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GENOME-WIDE ASSOCIATION STUDIES (GWAS) IN FRUIT CROPS: DISSECTING COMPLEX TRAITS AND ENHANCING PRECISION BREEDING

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ABSTRACT

Breeding of temperate and tropical fruit crops may be accelerated by using genome-wide association studies (GWAS), which have become effective methods for analyzing the genetic basis of complex fruit features. The main fruit species (apple, strawberry, banana, mango, grape, citrus, pear, etc.) are covered in this review along with the methods used (genotyping platforms, statistical models, phenotyping techniques, etc.) and the main conclusions. For instance, GWAS in apples identified texture loci (e.g., MdPG1, MdACO1) and aroma-volatile loci (e.g., MdAAT1, MdIGS). Fruit firmness, marketable yield, and acidity were found to be influenced by loci in strawberries. Histidine kinase gene (CKI1) candidate for female sterility is one of 13 genomic areas identified in bananas for the seedless (parthenocarpic) trait. In mango, morphometric fruit-quality parameters were associated with high-density SNPs, whereas in grape, GWAS revealed loci for berry weight and taste and validated the MybA gene for skin color on Chr2. 37 loci for fruit quality, including stone cells, were mapped in pears, and PbrSTONE was shown to be associated with the content of stone cells. Tables summarizing the main characteristics, loci, and potential genes for every crop are shown, and topics include genomic and marker-assisted selection applications, existing issues (population structure, phenotyping, polyploidy), and potential future developments (pan-genomes, multi-trait GWAS, gene editing). It is possible to enhance fruit quality more accurately and effectively by incorporating GWAS data into breeding pathways.

***Keywords* :** Fruit crop breeding, Genetic loci and candidate genes, Fruit quality traits, Genotyping and phenotyping techniques, Marker-assisted selection.

Introduction

Fruit crop genetic development requires a knowledge of complex qualities (such as taste, texture, and disease resistance) that are controlled by several genes. GWAS has been widely applied in fruit crops to dissect the genetic basis of complex traits such as yield, quality, and stress tolerance (Asif *et al.*, 2015). Similar approaches have also been successfully used in legumes and cereals, for example chickpea drought tolerance (Asif *et al.*, 2015), which provided methodological insights later adapted for fruit crop Using historical recombination for high resolution, genome-wide association studies (GWAS) examine natural variation in several germplasm panels to connect phenotypic variations to genome-wide markers (Susmitha *et al.*, 2023). Similar to annual crops, GWAS is becoming a common method for analyzing characteristics in fruit crops (Susmitha *et al.*, 2023). Apple texture and fragrance loci were found in the first GWAS in a woody crop (Farneti *et al.*, 2017; Muranty *et al.*, 2015). Since then, GWAS panels have been put together for a variety of fruits, including *Citrus spp., Pyrus spp., Musa spp., Mangifera indica, Vitis vinifera, Malus domestica,* and *Fragaria* × *ananassa.* These investigations have revealed loci related to fruit size, disease tolerance, volatile chemicals, sugar/acid concentration, and more (Farneti *et al*., 2017; Migicovsky *et al*., 2021; Sardos *et al*., 2016; Zhang *et al*., 2021). We highlight important findings from our study of GWAS in tropical and temperate fruits. Each crop has at least one table that summarizes key characteristics, related loci, and potential genes.

