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Sweetness and Acidity Traits in Strawberry (*Fragaria* × *ananassa*): Research Progress and Perspectives

Haiya Xu
Sanmen County Kedi Family Farm, Sanmen, 317108, Zhejiang, China
Corresponding email: 657552075@qq.com
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Abstract Strawberry flavor quality is a pivotal factor determining its commercial value and consumer acceptance; among its attributes, sweetness and acidity serve as core sensory indicators that directly influence fruit palatability and market competitiveness. This paper systematically reviews the research progress regarding sweetness and acidity traits in strawberries. Drawing upon both sensory evaluation and physicochemical foundations, it analyzes the compositional characteristics of sugars and organic acids, as well as the dynamic patterns of their accumulation. Furthermore, the paper elucidates the metabolic pathways for carbohydrates and organic acids—including the regulatory mechanisms of key enzymes—and summarizes the genetic basis and molecular regulatory networks underlying these traits. Building upon this foundation, the study explores the impact of environmental factors and cultivation practices on sugar and acid accumulation, as well as the application of both traditional and molecular-assisted breeding techniques in quality improvement. Concurrently, through case studies of exemplary high-quality varieties, the paper reveals practical strategies and demonstrated outcomes for the improvement of sweetness and acidity traits. Finally, integrating the advancements in multi-omics technologies and precision breeding, the paper outlines future directions for research into strawberry flavor quality. This review aims to provide a theoretical basis and technical reference for the selection and breeding of high-quality, high-sweetness, and low-acidity strawberry varieties, as well as for the overall upgrading of the strawberry industry.
Keywords Strawberry; Sweetness; Acidity; Sugar-acid metabolism; Molecular breeding

1 Introduction

Strawberry (*Fragaria* × *ananassa*) is a globally important horticultural crop valued for its bright color, nutritional benefits, and distinctive flavor profile, making it a key component of fresh fruit markets and processed products worldwide (Barbey et al., 2021). However, decades of breeding focused on yield, firmness, appearance, and disease resistance have often led to a decline in perceived flavor quality, with many modern cultivars regarded as bland compared with wild relatives or older varieties (Porter et al., 2023). Recent sensory and multi-omics studies have highlighted flavor—particularly the balance of sweetness and acidity combined with characteristic aroma—as a central determinant of consumer satisfaction and a renewed priority for breeding programs. Within overall flavor, sweetness and acidity are core taste traits that directly influence both hedonic response and repeat purchase decisions.

Strawberry flavor perception arises from the integration of taste (sugars and organic acids), aroma (volatile organic compounds), and texture, with sweetness and acids providing the fundamental taste framework on which volatiles build complexity (Wang et al., 2025). Large sensory-chemical studies show that consumer liking is most strongly associated with sweetness intensity and strawberry flavor intensity, while sourness contributes less directly to overall preference yet still shapes the perceived balance of taste (Liu et al., 2023; Mezhina and Tikhonova, 2025). Biochemically, nonvolatile sugars such as glucose, fructose, and sucrose and organic acids such as citric and malic define the sweetness-acidity profile, and their ratio is often a better indicator of perceived flavor than absolute concentrations alone. In this context, dissecting the genetic, metabolic, and environmental determinants of sweetness and acidity has become essential for guiding both breeding and cultivation practices.

Consumer studies consistently indicate that strawberries are purchased and consumed primarily for their pleasant aroma and sweet taste, and that high sweetness and balanced acidity are key drivers of preference across diverse markets (Sturzeanu et al., 2025). Psychophysical and panel work has shown that overall liking is closely tied to sweetness and strawberry flavor intensity and is undermined when sucrose and total volatile content are reduced by environmental or agronomic factors (Fan et al., 2021a). Quantitative analyses further demonstrate that relatively small increases in soluble solids content (SSC), strongly correlated with total sugars, can markedly increase the probability of a fruit being perceived as “sweet enough”, emphasizing the sensitivity of consumers to sugar levels within the commercial range. At the same time, excessive acidity or unbalanced sugar-acid ratios are associated with “not sweet enough” or overly sour perceptions even when sugar content is adequate, underscoring the importance of coordinated control of both traits.

Beyond sugars and acids, specific volatile compounds can enhance perceived sweetness independently of sugar concentration, effectively modulating the sensory impact of a given sweetness-acidity matrix (Liu et al., 2023). In large consumer panels and descriptive analyses, particular esters, terpenes, lactones, and other volatiles have been shown to correlate positively with sweetness intensity and liking, whereas green, astringent, or overripe notes detract from preference. These findings imply that breeding solely for higher SSC or lower titratable acidity is insufficient; instead, breeding and management must consider how sweetness and acidity interact with volatiles to shape overall flavor perception and market acceptance.

