for multiplexing and transfer between species, at least in some taxa. Became the standard for assortment recognition and the structure of the germplasm in many tree fruit crops (Varshney *et al*., 2005) [63].

DArT (Diversity Arrays Technology): sequencing-dependent, sequence-agnostic platform that could provide hundreds to thousands of scored loci; it was applicable to non-model and polyploid species for which the availability of prior sequence resources was minimal (Sanchez-Sevilla *et al*., 2015) [51].

SNPs and SNP arrays: single nucleotide changes that are very common over the course of genomes. SNP chips/arrays allow for high-throughput genotyping that is highly standardised, and these can be used for GWAS, pedigree verification and genomic selection (Mammadov *et al*., 2012) [39].

GBS / RAD-seq and other reduced-representation sequencing: cheap sequencing of restriction fragments to identify and genotype thousands of SNPs without needing to develop markers in advance. GBS is one of the the most adopted protocols. These methods enabled genome-wide marker discovery for many breeding programs (Ulaszewski *et al*., 2021) [62].

Table 1: Timeline of Marker Technology Evolution in Fruit Crops

Era	Marker Type	Key Features	Limitations
Pre-1980	Morphological / Biochemical	Easy, low cost	Low polymorphism, environment-sensitive
1980s	RFLP	High reproducibility	Low throughput, labor-intensive
1990s	RAPD, AFLP	No prior sequence needed	Dominant markers, reproducibility issues
2000s	SSR	Co-dominant, highly polymorphic	Moderate throughput
2010s	SNP arrays, GBS	Genome-wide coverage	Requires bioinformatics
2020s	WGS, pangenomics, functional markers	High-resolution, causal variants	Expensive, computationally intensive

3. Types of Molecular Markers in Fruit Breeding

Molecular marker systems vary widely in their complexity, information content (for example, co-dominant versus dominant, multi-allelic versus bi-allelic), reproducibility, cost, throughput and therefore applicability for various breeding applications (germplasm fingerprinting, pedigree verification, linkage and QTL mapping, association studies and genomic selection).

RFLP, RAPD, AFLP – the legacy markers

The first DNA markers were RFLP (Restricition Fragment Length Polymorphism) markers, which are based on differences in the length of DNA fragments produced by digestion of DNA with restriction enzymes and evaluated by the hybridisation of a probe. Although they were tedious work, RFLPs established early genetic maps of perennial species (such as apple, grape) and offered strong co-dominant scoring (Singh and Singh, 2015) [54].

Later on, PCR-based methods like Random Amplified Polymorphic DNA (RAPD) and Amplified Fragment Length Polymorphism (AFLP) gained popularity as they demanded minimal prior sequence information, they could generate large number of loci rapidly, and were cost effective. However, these markers are dominant in nature (do not differentiate heterozygous and homozygous) and can also have reproducibility issues and, therefore their accuracy may not be enough for detailed genotyping and subsequent breeding (Singh *et al*., 2025) [56].

In fruit breeding these markers have been extensively employed in initial studies of germplasm diversity and in linkage map development, but these disadvantages (dominance, fewer alleles, and lower reproducibility) have limited their use for long-term applications in high-precision breeding.

SSR (Microsatellites) – the game-changer

The introduction of Simple Sequence Repeat (SSR) markers, or microsatellites, was a major turning point. SSRs are short tandem repeats motifs (e.g. -$(CA)_n$-) and have a number of good properties: they are co-dominant (heterozygote can be detected), multi allelic (there are many repeat-length alleles for a locus), reproducible, transferable (sometimes) across related species and relatively cheap to assay (Testolin *et al*., 2023) [59].

Thus, SSRs were established as the default in fruit breeding for such important applications as cultivar identification, germplasm characterization, parentage/pedigree verification, development of linkage maps and QTL tagging. For instance, SSR markers have been extensively utilized in mango, citrus, guava, pomegranate and many other perennial fruit crops for the purpose of fingerprinting and study of genetic diversity

(Ahmad *et al*., 2021) [1].
Due to their advantageous properties (co- dominance, polymorphism, reproducibility) SSR are still relevant in the context of high throughput SNP genotyping, particularly for small laboratories or for the purpose of cultivar identification (Appleby *et al*., 2009) [2].