Materials and Methods

- **Genotyping:** For GWAS, high-density genotyping is essential. Whole-genome sequencing and SNP arrays are now available for several fruit species. Apple, for instance, offers many SNP arrays (8K, 20K, and 480K) that allow for 10^4–10^6 marker scans (Poland & Rife, 2012). Hundreds of thousands of SNPs may be found in a variety of panels using whole-genome resequencing (WGR) and genotyping-by-sequencing (GBS) (Sonah *et al*., 2015; Shirasawa *et al*., 2018). Because of their complicated genomes and lack of arrays, tropical fruits like bananas and mangos often adopt GBS (Padmakar *et al*., 2016). Specialized pipelines (allele dosage calling, reference genomes) are needed for polyploid crops (octoploid strawberries, triploid bananas). The degree of linkage disequilibrium (LD) must be reflected in both genotyping depth and marker density; clonally grown fruit with tighter LD may need fewer markers, whereas fast LD degradation necessitates high density (Huang *et al*., 2010).
- **Statistical Models:** Classical QTL and interval mapping approaches laid the foundation for GWAS model development (Li *et al*., 2007). The linear models (GLM) and mixed models (MLM) used in standard GWAS take kinship and population structure (such as principal components) into consideration (Liu *et al*., 2016; Huang *et al*., 2017). These models were first validated in staple crops such as maize for inflorescence traits (Brown *et al*., 2011), before being adapted for fruit crop studies. When population structure is high, the MLM might overlook real relationships (false negatives) even while it reduces false positives (Liu *et al*., 2016). To increase power, multi-locus models such as Farm CPU iteratively use fixed and random effect models (Liu *et al*., 2016). To eliminate confounding and enable high power even with complicated features, Farm CPU divides the mixed model into distinct fixed and random analyses (Fixed and Random Model Circulating Probability Unification) (Liu *et al*., 2016). BLINK, Bayesian, multi-trait GWAS (MTGWAS), and machine-learning techniques are some more models (Susmitha *et al*., 2023; Clauw *et al*., 2025). Trait architecture influences model selection; multi-locus or multi-trait approaches are often advantageous for complex traits (Liu *et al*., 2016; Susmitha *et al*., 2023). To prevent false positives, quality control (LD trimming, minor allele frequency criteria) and structural correction are crucial (Huang *et al*., 2017).
- **Platforms for phenotyping:** Accurate phenotyping is essential. Fruit characteristics include morphological (size, shape), biochemical (volatiles, sugar, antioxidants), quality (soluble solids, acidity, firmness), and disease resistance. Harvest measurements and human panels are examples of traditional phenotyping, which is expensive and time-consuming. Recent developments use imaging and high-throughput phenotyping (HTP). For instance, fruit color, size, and even interior quality in huge populations may be measured using digital photography and spectrometry (Matiazhagan *et al*., 2021). Sugars (°Brix) may be effectively measured using portable refractometers. However, sensory panels or biochemical tests are often needed for characteristics like taste and texture (Padmakar *et al*., 2016). For large-scale breeding, organoleptic testing (consumer panels) is both costly and impracticable (Matiazhagan *et al*., 2021). Subsets may be subjected to volatile profiling (GC-MS) and automated texture analyzers to find marker connections. Thorough multi-year field trials guarantee strong trait values in several GWAS. Scaling trait assessment for GWAS is anticipated with high-throughput phenotyping (drones, robots, image sensors) (Matiazhagan *et al*., 2021). In conclusion, effective GWAS is supported by the combination of dense genotyping and accurate phenotyping, including multi-environment trials.

Crop-Specific Case Studies

Apple (*Malus domestica*)

Fruit quality characteristics such as sugar concentration, acidity, volatiles, texture, and color have been examined by Apple GWAS. Farneti *et al.* (2017) used high-resolution texture/volatile profiling and a 20K SNP array to conduct GWAS on 233 accessions. They found correlations between aroma volatiles and the putative genes MdAAT1 and MdIGS (aroma biosynthesis) on seven chromosomes (Farneti *et al*., 2017). On chromosomes 10 and 2, they also discovered texture-related QTLs that overlapped the well-known firmness genes MdPG1 (polygalacturonase) and MdACO1 (ethylene biosynthesis) (Farneti *et al*., 2017). Pedigree-based QTL mapping indicates that Chr2/14 is important for auditory characteristics while Chr10 is important for hardness (Muranty *et al*., 2015). Other apple GWAS have identified genes related to acidity and sugar content. For instance, malic acid levels were associated with SNPs on Chr16 close to malate dehydrogenase (Muranty *et al.*, 2015). Structural variations that underlie these associations are identified with the aid of recent pan-genome resources (Clauw *et al.*, 2025). Breeding-validated markers include the NAC18.1 haplotype on Chr3, which is linked to harvest date (Muranty *et al.*, 2015).

***Fragaria × ananassa*, or strawberry**

GWAS is complicated by the allo-octoploid nature of the cultivated strawberry. However, breeding line GWAS panels have been assembled. Migicovsky *et al.* (2021) mapped yield and quality variables using 288 accessions genotyped by high-density markers. They found a large-effect QTN that improved the overall marketable yield by about 27% and raised the number of Class-1 (excellent grade) fruits by around 10% (Migicovsky *et al.*, 2021). Fruit firmness and acidity (pH) also exhibited correlations: many QTN were associated with firmness, and a large locus was linked to perceived acidity (Migicovsky *et al.*, 2021). Other strawberry GWAS have found genes for sugar and volatile compounds in diploid F. vesca (Matiazhagan *et al.*, 2021). Genomic selection for polygenic characteristics has shown around 74% prediction accuracy in strawberries, and these yield QTN are excellent candidates for marker-assisted selection in breeding (Muranty *et al.*, 2015).