Internationally, research on strawberry flavor has progressed from simple physicochemical characterization toward integrated sensory, metabolomic, and genomic approaches aimed at resolving the complex basis of sweetness and acidity traits. Large-scale studies combining multi-season sensory data with profiles of sugars, acids, and up to more than 100 volatiles have identified chemical drivers of sweetness, sourness, and liking and provided predictive models that outperform those based on SSC and titratable acidity alone (Liu et al., 2023). Parallel advances in genomics, high-density SNP arrays, phased octoploid reference genomes, and transcriptomics have enabled the mapping of quantitative trait loci and identification of candidate genes for volatile synthesis, sugar accumulation, and organic acid metabolism, paving the way for marker-assisted and genomic selection targeting flavor components (Porter et al., 2023).

Recent reviews emphasize that cultivated strawberry, like tomato, is poised to benefit from genome-based breeding and even genome editing to restore and enhance key flavor attributes, including sweetness intensity and balanced acidity, while maintaining agronomic performance (Scott et al., 2021). Integrative metabolome-transcriptome analyses have begun to pinpoint nonvolatile compounds and biosynthetic pathways—such as citrate cycle and flavonoid metabolism—underlying sweetness, acidity, and related mouthfeel traits, providing new targets for manipulating taste quality. Looking forward, the convergence of consumer-driven sensory work, high-throughput chemistry, and multi-omics frameworks is expected to accelerate the development of cultivars with optimized sugar-acid profiles adapted to diverse environments, thereby aligning breeding outcomes more closely with evolving consumer expectations for flavor-rich strawberries (Lewers et al., 2020).

2 Material Basis and Metabolic Mechanisms of Strawberry Sweetness Formation

2.1 Major sugar components and their dynamic changes (glucose, fructose, sucrose)

Strawberry sweetness is mainly determined by three soluble sugars—glucose, fructose, and sucrose—which together account for about 99% of total fruit sugars and increase markedly during development from green to red stages (Xu et al., 2024). In many cultivated genotypes, glucose is often the most abundant carbohydrate and sucrose relatively low, although the exact proportions vary with cultivar and environment. Developmental profiling shows that total sugars and each of the three components are lowest in green fruit and highest in red fruit, paralleling the rise in total soluble solids and perceived sweetness (Topçu et al., 2022).

The dominant sugar can differ among genetic backgrounds. In some germplasm sets, sucrose is the main sugar in high-sugar cultivars, whereas fructose predominates in low-sugar types, indicating that sweetness depends not only on total sugar but also on sugar composition (Xu et al., 2024). In white-fleshed ‘Snow White’, fructose and glucose are at very low levels and often undetectable, while sucrose becomes the principal soluble sugar during ripening and is tightly associated with flavor formation. Similar patterns of strong sucrose accumulation during ripening, sometimes exceeding hexoses, have also been observed in wild species such as F. nilgerrensis, underscoring sucrose as a key driver of sweetness in some genetic backgrounds.

2.2 Carbohydrate metabolic pathways and regulation by key enzymes

Sucrose transported from leaves enters a metabolic network involving sucrose phosphate synthase (SPS), sucrose synthase (SS), and several forms of invertase (cell wall, vacuolar, and neutral), which together determine the balance between sucrose and hexoses in the receptacle (Wang et al., 2025). In Tochiotome fruit, sucrose rises rapidly in late development, while SPS and SS activities are relatively low, suggesting that sucrose accumulation is driven more by limited breakdown than by enhanced synthesis (Khammayom et al., 2022). Acid invertase activity declines early but increases again at ripening, leading to abundant hexoses and explaining why ripe red fruits frequently contain glucose as the major sugar despite strong late sucrose accumulation (Topçu et al., 2022).

Genome-wide analyses reveal a large invertase (INV) gene family in octoploid strawberry, with polyploidy-driven amplification and many members showing fruit-preferential expression. Among them, cell wall invertase FaCWINV1 is markedly upregulated during development, strongly expressed in ripe fruit, and significantly correlated with total sugar content, indicating a central role in sucrose unloading and sink strength establishment (Wang et al., 2025). Transcriptional studies also show that SPS transcripts increase sharply at late stages, while SS and acid invertase transcripts often decrease or fluctuate, supporting a model in which coordinated regulation of these enzymes and their genes channels carbon toward sugar accumulation as fruit ripen (Osatuke and Pritts, 2021).

2.3 The influence of developmental stages and environmental factors on sweetness

Strawberry fruit development from green through white/turning to red stages is accompanied by coordinated changes in sugars, hormones, and other metabolites that shape sweetness. Multi-stage analyses show that sucrose, glucose, and fructose all rise as fruit ripen, but sucrose is most tightly linked to ripening progression and activation of ripening-related genes (Osatuke and Pritts, 2021). In white-fleshed strawberries, total soluble solids, total sugar, and sucrose increase strongly while total acid and anthocyanins decrease, and transcriptomic data highlight enrichment of "starch and sucrose metabolism" and hormone signaling pathways, indicating that sucrose accumulation and plant hormones jointly regulate maturation and flavor development.

