Calcium nutritional regulation in blueberry is highly complex. Doyle et al. (2021) systematically summarized the physiological processes involved in calcium nutrition in blueberry and indicated that calcium uptake into fruit mainly depends on xylem transport. However, as fruit development progresses toward maturity, reduced fruit transpiration limits calcium accumulation. Previous studies have shown that calcium concentration in blueberry fruit generally declines from approximately 0.2% during early development to below 0.05% at maturity. Consequently, preharvest calcium application has received considerable attention, although its effectiveness varies substantially depending on cultivar, application timing, and treatment method. Some studies have demonstrated that calcium treatments can increase fruit firmness and reduce weight loss and decay incidence, whereas others have reported limited effects on fruit calcium concentration, firmness, and shelf-life improvement (Lobos et al., 2021b; Hirzel, 2023; Lopes et al., 2026).

Boron is another essential nutrient involved in blueberry growth and quality formation. It contributes to the maintenance of cell wall and membrane functions and plays important roles in pollen germination, pollen tube elongation, cell expansion, and fruit development (Álvarez-Herrera et al., 2025). Blueberry has a relatively short flowering and fertilization period and is therefore highly sensitive to boron availability. Boron deficiency is more likely to occur under conditions of low organic matter content, coarse-textured soils, or drought stress. Studies have shown that foliar or fertigation-based boron applications can increase boron concentrations in blueberry leaves, roots, and fruits; however, improved boron status does not necessarily translate into increased yield, fruit weight, or firmness (Arrington and DeVetter, 2017; Leon-Chang and Bryla, 2024). In addition, because the optimal range of boron availability is relatively narrow, excessive application may cause toxicity, highlighting the need for precise boron management.

Both calcium and boron participate in cell wall stabilization, membrane maintenance, and fruit quality development. In several fruit crops, combined calcium and boron applications have been shown to further improve fruit firmness and storage performance. However, blueberry responses to calcium and boron nutrition remain highly variable, which may be associated with differences in nutrient uptake capacity, transport efficiency, cultivar characteristics, developmental stage, and environmental conditions. This study analyzes the effects of calcium and boron nutrition on blueberry fruit firmness and storage quality, with particular emphasis on firmness maintenance, weight loss regulation, and postharvest quality stability. The aim is to provide a theoretical basis for precision nutrient management and quality improvement in blueberry production.

## 2 Physiological Basis of Blueberry Fruit Firmness Formation

### 2.1 Cell wall structure and firmness development

Pectin is one of the major components determining fruit firmness and is primarily distributed in the middle lamella and primary cell wall. In the middle lamella, pectin regulates adhesion between adjacent cells, whereas in the primary cell wall, pectin forms a hydrated matrix structure that influences cell wall strength and porosity characteristics (Posé et al., 2019; Huang et al., 2023). Blueberry fruit texture is closely associated with pectin composition. Pectin maintains intercellular connections, while changes in pectin solubility and side-chain structure are highly consistent with the decline in fruit firmness during ripening. Hemicellulose and cellulose also contribute to fruit firmness by strengthening the structural framework of the cell wall. Chea et al. (2019) found that blueberry fruits with higher firmness or stronger crispness generally contained higher levels of hemicellulose polysaccharides and cellulose. In particular, hemicellulose content showed a positive correlation with fruit firmness during fruit development. Although cellulose content typically changes less markedly than matrix polysaccharides during ripening, its interactions with pectin and hemicellulose remain an important basis for maintaining cell wall mechanical properties (Wang et al., 2018).

Fruit softening is mainly driven by cell wall degradation processes, including pectin solubilization and depolymerization, matrix polysaccharide remodeling, and the loss of neutral sugars from pectin side chains (Wang et al., 2018; Huang et al., 2023). In blueberry, fruit firmness decreases progressively during ripening, with the most pronounced decline occurring between the light-green and red-purple stages. This reduction is generally