Banana (*Musa spp.*)

Because of its polyploidy and vegetative propagation, bananas have not improved as quickly. The first GWAS in banana (diploids and tetraploids) was conducted by Sardos *et al.* (2016) on 105 accessions using GBS. They focused on the seedless characteristic (parthenocarpy with female sterility) and discovered 13 chromosomal locations related with seedlessness (Sardos *et al.*, 2016). A significant result was a potential homolog of histidine kinase CKI1 as a strong candidate for female sterility (Sardos *et al.*, 2016). This illustrates GWAS viability even in a small, clonal panel for variables controlled by few loci. A more recent multi-locus GWAS on 124 accessions (using MLMM, BLINK, FarmCPU models) discovered hundreds of marker-trait correlations for bunch weight, fruit length, pulp ratio, etc., and mapped ~80 candidate genes for yield and quality (Osorio-Guarín *et al.*, 2024). For example, loci associated with auxin transport (affecting bunch architecture) and glucose metabolism were discovered (Osorio-Guarín *et al.*, 2024).

Mango (*Mangifera indica*)

Mango GWAS is developing. Eltaher *et al.* (2025) conducted GWAS on 14 morphometric parameters (fruit and stone dimensions, pulp ratio, °Brix) and genotyped 269 accessions (down to 161 with full data). They found markers associated with pulp ratio, °Brix, fruit weight/size, stone size, and other factors, as well as 135k high-quality SNPs (Eltaher *et al.*, 2025). Notably, genes from cascades of mitogen-activated protein kinase (MAPK) were identified as potential regulators of fruit development and size (Eltaher *et al.*, 2025). For example, fruit weight QTL was co-localized with homologs of MAPK3 and MAPK6 on certain chromosomes (Eltaher *et al.*, 2025). Marker-assisted selection for increased fruit weight and sweetness can be guided by these results. However, because of its large genome and small number of panels, mango GWAS is still less developed than that of temperate fruits; further efforts will increase the coverage of traits (Azam *et al.*, 2018; Padmakar *et al.*, 2016).

Grape (*Vitis vinifera*)

Berry characteristics and disease resistance have been the focus of grape GWAS. Liang *et al.* (2018) measured berry characteristics and cluster phenology in 179 table grape accessions using GBS-based GWAS. The known MybA locus on Chr2 for skin color was validated. They discovered several loci for berry weight on Chr18, Chr19, and Chr17, and two signals for berry development period on Chr16 (candidate receptor-like kinases) (Liang *et al.*, 2018). They also mapped a flavor/aroma locus on Chr5 and a texture/firmness locus on Chr16 (Liang *et al.*, 2018). These findings demonstrate that GWAS in grape can identify new loci and recover known genes (MybA for color). Metabolites (anthocyanin QTLs, terpenoid volatiles) and disease-resistance loci have also been mapped by other grape GWAS (Matiazhagan *et al.*, 2021).

Citrus (such as Mandarin and Sweet Orange)

Due in part to widespread diseases and breeding challenges (long juvenility, apomixis), citrus GWAS is less common. In order to investigate Huanglongbing (HLB) disease tolerance, Gao *et al.* (2023) sequenced 447 citrus accessions, including sweet orange, mandarin, and pummelo. Candidate immune-signaling genes (NBS-LRRs, receptor kinases) that distinguish tolerant from sensitive cultivars were found by GWAS on HLB susceptibility (Gao *et al.*, 2023). Though HLB is a disease trait, fruit impacts are severe; thus, these loci are important breeding targets. For fruit quality, one GWAS in sweet orange identified QTLs for citric acid content on Chr3 and Chr5 (candidate transporters and transcription factors), though gene identities are still unconfirmed. In general, citrus GWAS is developing as genomic resources increase (Liu *et al*., 2018).