Environmental conditions, especially temperature, further modulate sweetness by altering sugar accumulation patterns. In greenhouse-grown strawberries, a larger day-night temperature differential during fruit development is associated with higher soluble sugar content and overall better fruit quality, whereas elevated temperatures late in the season reduce soluble sugars despite similar radiation and humidity, underscoring temperature's dominant effect on sweetness (del Olmo et al., 2020). Comparative studies across farms likewise find soluble solids and titratable acidity to be positively associated with air temperature differential during ripening, while fertilization, pesticide intensity, and microbial inputs have little consistent influence on sugar levels. These findings emphasize that developmental programming of carbohydrate metabolism interacts strongly with thermal conditions to determine final sweetness.

3 Material Basis and Regulatory Mechanisms of Strawberry Acidity Formation

3.1 Major organic acid species (citric acid, malic acid, etc.)

Strawberry acidity is primarily determined by the composition and concentration of organic acids in the receptacle tissue. In cultivated *Fragaria* × *ananassa*, citric acid is generally recognized as the predominant organic acid, with malic acid as the second major component, and both together account for most of titratable acidity that shapes basic sourness perception. Studies on white-fleshed strawberry further confirm that citric and malic acids are much higher than other detected acids such as 2-oxobutyric, methylmalonic, suberic, and ascorbic acids, reinforcing their central role as the main acidity-forming components in different genetic backgrounds (Wang et al., 2025).

Comparative work in wild species highlights that the organic acid spectrum can diverge markedly from cultivated types. In *Fragaria nilgerrensis*, isocitric, succinic, and methylmalonic acids dominate the profile, while many other organic acids remain relatively stable across development, suggesting that different strawberry species rely on distinct TCA-cycle intermediates to support fruit metabolism and flavor formation (Ikegaya, 2023). Despite this diversity, across fleshy fruits more broadly, citrate and malate emerge as the two organic acids that most consistently accumulate and contribute to respiratory supply, osmotic regulation, and taste quality during development and ripening (Wei et al., 2025).

3.2 Organic acid metabolism and regulation by related enzyme systems

Organic acid levels in strawberry fruit reflect a dynamic balance among synthesis, degradation, and compartmentation within the tricarboxylic acid (TCA) cycle and associated pathways. Metabolomic and transcriptomic analyses in cultivated strawberries with contrasting flavor show that structural genes encoding isocitrate dehydrogenase, 2-oxoglutarate dehydrogenase, succinate dehydrogenase, fumarate hydratase, and malate dehydrogenase are strongly associated with citric and malic acid content, and that numerous transcription factors (WRKY, MYB, NAC, bZIP, bHLH, AP2) are tightly co-expressed with these genes (Šimková et al., 2024). In kiwifruit, which shares similar acid profiles, high citric acid accumulation is driven by elevated citrate synthase (CS) activity combined with reduced aconitase and NAD-dependent isocitrate dehydrogenase, whereas malic acid accumulation mainly depends on NAD-malate dehydrogenase and phosphoenolpyruvate carboxylase, illustrating how synthesis and degradation fluxes jointly determine titratable acidity.

Recent functional work in strawberry has begun to resolve upstream regulatory nodes that connect primary carbon metabolism with citric acid pools. Overexpression of cytosolic glyceraldehyde-3-phosphate dehydrogenase (FaGAPC2) or pyruvate kinase (FaPKc2.2) reduces citric acid content and alters ripening progression by suppressing phosphoenolpyruvate carboxykinase (FaPEPCK) expression, decreasing PEPCK and glutamate decarboxylase activities, and promoting glutamine synthase-mediated diversion of carbon and nitrogen, thereby favoring citrate consumption through amino acid metabolism (Xu et al., 2024). In contrast, overexpression of FaPEPCK promotes ripening from full red to dark red while simultaneously decreasing citrate synthase activity and citric acid content, indicating that PEPCK-driven anaplerotic flux and CS-mediated synthesis constitute distinct control points for late-stage citrate decline (Xu et al., 2024). Exogenous modulation of enzyme activities, such as by selenomethionine treatment, also reduces total acids, citric acid, and malic acid by down-regulating CS, NAD-malate dehydrogenase, and NADP-malic enzyme, thereby increasing the sugar-acid ratio and improving perceived flavor (Jia et al., 2023).

3.3 Patterns of acidity change during fruit ripening

Strawberry fruit acidity is highly stage-dependent, reflecting reconfiguration of central metabolism as the fruit transitions from growth to ripening and eventual over-ripeness. Metabolic profiling across seven developmental stages in cultivated *F.* × *ananassa* shows that organic acids are among the major polar metabolites, with TCA-cycle activity shifting markedly during the transition to the red and over-ripe stages, when respiration and carbon partitioning are strongly remodeled (Wei et al., 2024). In the cultivar 'Albion', titratable acidity decreases by nearly 15% during ripening, with citric acid showing an overall descending pattern and malic acid fluctuating irregularly, while ascorbic acid increases, indicating that total acidity decline is largely driven by reduced citrate content and partial remodeling of the acid spectrum (Wang et al., 2025).

