capacity, fruit weight, and pulp proportion. These effects were associated with enhanced cell division, improved cell membrane integrity, and more efficient assimilate transport (Sahu et al., 2022). However, responses to boron application in blueberry production are not always consistent. Although foliar or soil boron application can improve plant boron nutritional status, it does not necessarily increase berry weight, suggesting that fruit enlargement responses to boron depend on whether plants are actually limited by boron availability, as well as on cultivar characteristics and environmental conditions (Leon-Chang and Bryla, 2024).

The effects of boron on fruit tissue strength are mainly associated with its regulation of cell wall structure. Most boron within plants is located in the cell wall, where it contributes to tissue formation by maintaining cell wall integrity and mechanical stability. Zhang et al. (2022) found that boron deficiency increased cell wall porosity, disrupted cellulose arrangement, and reduced cell wall mechanical strength, thereby promoting tissue weakening and fruit softening. In fruit crops, boron supplementation generally delays softening by reducing the activities of cell wall-degrading enzymes, such as polygalacturonase and pectin lyase, while maintaining interactions between boron and structural components including pectin, cellulose, and hemicellulose (Zhang et al., 2024; Álvarez-Herrera et al., 2025). Studies in strawberry have shown that foliar boron application can increase fruit firmness and extend shelf life, while appropriate boron supply similarly improves pulp firmness in pitaya (Sahu et al., 2022; Zhang et al., 2024). However, in blueberry, the direct effects of boron on fruit firmness remain highly variable. Leon-Chang and Bryla (2024) reported that boron treatments increased boron concentrations in leaves and fruits but did not significantly improve berry firmness. Thus, although boron has a clear physiological basis for maintaining fruit firmness, whether this function translates into measurable firmness improvement depends on specific cultivation conditions and plant nutritional status.

4.2 Boron effects on carbohydrate metabolism and quality formation

Boron participates in carbohydrate metabolism and sugar transport in plants, and boron deficiency can affect photosynthetic efficiency as well as the translocation and distribution of photosynthetic products within the plant. Overall, sugar accumulation in fruits is regulated by the coordinated effects of multiple factors, including the activities of related metabolic enzymes, sugar transport processes, mineral nutrition status, and environmental conditions (Du et al., 2024; Wu et al., 2025). In sweet cherry, boron application can induce sugar homeostasis pathways and promote the accumulation of fructose, glucose, and organic acids during early fruit development (Michailidis et al., 2023). In pitaya, boron supply increased soluble solids, sugar content, and total carbohydrate levels, while enhancing the activities of invertase and sucrose synthase, indicating that boron participates in assimilate metabolism regulation during fruit maturation (Sahu et al., 2022). Similar trends have been observed in blueberry, although the positive effects appear to be relatively limited. For example, Leon-Chang and Bryla (2024) found that boron fertigation or foliar application did not significantly increase yield or berry size, but soluble solids content increased in some cultivars, suggesting that boron may promote sugar accumulation without necessarily causing concurrent changes in external fruit characteristics.

Because sugars, organic acids, and their balance are key determinants of fruit flavor, boron nutrition can indirectly regulate flavor development by influencing carbon metabolism and fruit biochemical processes. Reviews of various fruit crops have shown that boron application generally increases soluble solids content, regulates titratable acidity and pH, and contributes to the maintenance of ascorbic acid levels, all of which are closely associated with sensory fruit quality (Thakur et al., 2023; Álvarez-Herrera et al., 2025). In citrus, Luo et al. (2024) reported that excessive boron supply reduced soluble solids, sugar content, vitamin C concentration, and sugar-acid ratio, indicating that both boron deficiency and excessive boron availability may negatively affect flavor-related quality formation. In blueberry, direct evidence regarding the effects of boron on flavor quality remains limited. However, increases in soluble solids content observed in some cultivars following foliar or fertigation-based boron application suggest that, under appropriate conditions, boron may contribute to the development of sweeter fruits (Leon-Chang and Bryla, 2024).