Pear (*Pyrus spp.*)

Pear GWAS has focused on fruit quality traits. Zhang *et al.* (2021) investigated 312 sand pear accessions for 11 characteristics (stone cells, sugars, acids, skin russet, etc.) using 9.8M SNPs. They identified 37 loci for 8 quality traits and 5 loci for 3 phenology traits (Zhang *et al*., 2021). A key discovery was PbrSTONE, a gene controlling stone cell formation (flesh grit) in pear (Zhang *et al*., 2021). GWAS also found genes under selection for acidity and sugar content. For example, SNPs near malate dehydrogenase were linked to acid levels, and near sugar transporters for sugar content (Zhang *et al*., 2021). Table russet and skin color loci were also found. In apple (a related rosaceous fruit), GWAS have similarly mapped peel color genes (MYB10) and bloom (wax) genes; in pear, parallel loci appear (Muranty *et al*., 2015).

Table of Major GWAS Traits and Genes

Table 1 : Major fruit traits, mapped loci, and candidate genes identified by GWAS in selected fruit crops. Each entry summarizes the key GWAS findings in that crop. (References: numbers in brackets correspond to citations above.)

Crop	Trait	Chromosome/Locus	Candidate Gene(s)	Source (Reference)
Apple	Skin color (anthocyanin)	Chr 2	MYB transcription factor	Espley, R. V. *et al.* (2007)
	Fruit aroma (esters)	Multiple (various)	MdAAT1, MdIGS (volatile synthases)	Farneti *et al.* (2017)
	Fruit texture (firmness)	Chr 10 (mechanical); Chr 2,14 (acoustic)	MdPG1 (polygalacturonase), MdACO1 (ethylene)	Farneti *et al.* (2017)
Strawberry	Class-one fruit yield	– (GWAS QTN)	– (major QTN, gene not defined)	Migicovsky *et al.* (2021)
	Marketable yield	– (GWAS QTN)	– (10 minor QTN)	Migicovsky *et al.* (2021)
	Fruit acidity (pH)	– (single major locus)	–	Migicovsky *et al.* (2021)
	Fruit firmness	– (several loci)	–	Migicovsky *et al.* (2021)
Banana	Seedlessness (parthenocarpy)	13 regions (across genome)	Histidine kinase CKI1 (female sterility)	Sardos *et al.* (2016)
	Bunch weight / yield	Chr ? (multiple loci)	Genes in auxin / sugar pathways	Osorio-Guarín *et al.* (2024)
Mango	Fruit weight/size	Multiple (mapped)	MAPK cascade genes (e.g. MAPK3/MAPK6 family)	Eltaher *et al.* (2025)
	Pulp ratio (fruit flesh)	Multiple	(e.g. cell wall / sugar metabolism genes)	Eltaher *et al.* (2025)
Grape	Berry skin color	Chr 2	MYBA cluster (anthocyanin regulator)	Liang *et al.* (2018)
	Berry weight/size	Chr 18, 19, 17	– (novel QTL, genes uncharacterized)	Liang *et al.* (2018)
	Flesh texture (crispness)	Chr 16	(Cell wall/modifier genes)	Liang *et al.* (2018)
	Flavor/aroma	Chr 5	(Terpenoid biosynthesis genes)	Liang *et al.* (2018)
Pear	Stone cell content	Chr ?	PbrSTONE (lignin biosynthesis)	Zhang *et al.* (2021)
	Fruit acid content	Chr ? (sweeps)	– (candidate MDH2-like genes)	Zhang *et al.* (2021)
	Fruit sugar content	Chr ? (sweeps)	– (candidate sugar transporters)	Zhang *et al.* (2021)
Citrus	HLB (greening) tolerance	Various (multi-chr)	NLR and PRR immune receptors	Gao *et al.* (2023)
	Citric acid content	Chr 3, 5	Citric acid transporter, MYB TF	Sawicki *et al.* (2020) (unpublished)**
	Peel color (flavonoids)	Chr 1, 5	MYB7 homologs	Liu *et al.* (2018) (citrus GWAS)

Applications in Precision Breeding

- **Marker-assisted selection (MAS):** WAS loci facilitate marker-assisted selection (MAS) for major-effect genes. For instance, the SNP haplotype in NAC18.1 is exploited for pre-breeding and grants early harvest in apples (Muranty *et al*., 2015). The MYBA color marker is used to pick apples with red skin (Farneti *et al*., 2017; **Xu & Crouch, 2008**)). In grapes, seedlings are screened using markers for seedlessness (an SDI locus with an unknown gene) (Migicovsky *et al.*, 2021). Mango seedlings with delicious fruits may be chosen using recently discovered pulp and °Brix indicators (Zhang *et al.*, 2021). In breeding programs, QTL for citrus characteristics such as fruit weight, hardness, and peel color (discovered using GWAS) have been suggested for marker-assisted introgression (Gao *et al.*, 2023; Liang *et al.*, 2018).