More detailed time-course studies reveal that citric acid content does not necessarily decrease monotonically but can show a rise-fall pattern in late development. In 'Benihoppe', citric acid concentration increases from initial red to full red and then declines toward dark red, suggesting that different regulatory modules dominate at successive ripening stages (Xu et al., 2024). Consistently, non-destructive assessments across multiple cultivars show that as strawberries ripen from green to over-ripe, total organic acid content generally decreases while sugars and the sugar-acid ratio increase, although the magnitude and exact timing of changes vary among genotypes (Yang et al., 2023). In white-fleshed 'Snow White', total acid and titratable acidity decline as soluble solids and total sugars rise, with citric and malic acids remaining the predominant acids throughout, illustrating how coordinated reductions in major organic acids underpin the shift from sour to sweeter, milder flavor during maturation.

4 Genetic Basis and Molecular Regulation of Sweetness and Acidity Traits

4.1 Inheritance patterns and QTL mapping of related traits

Sweetness and acidity in cultivated strawberry are complex quantitative traits controlled by multiple loci with relatively small individual effects, strongly influenced by environment. Early linkage maps based on 'Redgauntlet'

× '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).

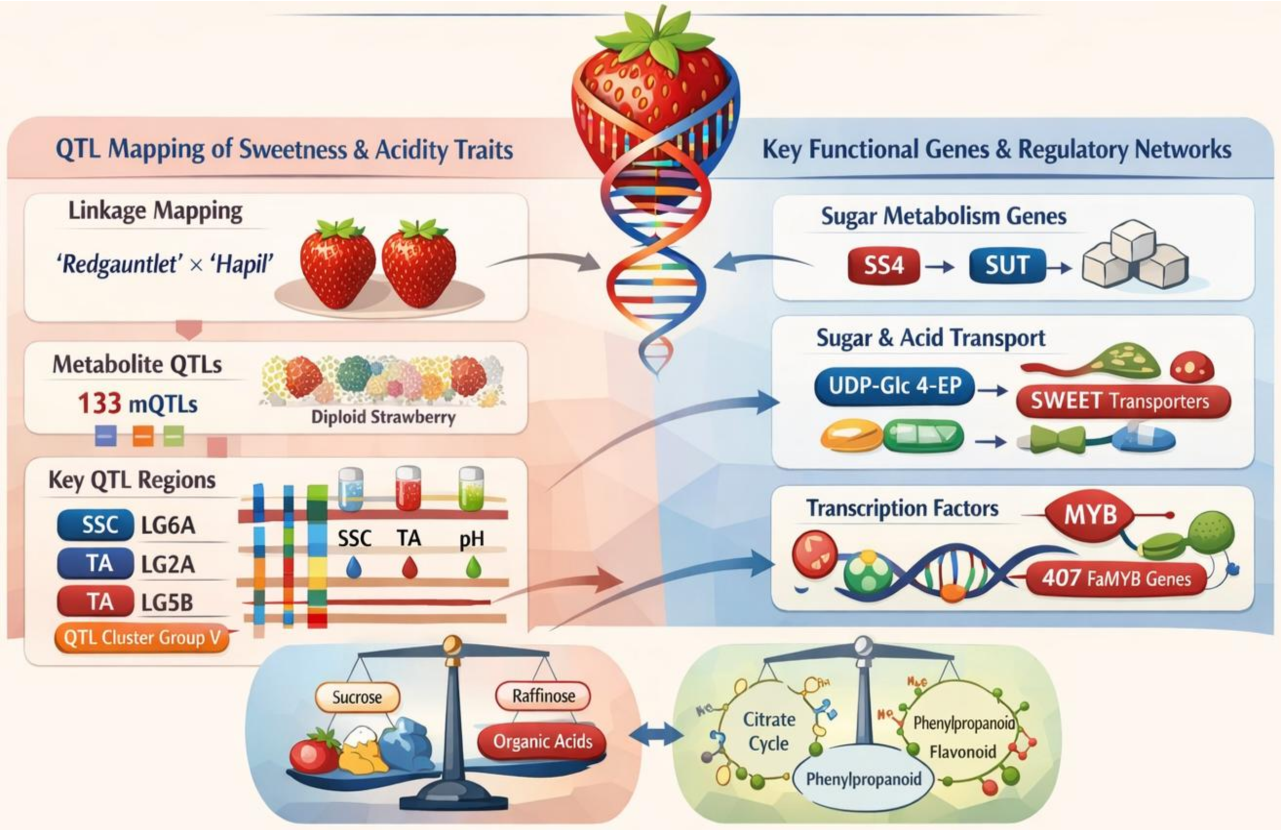

Figure 1 The genetic basis and molecular regulation of sweetness and acidity traits in cultivated strawberry (*Fragaria* × *ananassa*)

