in hardy kiwifruit the accumulation period can also vary by cultivar (Lin et al., 2022). Enzyme and transcript data indicate that AGPase is a key determinant of starch accumulation, while AMY, BAM, SPS, SUS, and related enzymes regulate starch degradation and sugar production during maturation and ripening (Shu et al., 2023).

2.2 Organic acid composition and metabolic dynamics

The dominant organic acids in kiwifruit are citric acid, quinic acid, and malic acid, although their proportions vary among species, cultivars, and developmental stages. Quinic acid is often abundant in young fruit and contributes strongly to the characteristic acidity of fresh kiwifruit (Fu et al., 2023). During development, quinic acid generally declines, whereas citric acid accumulates progressively and becomes the major contributor to total acidity near harvest in several cultivars including 'Hongyang', 'Hayward', and 'Zesy002' (Lievre et al., 2021). Malic acid usually occurs at lower levels and shows a more variable pattern, including transient early peaks or stage-specific fluctuations rather than a single uniform trajectory.

Acid content also varies systematically across developmental phases. In early growth, glucose and quinic acid tend to accumulate together, whereas the transition to slower growth and maturation is associated with declining quinic acid and increasing citric acid (Lievre et al., 2021). During postharvest ripening, titratable acidity generally falls, and this decline is driven mainly by citrate loss rather than by major changes in malate (Mao et al., 2023). Even so, malic acid can remain stable or increase under some storage conditions, which helps explain differences in perceived acidity after ripening. Mechanistically, citrate and malate accumulation depend on coordinated regulation of synthesis, degradation, and transport, including citrate synthase, aconitase, isocitrate dehydrogenase, NAD-MDH, PEPC, and the citrate transporter AcALMT1 under AcNAC1 control (Jia et al., 2023).

2.3 Cultivar differences in sugar–acid profiles

Substantial cultivar variation exists in sugar–acid profiles among green-, yellow-, and red-fleshed kiwifruit. Comparative studies by Li et al. (2021) show that green-fleshed 'Hayward', red-fleshed 'Hongyang', and hardy 'Kuilv' share the broad pattern of starch accumulation followed by sugar increase, but differ in developmental duration, sugar composition, and acid trajectories. 'Kuilv' matures earlier, has lower late-stage glucose, fructose, quinic acid, and malic acid, but higher sucrose than 'Hongyang' and 'Hayward'. In broader market comparisons, red-fleshed cultivars tend to receive higher consumer preference, with sugar–acid ratio, soluble sugars, and malic acid among the major drivers of liking, while green- and yellow-fleshed cultivars appear more environmentally sensitive (Wang et al., 2025).

Genetic and cultivar-level variation in sugar–acid ratio is therefore a major basis for flavor diversity in kiwifruit. High-sugar or high-dry-matter genotypes accumulate more starch reserves and soluble sugars, while differences in citrate, quinate, and malate metabolism shift acidity and final taste balance (Nardozza et al., 2013). Orchard and carbohydrate-supply effects further modify these inherited tendencies, changing sugar/acid ratios, maturity timing, and sensory quality even within the same cultivar. Kiwifruit development is characterized by a transition from starch and organic acid accumulation to starch remobilization, soluble sugar accumulation, and progressive organic acid remodeling. Although the timing and relative abundance of individual sugars and organic acids vary among cultivars, the overall developmental pattern is relatively conserved (Figure 1).

3 Regulation of Sugar Metabolism in Developing and Ripening Kiwifruit

3.1 Starch metabolism and sugar release

During early fruit development, net starch synthesis begins after cell division and becomes a major feature of the slower enlargement phase (Kang et al., 2021). Comparative metabolic analyses identify AGPase as a key control point for starch accumulation, with high-starch genotypes showing 2- to 5-fold higher and more sustained AGPase activity than low-starch genotypes. Additional evidence indicates that SPS also contributes to maximizing starch accumulation, likely through sucrose cycling that supports carbon supply to the starch pathway (Nardozza et al., 2013). In hardy kiwifruit, expression correlations further suggest genotype-specific regulation, with neutral invertase positively associated with starch and fructokinase linked to the conversion of fructose into starch in some cultivars (Lin et al., 2022).