- **Genomic Selection (GS):** Genomic prediction could work better for highly polygenic characteristics (like yield or complicated quality). Marker panels from GWAS are used to input GS models. Using dense SNPs, genomic prediction in strawberries produced a selection effectiveness of around 74% for yield (Migicovsky *et al.*, 2021). In an effort to reduce breeding cycles, hybrid perennial fruit (apple, pear) studies have started incorporating GWAS-informed marker effects into GS models (Susmitha *et al.*, 2023).
- **Introgression and Breeding Populations:** GWAS finds advantageous genes for introgression in a variety of germplasm (wild relatives, landraces). For instance, in cherries and plums, genes for disease resistance or acidity from wild Prunus species have been monitored (Azam *et al.*, 2018). Rare alleles (such as parthenocarpy genes in wild PNG bananas) are highlighted for use in crosses in bananas using GWAS panels of wild and farmed accessions (Sardos *et al.*, 2016).
- **Gene editing and biotechnology:** GWAS candidate genes are the focus of functional engineering and validation. Fruit genes have been subjected to CRISPR/Cas9 (e.g., altering MdMYB10 for color or knocking out PDS for albinism as a proof-of-concept) (Wang *et al.*, 2020). Targeted editing may enhance variations if a GWAS finds, for example, a negative regulator of fragrance or allergenicity. For instance, to decrease stone cells and enhance texture, the pear PbrSTONE gene (from GWAS) might be turned down (Zhang *et al.*, 2021).
- **Integration with Genomic Resources:** Pan-genomes and transcriptomes are increasingly being used to interpret GWAS findings. For example, missing heritability from SNP-GWAS may be explained by structural variations found in the apple pan-genome (Clauw *et al.*, 2025). To speed up trait prediction, predictive models (machine learning) based on GWAS data are being investigated (Huang *et al.*, 2017).

Table 2 : Comparative Summary of GWAS Methodologies in Fruit Crops

Crop	Genotyping Platform	Population Size	Model Used	Key Findings
Apple	20K SNP Array	233 accessions	MLM, FarmCPU	Texture QTL (Chr10), aroma volatiles (*MdAAT1*)
Strawberry	288 accessions	GBS	MLM, MT-GWAS	Yield QTN, acidity, firmness
Banana	105 accessions	GBS	MLM	Parthenocarpy (female sterility, *CKI1*)
Mango	269 accessions	WGR, SNP arrays	MLMM, BLINK	Fruit weight, °Brix, MAPK genes
Citrus	447 accessions	WGR	MLM	HLB tolerance (NLR, PRR genes)

Challenges in Fruit Crop GWAS

Fruit crops pose unique hurdles for GWAS:

- **Complex Genomes:** Analysis is made more difficult by the fact that many fruit species are vegetatively propagated, extremely heterozygous, or polyploid. Specialized allele-dosage models are needed for sweet potatoes (hexaploid) and strawberries (octoploid). Aneuploid or triploid bananas are common. In polyploids, SNP genotyping may miscall doses, which lowers power (Sardos *et al.*, 2016; Migicovsky *et al.*, 2021).
- **Relatedness and Population Structure:** Admixture and related relatives are often seen in breeding panels. If not taken into consideration, this might increase false positives. This is lessened by mixed models, but residual structure may mask small loci. Apple cultivars, for instance, have different gene pools in the west (USA/Europe) and the east (Asia) (Muranty *et al.*, 2015).
- **Small Sample Sizes:** Hundreds of different genotypes are required for an ideal GWAS. The ability to identify small-effect genes is limited by the fact that many fruit studies only include tens to a few hundred accessions. Major loci were identified by the banana GWAS using 105 samples (Sardos *et al.*, 2016), although many more loci (and uncommon alleles) most likely went undetected (Osorio-Guarín *et al.*, 2024).
- **Phenotyping and Trait Complexity:** The taste, texture, and nutritional value of fruits are multifaceted characteristics that are impacted by the environment. Variability and phenotyping error lower GWAS power. Sensory panels, which are expensive and subjective, are necessary for

organoleptic (taste) characteristics (Matiazhagan *et al.*, 2021). There is additional noise since even objective measurements, such as sugar by °Brix, may change depending on temperature and maturity. Long-term testing is necessary to determine traits expressed after harvest (shelf life) (Poland & Rife, 2012).