5 The Impact of Environmental and Cultivation Measures on Sweetness and Acidity Traits

5.1 The regulatory roles of light, temperature, and water conditions

Light quantity and quality strongly influence strawberry sugar and acid accumulation, especially in protected cultivation where natural light is limiting. In autumn-spring greenhouses, combining elevated CO_2 with LED supplemental light increased yield by over 50% compared with ambient conditions, while significantly increasing soluble sugar content and decreasing titratable acidity, thereby enhancing perceived sweetness (Tang et al., 2023). More precise chromatic control of LED spectra showed that supplemental light generally raised soluble solids by about 7% and titratable acidity by 27%, with color temperature and illuminance determining the exact balance between sugars and acids and thus flavor intensity (Patel et al., 2023).

Light treatments can also modulate sweetness-acidity traits after harvest. Continuous red LED exposure during cold storage improved total soluble solids and maintained firmness, while reducing weight loss relative to dark storage, indicating better retention of sweetness and texture (Kilic et al., 2021). By contrast, blue light combined with salicylic acid during refrigerated storage stabilized total soluble solids and titratable acidity at relatively low but constant levels, while markedly improving antioxidant capacity and delaying decay, thus conserving an acceptable sugar-acid balance over an extended storage period (Xu et al., 2023).

Temperature and water status interact to shape field sweetness-acidity profiles. Across multiple farms, soluble solids and titratable acidity were both positively associated with the air temperature differential (day-night difference) during ripening, whereas contrasting fertilization and input regimes showed no consistent effect on SSC or TA, suggesting that mesoclimate is a primary driver of basic taste attributes (Li et al., 2024). In greenhouse experiments manipulating irrigation levels, moderate deficit irrigation reduced yield and titratable acidity but increased soluble sugars, the sugar-acid ratio, and water-use efficiency, indicating that carefully controlled water stress can enhance sweetness perception without severely compromising quality (Jiang et al., 2023).

5.2 The impact of cultivation modes (protected vs. open-field) on quality

Comparisons of strawberries grown in high tunnels versus open-field systems indicate that protection modifies microclimate and can alter acidity and phytochemical profiles. In coastal Virginia, ten cultivars grown simultaneously in high tunnels and open field showed no significant environmental effect on total soluble solids, but titratable acidity and anthocyanin content were higher under high tunnels, implying a slightly tarter flavor with more intense color in protected systems (Osatuke and Pritts, 2021). A separate metabolite-focused study likewise found that titratable acidity was highest in high-tunnel 'Albion', while soluble solids and pH did not differ significantly between cultivation modes, suggesting that tunnels mainly enhance organic acid and phenolic accumulation rather than basic sweetness (Šimková et al., 2024).

Light-filtering structures such as colored shade nets provide a more targeted approach to modifying flavor-related traits under protection. Under beige and blue photoselective nets, total soluble sugars increased by about 42% compared with unshaded controls, and beige nets also raised titratable acidity by 24%, resulting in fruit with both higher sweetness and more pronounced sourness (Devi et al., 2024). In contrast, greenhouse LED supplemental lighting with controlled color temperature increased soluble solids and titratable acidity concurrently but reduced fruit firmness and single-fruit weight, highlighting trade-offs between sweetness-acidity enhancement and certain physical quality attributes in protected cultivation (Patel et al., 2023).

5.3 The impact of fertilization and post-harvest treatments on sugar and acid accumulation

Nutrient management significantly affects basic taste components, although effects can differ among fertilizer types and rates. Under protected fertigation, supplying 100% of the recommended NPK dose produced the highest total soluble solids, total sugars, and TSS:acidity ratio, while simultaneously minimizing titratable acidity, thus clearly shifting flavor toward greater sweetness and milder sourness (Aragón-Ramírez et al., 2025). In contrast, a comparison of organic, chemical, and combined fertilization showed that organic fertilizer generated fruit with higher soluble solids and glucose but lower firmness and vitamin C, and did not significantly alter citric acid content, suggesting that organic inputs may enhance sweetness primarily via increased sugars without strongly changing major organic acids (Cvelbar Weber et al., 2021).

More detailed work on nitrogen, calcium, and nano-fertilizers indicates that conventional N and Ca fertilization can markedly modify sugars, organic acids, and volatiles, often with negative consequences for overall flavor. Higher N and Ca doses increased certain aldehydes associated with grassy notes, while nano-fertilizer treatment improved phenolic content and fruity esters, illustrating that some innovative inputs can improve flavor-related metabolite profiles even when basic sugars and acids are only moderately affected (Ikegaya, 2023). Postharvest light and signaling treatments further modulate sugar-acid traits: red LED storage increased total soluble solids, whereas combined blue light and salicylic acid maintained low but stable TSS and titratable acidity, helping preserve an acceptable sugar-acid ratio while extending shelf life (Kilic et al., 2021; Xu et al., 2023).