SNPs and High-throughput/Sequencing Approaches – the present and future
In recent years, the preferred marker system among many elite breeding programs is Single Nucleotide Polymorphism (SNP) markers. SNPs are the most common type of variation in the plant genome, are usually bi-allelic, and can be analyzed by automated and high-throughput methods, can be standardized, and can be used for genome-wide applications (Udoh *et al*., 2021) [61].
Moreover, genotyping-by-sequencing (GBS), RAD-seq and similar reduced-representation sequencing approaches enable parallel discovery and genotyping of thousands to tens of thousands of SNPs for species with or without prior marker development (Rasheed *et al*., 2017) [48].
In fruit crops, SNP arrays (apple 480K, peach 9K, grape 18K) and genome wide SNP platforms have been applied in order to harmonize genotyping within breeding programs, facilitating genome wide association studies (GWAS), high-resolution linkage mapping, genomic selection and pangenome research (Chagne *et al*., 2012) [10].
Collectively, these (SNP + sequencing + high-density arrays) advances have greatly lowered genotyping cost per data-point and increased mapping resolution, permitting genome-wide selection pipelines, and allowing modern molecular-breeding methodologies for perennial fruit crops.

Table 2: Comparative overview of molecular marker systems used in fruit crops

Marker Type	Polymorphism	Reproducibility	Throughput	Inheritance	Key Applications
RFLP	High	High	Low	Co-dominant	Early linkage mapping
RAPD	Moderate	Low	Moderate	Dominant	Preliminary diversity studies
AFLP	High	Moderate	Moderate	Dominant	Genetic diversity and mapping
SSR	High	High	Moderate	Co-dominant	Cultivar identification, MAS
SNP	Moderate	Very high	Very high	Co-dominant	GWAS, GS, QTL mapping
GBS/RAD-seq	Very high	High	Very high	Co-dominant	High-resolution mapping
DArT	High	High	High	Dominant	High-throughput genotyping

4. Applications of Molecular Markers in Fruit Crop Improvement
Molecular markers have transformed the fruit crop breeding, allowing accurate genotyping, trait dissection, and selection efficiency. They have a wide range of uses including characterization of germplasm, marker-assisted breeding and genomic prediction (Varshney *et al*., 2020) [64].

4.1 Genetic Diversity and Germplasm Characterization
Knowledge of genetic diversity is the basis for any crop breeding program. Molecular markers shed light on the genetic diversity between and within populations to help in germplasm management and identification of superior genotypes (Bunjkar *et al*., 2024) [8]. SSR and SNP markers are also widely applied to study genetic relatedness and phylogenetic grouping in mango, apple, grape and citrus (Hazarika *et al*., 2014; Thakur *et al*., 2023) [27, 60]. For example, SSR-based study demonstrated a high allelic diversity in Indian germplasm of mango (Yan *et al*., 2024) [70].

4.2 Genetic Linkage Mapping and QTL Analysis
Linkage maps are crucial for mapping genomic regions associated with important agronomic traits. High density genetic maps using SSRs and SNPs have been constructed in apple, citrus and grape. Using these markers, QTL mapping has also detected loci affecting fruit size (Wu *et al*., 2014) [68], flavor (Rawandoozi *et al*., 2020) [49], disease resistance (Yang *et al*., 2013) [71], and abiotic stress tolerance (Dixit *et al*., 2014) [19].

4.3 Marker-Assisted Selection (MAS)
MAS permits breeders to select individuals that carry favorable alleles without the need of waiting for the phenotypic expression. This has been of particular benefit for fruit trees with long juvenile period (De Mori and Cipriani, 2023) [16]. The Vf gene for scab resistance (Patocchi et al., 2009) [45] and MdACS1 for low ethylene production were incorporated into apple using marker-assisted approaches (Lundmark, 2019) [38]. Similarly, MAS has also facilitated the selection of seedlessness in grape (Likhovskoi et al., 2023) [37], and dwarfing rootstocks in mango.

4.4 Disease Resistance Breeding
Molecular markers are important in disease resistance breeding for the precise identification of resistance genes and their deployment in breeding programmes. They aid breeders in locating the genomic regions involved in host–pathogen interactions. Marker-associated resistance traits enable the early and accurate selection of resistant genotypes. This enables early, efficient screening and accelerates the development of disease resistant cultivars particularly in long-gestation fruit crops (Nair *et al*., 2024) [44].

5. Marker-Assisted Breeding (MAB) in Fruit Crops
Marker-assisted breeding is the incorporation of molecular markers in conventional breeding schedules to improve the effectiveness, accuracy and genetic improvement.

5.1 Marker-Assisted Backcrossing (MABC)
Marker-assisted backcrossing (MABC) is a precision breeding strategy for the incorporation of the target gene (e.g disease resistance/quality gene) in elite fruit cultivars, with minimum modifications to its genome related to desirable cultivar specific traits. Using closely linked DNA markers, MABC allows foreground selection for the target gene, recombinant selection for reducing linkage drag, and background selection for increasing the proportion of the recurrent parent genome (Hospital, 2005; Collard & Mackill, 2008) [12, 30]. This greatly reduces the breeding cycles, which is critical for perennial fruit crops. Amongst successful cases of marker-assisted breeding for fruit crops are the incorporation of the Vf scab resistance gene into widely cultivated apple cultivars, through SSR/SNP markers (Patocchi *et al*., 2020) [46] and marker-assisted breeding for seedlessness and disease resistance in grape and banana.