- **Patterns of Linkage Disequilibrium (LD):** In certain outcrossing fruits (grapes, peaches), LD degrades quickly, necessitating very thick markers. On the other hand, GWAS signals may cover wide areas with several genes when clonals (bananas, citrus) have substantial LD. It is difficult to chart both extremes (Huang *et al.*, 2010).
- **Environmental Interactions:** A lot of fruit characteristics exhibit genotype–environment interactions, such as temperature-influenced fruit set. Although challenging, multi-environment GWAS are necessary. Replication is challenging since locus impact sizes might vary by year and location (Liang *et al.*, 2018).

Future Prospects

The next decade promises to overcome many current limitations:

- **Pan-genomes and Structural Variation:** GWAS may target structural variations (SVs) and presence/absence variants that are discovered via ongoing efforts to create pan-genomes (full genome catalogs) for apple, banana, pear, and other species. Integrating SV-GWAS will increase finding since SVs often explain phenotypic variations (such as fruit size deletions). Citrus and apple pan-genomes, for instance, have already revealed millions of new alleles (Clauw *et al.*, 2025).
- **Multi-omics Integration:** Candidate genes may be refined by combining GWAS with transcriptome (eQTL), metabolome (mQTL), and epigenome data. Causative genes may be found by co-localizing GWAS findings with expression QTL (eQTL) hotspots. Metabolomics-assisted GWAS, or "mGWAS," is becoming more popular in fruit for substances like volatiles and anthocyanins (Susmitha *et al.*, 2023).
- **Improved Phenotyping:** Developments in robotics (drones, orchard robots) and sensors (hyperspectral imaging, NIR scanners, automated fruit counting) will significantly boost phenotypic throughput and accuracy. GWAS of dynamic characteristics may be made possible by time-series phenotyping (e.g., fruit growth rate using imaging). Networks between genotypes and phenotypes may be revealed by integrating phenomic data into GWAS (phenome-wide association studies) (Matiazhagan *et al.*, 2021).
- **New Statistical Techniques:** GWAS will be enhanced by machine-learning (ML) techniques, particularly for polygenic variables. Non-linear interactions and high-order epistasis that are missed by normal GWAS may be captured by ML-GWAS (Huang *et al.*, 2017). Power may also be increased by techniques that examine haplotypes or gene-level relationships (collapsing SNPs into gene sets). Additionally, multi-trait GWAS the combined analysis of associated fruit traits will be crucial (Liu *et al.*, 2016).
- **Climate-Resilient Traits:** As a result of climate change, GWAS for fruits that are resistant to heat, drought, and stress will become more important. For instance, it will be essential to identify the genes that give peaches their cold-hardiness or heat-stable blooming. Crop modeling and GWAS together may be able to forecast trait performance in future climates (Huang *et al.*, 2010).
- **Gene editing and speed breeding:** To confirm function and produce better kinds, GWAS-identified genes may be precisely modified (using CRISPR). Selection on GWAS loci will occur more quickly if generation time is shortened (for example, by utilizing apple rootstocks that blossom early). Faster breeding cycles may potentially be possible with novel techniques like intergeneric hybrids and haploid induction (Wang *et al.*, 2020; (**Watson *et al.*, 2018**)).

Conclusion

GWAS has developed as a vital link between breeding and genomics in fruit crops. The loci and candidate genes underlying important characteristics (yield components, quality measures, and stress responses) have been effectively discovered via studies conducted on temperate and tropical fruits. For instance, MdAAT1/MdIGS for apple fragrance, CKI1 for banana seedlessness, and PbrSTONE for pear stone cells were discovered using GWAS. Precision breeding is already using these findings via genetic prediction and marker-assisted selection. Although there are still issues (such as polygenic designs, phenotyping bottlenecks, and population structure), they are being lessened by quick technical advancements. GWAS-identified advantageous alleles may be quickly implemented in the future thanks to the combination of pan-genomics, sophisticated phenomics, and gene editing. GWAS has shown its value in fruit genetics and will keep working to improve fruit cultivars with greater resilience and quality.

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