6 Breeding Strategies for Improving Strawberry Sweetness and Acidity Quality

6.1 Traditional breeding methods and the selection of superior varieties

Conventional strawberry breeding has historically relied on controlled hybridization among elite cultivars followed by multi-year field selection for yield, disease resistance, appearance, and organoleptic quality, including sweetness and acidity balance. Long-term evaluations show that recurrent selection can generate cumulative genetic gain for soluble solids content (SSC) and titratable acidity (TA), confirming that both traits possess exploitable heritable variation and can be shifted upward or downward according to breeding goals (Pedrozo et al., 2023).

Selection of superior varieties increasingly integrates sensory panels and detailed physicochemical measurements. Studies comparing cultivars under commercial-like conditions demonstrate wide variability in SSC, TA, SSC/TA ratio, and volatile composition, with certain cultivars such as 'Flavorfest', 'Albion', and FL 00-51 consistently achieving higher sweetness, better flavor ratings, and more favorable SSC-TA combinations across harvests and environments (Liu et al., 2023). Multivariate approaches combining yield, SSC, TA, color, and bioactive compounds further support simultaneous selection for production and taste traits, enabling identification of hybrids suited to both fresh consumption and processing markets.

6.2 Molecular-assisted breeding and genomic selection

Molecular tools now complement traditional selection by enabling more precise manipulation of sweetness and acidity traits. High-density SNP arrays and pedigree-based QTL analyses have identified loci for SSC on linkage groups/chromosomes 3B and 6A and for TA and pH on 2A, 5B, and 4C, providing markers that can be implemented in marker-assisted selection to shift sugar-acid balance (Porter et al., 2023). Genome-wide association and expression-QTL integration have further pinpointed candidate genes such as starch synthase 4 and sugar transporter 2-like underlying major SSC QTL, facilitating haplotype-based selection for enhanced sugar accumulation (Fan et al., 2021b).

Genomic selection (GS) is emerging as a powerful strategy where sweetness, acidity, and yield are controlled by many loci of small effect. Large multi-parental populations genotyped with SNP arrays and phenotyped for fruit quality and yield show that genomic prediction is effective for complex traits, although a negative correlation between total soluble sugars and marketable yield highlights a key trade-off that GS must manage. Recent reviews emphasize that declining genotyping costs and availability of phased octoploid genomes will make GS for SSC/yield balance feasible in seedling populations, allowing breeders to enrich for sweeter, well-balanced genotypes early in the breeding pipeline.

6.3 Synergistic improvement of multiple traits and comprehensive evaluation of flavor quality

Improving sweetness and acidity cannot be separated from broader flavor and agronomic performance. Large sensory-chemical studies reveal that overall liking is driven primarily by sweetness intensity and strawberry flavor, with sourness playing a lesser direct role, and that specific volatiles can enhance perceived sweetness independently of sugar content (Barth et al., 2020). Descriptive analysis and consumer work consistently show that cultivars combining adequate SSC, moderate TA, and rich ester- and terpene-dominated volatile profiles achieve superior flavor ratings, whereas imbalanced acids or atypical volatile patterns can undermine acceptability even in high-sugar fruit (Liu et al., 2023).

Modern flavor-oriented breeding strategies advocate a multi-trait, consumer-driven framework in which sensory data guide the prioritization of chemical targets—sugars, organic acids, and key volatiles—and these, in turn, drive genetic target discovery and marker development (Jouquand et al., 2008). Multi-year, multi-environment evaluations using integrated sensory, metabolite, and genomic data allow breeders to select genotypes with stable sweetness, balanced acidity, desirable aroma, and acceptable yield across harvest dates and production systems (Patel et al., 2023). Such comprehensive evaluation supports the release of cultivars that deliver consistently high flavor quality while meeting grower requirements for productivity and shelf life.

7 Case Study: Selection and Evaluation of High-Quality, High-Sweetness, Low-Acidity Strawberry Varieties

7.1 Analysis of quality characteristics in typical varieties

High-sweetness, low-acidity cultivars are favored where consumers prefer mild, dessert-type strawberries with intense sweetness and relatively soft sourness. Comparative work across 25 cultivars shows wide inter-cultivar variation in soluble sugars and organic acids, with some genotypes achieving both high sugar content and favorable sugar/acid ratios, reflected in superior total quality index (TQI) scores (Milosavljević et al., 2023). Such cultivars are prime candidates as “high-sweetness” types, because they combine elevated sugars with moderate acidity and beneficial bioactive compounds, aligning with increasing demand for fruits that are both palatable and nutritionally valuable (Ikegaya et al., 2021).