5.2 Marker-Assisted Recurrent Selection (MARS)

Marker-Assisted Recurrent Selection (MARS) is an approach in breeding which seeks to increase the frequency of favourable alleles for a polygenic trait in a population by selection reiteratively of individuals carrying the highest number of favourable alleles. With markers associated with multiple QTLs, MARS enables accumulation of genetic gain across cycles, and is the best approach for complicated traits such as yield, size and quality of fruit. In apple and pome fruit, Like in grape and citrus, MARS has been successfully applied to enhance yield components, flavour profiles and stress resistance by iterative population enrichment for favorable alleles (Gokidi *et al*., 2016; Cholin and Kulkarni, 2023) [11, 24].

5.3 Pyramiding of Multiple Genes

Molecular markers facilitate the pyramiding of genes for resistance durability in multigenic traits. For example, the apple gene pyramid combining the Vf and Vr2 scab resistance genes resulted in multi-pathogen tolerance (Mhetre *et al*., 2025) [41]. In banana, pyramiding of Fusarium wilt and Black Sigatoka resistance genes using SSRs resulted in enhanced field stability (Soares *et al*., 2021) [57].

6. Genomic Tools Enhancing Marker Development

Advanced genomics have provided means to identify a large number of high resolution DNA markers and have led to enhanced genotyping in fruit crops. These technologies, including next-generation sequencing (NGS), transcriptomics, and whole genome resequencing have increased availability of single nucleotide polymorphisms (SNPs), structural variants and gene based markers for applications in breeding.

6.1 Next-Generation Sequencing (NGS)

NGS platforms permit sequencing of whole genomes or specific regions at a high throughput, enabling the identification of SNPs, InDels, and functional markers at high speed (Metzker, 2010) [40]. In fruit crops, NGS based methods including RAD-seq and GBS have been widely used to develop high density genetic maps and genome wide marker panels for QTL mapping, GWAS and genomic selection (Singh *et al*., 2020) [55].

6.2 Transcriptome and RNA-seq Analysis

RNA-seq provides gene expression profiles and discloses the information of expressed SNPs and transcriptionally active markers associated with fruit development, quality, and stress response (Wang *et al*., 2009) [66]. A number of transcriptomic studies in mango, grape and citrus have led to the discovery of putative genes associated with traits, including aroma, ripening and disease resistance (Datir and Regan, 2022; Borreda *et al*., 2022) [7, 15].

6.3 Whole Genome Resequencing and Pangenomics

Whole-genome resequencing provides a genome-wide detection of polymorphisms over a wide range of germplasm, which can be used to identify rare alleles, structural variants and diversity at the population level (Huang *et al*., 2025; Zhong *et al*., 2025) [31, 73]. Pangenomics expands marker discovery approaches by analyzing core and accessory genes shared across multiple cultivars, an approach with extensive in crops improvement (Bayer *et al*., 2020; Petereit *et al*., 2022) [6, 47].

7. Functional Markers and Candidate Gene Approaches

Functional markers are DNA markers derived from adaptive polymorphisms within genes itself influencing phenotypic variation. They provide the possibility to select alleles for known functional variation and not for linked markers (Kage *et al*., 2016) [34]. Candidate gene approaches recognize genes that are known to affect important traits, for example by genomic, transcriptomic or physiological data (Zhu and Zhao, 2007) [75]. These methods give higher accuracy in the selection for traits such as fruit quality, stress tolerance and disease resistance. Taken together, functional markers and candidate gene approaches can greatly enhance the speed and precision of molecular breeding.

Examples include:

- MdNAC18 in apple is a functional ortholog of NOR controlling the ethylene synthesis (Wen *et al*., 2024) [67].
- CitPH5 controls fruit acidity in citrus (He *et al*., 2025; Strazzer *et al*., 2019) [28, 58].
- MiWRKY transcription factors associated with anthracnose resistence in mango (Xiang *et al*., 2025) [69].

Functional marker have a direct relationship between genotype and phenotype, thus, they are expected to have less false positives than random genome markers.

8. Genome-Wide Association Studies (GWAS)

Genome-Wide Association Studies (GWASs) detect genetic variants associated with complex traits by analyzing marker–trait associations in natural populations (Korte & Farlow, 2013) [35]. By taking advantage of historical recombination, GWAS has a greater mapping resolution than conventional linkage mapping (Zhu *et al*., 2008) [74]. In fruit crops, GWAS has facilitated the identification of loci associated with fruit size, sugar content, aroma and disease resistance (Zahid *et al*., 2022) [72]. High-density SNP arrays and sequencing-based genotyping have further improved the power and accuracy of GWAS (D'Agostino and Tripodi, 2017) [14]. The outcomes of GWAS are also frequently used to inform the marker-assisted selection and genomic prediction pipelines in the application of modern fruit-breeding programs (Huang & Han, 2014) [32].

