studies and enzyme assays indicate that starch-to-sucrose conversion involves active sucrose cycling, rather than simple one-way accumulation (Nardozza et al., 2013). Cultivar comparisons support this developmental shift, with SS highly expressed in immature fruit and SPS increasing in mature stages, while SPS expression is positively associated with sugar accumulation in some genotypes (Lin et al., 2022).

Invertases provide a second route for sucrose cleavage and help shape the balance between sucrose and hexose accumulation. Invertases occur as cell wall, vacuolar, and neutral isoforms, and their functions differ by compartment and developmental stage (Huang et al., 2025). In kiwifruit fruit, neutral invertase is generally more important than acid invertase during development, and early changes in glucose and neutral invertase activity mark the transition into starch accumulation (Kang et al., 2021). During softening, acid and neutral invertase activities increase alongside amylase activities and correlate with sucrose, fructose, starch, and soluble solids, indicating a broader role in remobilizing carbon during ripening. Gene-expression data from 'Donghong' further suggest that specific NINV members participate in postharvest sugar accumulation, because several sugar-metabolism genes were upregulated during ripening but inhibited by 1-MCP (Yuan et al., 2023).

3.3 Sugar transport and sink strength

Sugar accumulation also depends on transport capacity and sink strength, because imported assimilates must be unloaded from the phloem and partitioned into storage parenchyma (Falchi et al., 2020). In general, sucrose can be unloaded symplasmically through plasmodesmata or apoplasmically into the cell wall space, after which SUTs, SWEETs, or hexose transporters mediate membrane transfer (Braun, 2022). Work across crops shows that these transporters strongly influence sink development, soluble sugar levels, and carbon allocation (Braun et al., 2014; Li et al., 2021). In kiwifruit leaves, Zhang et al. (2026) found that SPS in source tissues is itself a central regulator of sucrose synthesis and export capacity, and distinct SPS isoforms appear to differ in their contributions to whole-plant carbon allocation.

For kiwifruit fruit specifically, the strongest anatomical and tracer evidence supports predominantly apoplastic phloem unloading in the flesh during development. This conclusion contrasts with an earlier metabolite-based inference of symplastic unloading, showing that the unloading route remains somewhat debated (Nardozza et al., 2013). Within this apoplastic framework, low cell wall acid invertase but high sucrose synthase activity suggests that post-unloading sucrose is metabolized mainly through the sucrose synthase pathway rather than extensive extracellular hydrolysis (Chen et al., 2017). More broadly, sugar partitioning in fruit tissues depends on the interaction between unloading route, transporter function, and sucrose-cleaving enzymes that maintain concentration gradients and sustain sink activity.

4 Regulation of Organic Acid Metabolism in Kiwifruit

4.1 Biosynthesis and accumulation of major organic acids

Citrate in kiwifruit is formed through the tricarboxylic acid cycle in mitochondria, and its accumulation depends on both strong synthesis and restricted degradation (Baiquan et al., 2018). In developing kiwifruit, citrate often accumulates continuously and becomes the predominant contributor to total acidity by harvest, as shown in both 'Hongyang' and 'Hayward' backgrounds (Fu et al., 2023). Jia et al. (2023) conducted enzyme activity analyses in *Actinidia eriantha* and found that high citrate accumulation was associated with increased citrate synthase activity, accompanied by decreased activities of mitochondrial aconitase and NAD-dependent isocitrate dehydrogenase. These findings suggest that substantial citrate accumulation may result from the combined effects of enhanced biosynthetic flux and reduced citrate utilization. This interpretation is consistent with broader fruit studies showing that citrate synthesis is controlled by the pyruvate-to-acetyl-CoA-to-citrate pathway and that TCA-cycle protein abundance can shift citrate accumulation capacity (Zheng et al., 2021; Wu et al., 2025).

Malate and quinate show distinct developmental trajectories from citrate. In kiwifruit, malate often peaks earlier or accumulates less strongly than citrate, while quinate is high in young fruit and declines during development (Qi et al., 2025). In *A. eriantha*, malate accumulation increased during fruit development and was positively associated with titratable acidity, with NAD-MDH and PEPC identified as major synthetic drivers and AeMDH2