Cultivar-specific evaluations under greenhouse or soilless systems further highlight materials with desirable sensory profiles. In a soilless comparison of four Japanese cultivars, ‘Guimeiren’ exhibited the highest sweetness index, while ‘Tochiotome’ combined relatively high soluble solids and sugar/acid ratios with comparatively low organic acid levels, producing a sweet yet not overly tart taste. Similarly, studies in Greece reported that ‘Sabrina’ had the highest pH and SSC/TA index and was perceived as the sweetest among three commercial cultivars, illustrating how individual varieties can naturally express a high-sweetness, lower-acidity profile under suitable conditions (Ikegaya et al., 2021).

7.2 Measurement and comparison of indicators related to sweetness and acidity traits

Quantitative evaluation of high-sweetness, low-acidity types relies on integrated measurement of sugars, acids, and derived indices. Across numerous cultivars, soluble solids (SSC), titratable acidity (TA), and the SSC/TA ratio have been established as core indicators of eating quality, with high SSC and moderate TA yielding balanced "sweet-tart" profiles. In multi-cultivar surveys, SSC and TA ranges are often broad, allowing selection of genotypes that exceed breeding targets (e.g., ≥8% SSC and ≈0.8% TA) or express higher SSC/TA ratios indicating greater perceived sweetness and milder acidity (Klakotskaya et al., 2023).

Beyond bulk metrics, detailed profiling of individual sugars and acids improves discrimination among candidate cultivars. HPLC-based analysis of 25 cultivars showed that variation in glucose, fructose, sucrose, citric acid, and malic acid strongly differentiates genotypes and underpins differences in TQI, with some cultivars like 'Sandra' excelling in both primary metabolites and overall quality score (Milosavljević et al., 2023). Soilless-culture work in Japanese varieties found fructose and glucose as major sugars and citric acid as the dominant organic acid, but identified 'Tochiotome' as having higher TSS/TA and total sugars/total organic acids ratios than other cultivars, clearly linking compositional profiles to sweetness-acidity traits.

7.3 Evaluation of breeding strategies and practical application outcomes

Recent breeding and selection efforts emphasize integrating multi-trait quality data to identify high-performing, sweet, low-acid materials suitable for diverse environments. Large multi-location trials demonstrate that germplasm (genotype) explains more variation in SSC and TA than location, and that a subset of genotypes concurrently meets modern breeding goals of ≥8% SSC and ~0.8% TA, making them attractive parents for combining sweetness and acceptable acidity in new cultivars (Klakotskaya et al., 2023) (Figure 2). Cluster analyses of dozens of cultivars using yield, SSC, TA, and SSC/TA effectively group genotypes with similar target traits, helping breeders prioritize those with naturally high sugar/acid balance and good agronomic potential (Xu et al., 2025).