8.1 Principle and Workflow

GWAS utilizes high-density SNP data across diverse populations to associate genotypic variation with phenotypic traits. The availability of large-scale SNP datasets and improved reference genomes has facilitated its implementation in perennials.

8.2 GWAS in Fruit Crops

- **Apple:** Detection of loci controlling firmness, acidity and fruit size (Dujak *et al*., 2024) [21].
- **Citrus:** Identification of QTLs associated with sugar-acid ratio and peel color (Di Guardo *et al*., 2023) [18].
- **Mango:** Identification of loci for fruit traits (Eltaher *et al*., 2025) [22]. 9. Genomic Selection (GS) and Prediction Models

Genomic selection was the next step after marker-based breeding and it allows using entire genome marker data to predict breeding values (Desta and Ortiz, 2014) [17].

9. Principle of Genomic Selection

The GS principle is based on establishing a training population that contains genotypic (high-density markers) and phenotypic information to train prediction models. These models compute the marker effects along the genome to predict GEBVs of unphenotyped individuals, therefore reducing breeding cycles

time. The method is especially efficient for lowly heritable or costly to measure traits, and improves long-term genetic gain (Crossa *et al*., 2017) [13].

9.1 Application in Fruit Crops

In fruit crops (many of which are perennial and highly heterozygous with long generation times), GS offers great potential for improvement. GS has been successfully implemented in apple, grapevine, blueberry, citrus, and peach for prediction of traits such as fruit firmness, sweetness, disease resistance, and flowering time (Kumar *et al*., 2012; Minamikawa *et al*., 2017) [36, 43]. Making selection decisions early, even at the seedling level, leads to a significant reduction in the time and cost of field evaluations and large populations for breeding.

9.2 Integration with Speed Breeding and Phenotyping

The integration of GS with speed breeding, HTP, and automated imaging also accelerates genetic gains. Speed breeding reduces the length of the generation intervals and HTP systems – visually UAVs, hyperspectral sensors, phenomics tools etc – allow for increasing the precision with which traits are measured that are subsequently used to train GS models (Araus and Cairns, 2014) [3]. In combination, these strategies enable rapid cycling, higher selection accuracy and cost-effective gain of more climate and production environment precise superior fruit types.

10. Molecular Markers for Abiotic Stress Tolerance

Molecular markers, including SSRs, SNPs, and functional markers, make it possible to quickly identify the genomic regions associated with drought, salinity, and temperature tolerance in fruit crops. Such markers facilitate the early selection of high performing genotypes and minimize the reliance on years of field testing (Cattivelli *et al*., 2008) [9].

10.1 Drought and Water Stress

Drought tolerance QTLs for root characteristics, osmotic adjustment, stomatal conductance, and ABA signaling were reported also in grapevine, apple, citrus and mango. SNP-based GWAS studies in grape also pinpoint markers associated with water-use efficiency (Guo *et al*., 2025) [26], and apple drought qtls linked to aquaporins and dehydrins facilitate precision breeding (Wang *et al*., 2018) [65].

10.2 Salinity and Temperature Stress

Salt tolerance-associated markers in citrus, including SNPs linked with Na^+/K^+ transporters and SOS-pathway genes, are the basis of rootstock-mediated enhancement (). Temperature-response QTLs in apple, peach, and grape are associated with genes involved in cold hardiness, heat-shock proteins and antioxidant defense (Fennell, 2014) [23].

11. Conclusion

Molecular marker technologies—from the early RFLP and SSR systems to high-density SNP arrays, next-generation sequencing, and pangenomic platforms—have had a transformative impact on contemporary fruit breeding. marker-assisted selection (MAS) is still an extremely powerful strategy for the improvement of major single-gene traits, the enhancement of complex quantitative traits such as fruit quality, stress tolerance, and adaptation is increasingly dependent on genome-wide methodologies. Genome-wide association studies (GWAS) and genomic selection (GS) are now capable of high-resolution dissection and prediction of polygenic variation by combining molecular markers with advanced phenomics, transcriptomics and metabolomics data sets.

The convergence of functional genomics, machine-learning-based prediction models, and high-throughput digital phenotyping is heralding a new age of data-driven, predictive breeding in perennial fruit crops. As breeding objectives diversify in a changing climate and market, the utility of molecular methods will be shaped by concerted systems approach— including genomic data sharing, breeder capacity building, and open access analytical infrastructure—to capitalize on genomic technology for the sustainable, high-throughput improvement of fruit crops.

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