× 'Hapil' established collinearity with the diploid *Fragaria* reference genome and enabled dissection of fruit quality QTL, providing a structural framework for mapping sugar and acid-related traits in the octoploid background (Porter et al., 2023). Subsequent metabolite-focused QTL work detected 133 mQTL for 44 primary metabolites, soluble solids content (SSC), titratable acidity (TA), and pH, with only 12.9% stable across years, underlining strong genotype × environment interactions for sugar-acid balance (Alarfaj et al., 2021).

Specific genomic regions contributing to sweetness and acidity have now been repeatedly identified. Pedigree-based analysis in U.S. breeding populations mapped a moderate-effect SSC QTL on linkage group (LG) 6A and TA QTL on LGs 2A and 5B, together explaining up to 22% of phenotypic variance for acidity-related traits. Independent F_1 and F_2 populations and GWAS have revealed additional SSC QTL on chromosomes 3B and 6A, often with antagonistic effects on yield, and co-localized QTL blocks in homoeology group V controlling sucrose, raffinose, and organic acids, suggesting hotspots for coordinated regulation of sweetness and acidity (Liu et al., 2020).

4.2 Key functional genes and transcriptional regulatory networks

High-resolution QTL and multi-omics analyses are beginning to pinpoint functional genes underlying sugar and acid variation. Genome-wide association combined with eQTL mapping has implicated a starch synthase 4 gene and a sugar transporter 2-like gene within major SSC QTL on chromosomes 3B and 6A, linking allelic variation in carbohydrate metabolism and transport to differences in soluble sugar accumulation and SSC-yield trade-offs (Liu et al., 2020). Similarly, mQTL in homoeology group V co-controlling sucrose, raffinose, and succinic acid co-localize with genes involved in sugar interconversion and transport, such as UDP-glucose 4-epimerase and SWEET-type sugar transporters, indicating pleiotropic regulators of both sweetness and acidity (Alarfaj et al., 2021).

At the transcriptional level, integrated metabolome-transcriptome studies identify broad networks connecting sweetness, acidity, and other non-volatile flavor components. Comparative analyses of three *F.* × *ananassa* cultivars with contrasting flavor profiles showed that differences in fructose and citric acid contents were associated with differential expression of structural genes in the citrate cycle, phenylpropanoid, and flavonoid pathways, highlighting central metabolic nodes that affect both acid accumulation and downstream flavor traits (Natarajan et al., 2020). In parallel, genome-wide surveys of the MYB transcription factor family identified 407 FaMYB genes, with specific loci predicted to regulate sugars and organic acids; several MYBs showed cultivar- and ripening-dependent expression linked to fruit quality, nominating them as key regulators of sugar-acid metabolism and transport (Figure 1).

4.3 Progress in the application of molecular markers and gene editing technologies

Rapid advances in strawberry genomics are transforming sweetness and acidity improvement from purely phenotypic selection to genomics-assisted strategies. High-density SNP arrays (IStraw90, IStraw35) and ddRAD-based maps have enabled finer QTL resolution for SSC, TA, and SSC/TA, and marker haplotypes in validated regions such as LG 6A for SSC and LG 2A/5B for TA are now available to support marker-assisted selection for improved sugar-acid balance. In some cases, functional markers linked to sugar metabolism genes (e.g., UDP-glucose 4-epimerase) differentiate high- and low-sugar genotypes with >80% accuracy, illustrating the potential of trait-specific markers for routine screening in breeding programs (Wang et al., 2022).

Beyond markers, genome-scale resources and CRISPR technologies are opening prospects for direct manipulation of sweetness and acidity pathways. Phased octoploid reference genomes, dense SNP arrays, and extensive fruit transcriptomes now allow precise localization of genes controlling sweetness intensity and acid metabolism, while early CRISPR applications in *Fragaria* demonstrate the feasibility of targeted editing of fruit quality genes, including those for volatile synthesis and sugar perception. Recent reviews emphasize that integrating marker-assisted and genomic selection for SSC with editing of key metabolic and regulatory genes (e.g., sugar transporters, MYBs) will accelerate the development of cultivars combining high sweetness, balanced acidity, and strong agronomic performance (Liu et al., 2020).