

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’