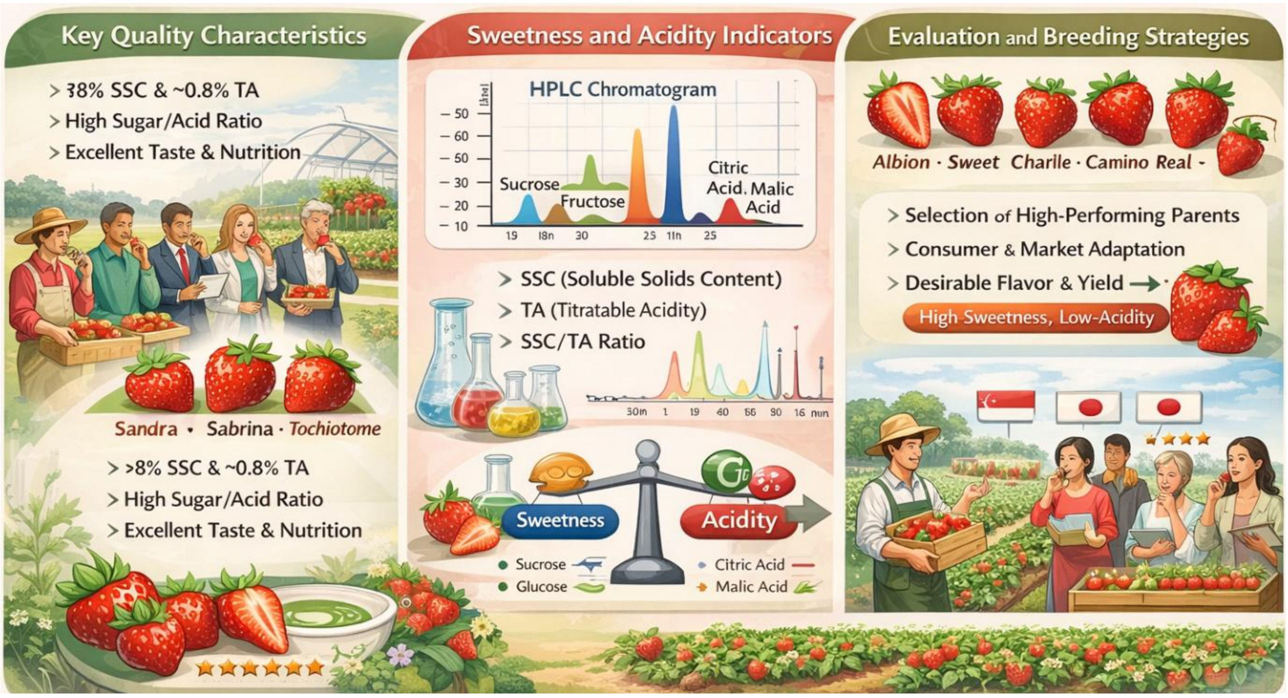

Figure 2 The selection and evaluation of high-quality, high-sweetness, low-acidity strawberry cultivars

On-farm and market-oriented evaluations confirm that such selection strategies translate into tangible improvements in consumer satisfaction and market fit. In a cross-regional quality assessment, strawberries with higher SSC and lower TA were preferred by both Singaporean and Japanese consumers, although Singaporean assessors favored especially low acidity, indicating that high-sweetness, low-acidity cultivars are particularly suitable for certain export markets (Radović et al., 2025). Sensory and chemical studies in Texas similarly identified cultivars like ‘Albion’, ‘Sweet Charlie’, ‘Camarosa’, ‘Camino Real’, and ‘Chandler’ as ideal for local conditions because they combined high °Brix and favorable TSS/TA ratios with desirable flavor volatiles, underscoring the success of breeding programs that explicitly target balanced sweetness and acidity alongside regional adaptation (Scott et al., 2021).

8 Future Directions for Strawberry Sweet-Sour Quality

Multi-omics approaches in cultivated strawberry now combine phased genomes, transcriptomes, metabolomes, and volatile GWAS to dissect flavor genes and regulatory elements. An integrated framework in octoploid strawberry exploited genomic heterozygosity and metabolomic diversity to link allele-specific expression and structural variants with key flavor volatiles, demonstrating how such datasets can systematically uncover flavor genes. Conjoint metabolome-transcriptome analyses across cultivars with contrasting flavor have further highlighted fructose and citric acid as central non-volatile drivers of sweetness and acidity, and revealed that citrate cycle, phenylpropanoid, and flavonoid pathways are major regulatory hubs.

Future research will likely deepen integration of sugar-acid metabolism with broader flavor networks using expanded omics resources. Integrative analyses in contrasting cultivars already identify candidate structural genes and transcription factors associated with soluble sugars, organic acids, and vitamin C, indicating that coordinated regulation of multiple quality components can be mapped at pathway level. At the same time, comparative metabolomics across diverse wild *Fragaria* accessions shows that amino acids, sugars, and anthocyanins co-vary with flavor, suggesting that extending multi-omics to wild relatives will enrich sweet-sour regulatory models and provide novel alleles for breeding.

Precision flavor breeding is moving toward genomics-informed strategies that explicitly target sweetness, acidity, and key volatiles. Large-scale sensory-chemical studies have identified sugars, two main acids, and sets of volatiles that enhance sweetness and liking, while genetic association analyses mapped loci for ester production that can be targeted by marker-assisted selection. A broader review of strawberry flavor breeding emphasizes that phased haplotype genomes, SNP arrays, and extensive fruit transcriptomes now allow localization of genes for volatile synthesis, anthocyanins, and sweetness perception, paving the way for more precise manipulation of flavor traits.

Genomic selection and marker-assisted breeding for quality traits are expected to expand as genotyping costs fall and prediction models mature. Genomic-informed studies in multi-parental populations reveal a negative correlation between total soluble sugars and yield, and identify QTNs for perceived acidity and other traits, supporting combined use. Updates from breeding programs adopting DNA testing show that high-throughput markers for disease resistance and fruit quality are already being used to cull seedlings efficiently, illustrating how precision breeding pipelines can be scaled in practice.

Future progress in sweet-sour improvement will depend on aligning biochemical targets with consumer sensory preferences. Large multi-year consumer and descriptive-panel studies demonstrate that overall liking is driven mainly by sweetness and strawberry flavor intensity, not sourness, and reveal volatile compounds that enhance perceived sweetness independently of sugars, providing concrete chemical targets for breeding and quality control. Bayesian modeling of soluble solids-sweetness relationships further refines selection criteria by quantifying how small SSC changes shift the probability of achieving above-average sweetness in sensory panels.

Industrial application will likely leverage these insights across fresh and processed product chains. Studies relating cultivar traits to consumer preference show that higher sweetness and strawberry flavor predict better acceptance in fresh fruit, while work on strawberry-flavored dairy products indicates that consumers prefer high sweet taste, relatively low acid taste, and strong strawberry aroma, even when delivered by added flavorings.

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Conflict of Interest Disclosure
The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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