

of the recommended fertilization rate did not provide additional benefits and may instead increase the risks of soil acidification and ammonium toxicity (Quaggio et al., 2019). Excessive potassium application may also cause nutrient imbalance. For example, in hydroponically grown lemon, high potassium concentrations reduced the overall uptake of phosphorus, calcium, magnesium, boron, manganese, and zinc, with these effects being particularly evident under the 6 mM potassium treatment (Papadakis et al., 2023).

Therefore, the positive effects of potassium fertilization on citrus fruit enlargement can only be achieved consistently when fertilizer rate, potassium source, application timing, cultivar characteristics, rootstock traits, and water availability are properly coordinated. Rational potassium management should be based on local production conditions and tree nutrient requirements, rather than simply increasing potassium input.

## **4 Effects of Potassium Fertilization on Sugar Accumulation**

### **4.1 Potassium regulation of carbohydrate metabolism**

Potassium regulates sucrose degradation during the early stage of citrus fruit development and sucrose resynthesis during the later stage, thereby affecting sugar accumulation in fruits. Wu et al. (2021) reported that potassium application in Cara Cara navel orange increased the cleavage activities of invertase and sucrose synthase (SS) during the early fruit development stage, promoting sucrose degradation into fructose and glucose. During the later ripening stage, potassium enhanced the synthesis direction activity of sucrose synthase and increased the activity of sucrose phosphate synthase (SPS), indicating that potassium promotes sucrose resynthesis during fruit maturation. This stage-dependent regulatory pattern is consistent with the general characteristics of citrus sugar metabolism, in which sucrose is the major storage sugar in citrus fruits. As a rate-limiting enzyme in sucrose biosynthesis, SPS generally shows increasing expression levels during fruit maturation and is positively correlated with sucrose accumulation (Lu et al., 2024). Studies on other fruit crops also provide supporting evidence, showing that potassium generally enhances SPS and SS activities, thereby promoting the accumulation of sucrose, glucose, and fructose and shifting carbon metabolism toward higher sugar accumulation (Zhang et al., 2018; Wang et al., 2024).

Potassium also promotes sugar accumulation by enhancing phloem loading, long-distance transport, and the capacity of fruits to absorb carbohydrates. In Newhall navel orange, <sup>13</sup>C tracing analysis showed that potassium application increased <sup>13</sup>C-sucrose accumulation in fruits during the enlargement stage and increased both <sup>13</sup>C-sucrose and <sup>13</sup>C-glucose contents during the coloration stage, demonstrating that potassium enhances carbon transport from source leaves to sink fruits (Wu et al., 2024). The study further indicated that approximately half of the sugars in citrus fruits originate from transported carbohydrates, and potassium strengthens carbon flow between source and sink tissues by regulating the symplastic loading pathway.

In Nanfeng mandarin, continuous foliar application of K<sub>2</sub>SO<sub>4</sub> throughout fruit development increased soluble sugar content, mainly due to enhanced fruit sink strength and sugar transport capacity induced by potassium (Thu et al., 2024). This transport-centered regulatory model is also supported by broader studies in plant nutritional physiology, which demonstrate that potassium is closely associated with the translocation of photosynthetic products from source leaves to sink fruits (Shah et al., 2024; 2025).

### **4.2 Molecular mechanisms of potassium-induced sugar accumulation**

One of the important molecular mechanisms by which potassium promotes sugar accumulation is through enhancing the expression of sugar transport-related genes in leaves and fruits. In Nanfeng mandarin, foliar application of K<sub>2</sub>SO<sub>4</sub> increased the expression of CsCWINV-2/6 in the segment membrane tissues and enhanced the expression of CsSUT-1/2 and CsVPP-1/2 in juice sac tissues, linking potassium nutrition with stronger fruit sink activity and sucrose unloading processes (Thu et al., 2024). In Newhall navel orange, potassium enhanced symplastic loading capacity, increased carboxyfluorescein signal intensity, and promoted plasmodesmata density in leaves, indicating that potassium not only affects the expression of sugar transport proteins but also modifies the structural pathways involved in carbohydrate transport (Wu et al., 2024). Sugar storage in citrus fruits also depends on vacuolar transport capacity. A proteomic study by Mao et al. (2024) revealed that tonoplast