accompanied by disruption of parenchyma tissue microstructure, degradation of cell wall materials, increased levels of water-soluble pectin, and decreased contents of hydrochloric acid-soluble pectin and hemicellulose (Chea et al., 2019). During ripening, the activities of enzymes associated with cell wall loosening gradually increase. Changes in the activities of polygalacturonase, α-arabinofuranosidase, β-galactosidase, and xylanase-related enzymes during late ripening collectively contribute to the degradation of pectin and hemicellulose, thereby accelerating fruit softening (Hocking et al., 2016; Chea et al., 2019).

2.2 Calcium-mediated regulation of cell wall stability

Calcium primarily enhances cell wall stability by binding to de-esterified homogalacturonan (HG) regions, forming cross-linked calcium pectate networks that strengthen pectin gel structure and improve intercellular adhesion, thereby increasing fruit tissue stability. This process depends on pectin methylesterase-mediated de-esterification of pectin, as block-wise de-esterified homogalacturonan provides binding sites for Ca^{2+} cross-linking (Huang et al., 2023). Calcium-pectin interactions are particularly important in the middle lamella and tricellular junction regions, which serve as key sites for cell adhesion. Calcium stabilizes these cell connection areas and enhances tissue resistance to cell separation caused by internal turgor pressure (Wang et al., 2018). In blueberry, Doyle et al. (2021) found that higher fruit calcium concentrations were generally associated with increased tightly bound pectin, reduced loosely bound pectin, lower pectin solubilization, and decreased postharvest softening and water loss, indicating the important role of calcium in maintaining cell wall stability.

Studies have further demonstrated that calcium improves fruit firmness retention by maintaining cell membrane integrity and structural stability (Doyle et al., 2021; Lopes et al., 2026). Calcium deficiency often results in increased membrane leakage, abnormal cell wall degradation, and impaired fruit tissue development (Hocking et al., 2016). Although calcium plays important physiological roles in blueberry production, its accumulation in fruit is relatively limited. This is mainly because calcium is transported predominantly through the xylem and has restricted mobility via the phloem, while fruit calcium concentration generally declines during fruit development. These physiological constraints contribute to the variable quality responses observed following calcium fertilization in blueberry production (Manzi and Lado, 2019; Doyle et al., 2021).

2.3 Boron functions in cell wall formation and fruit development

Boron contributes to cell wall stability by promoting covalent cross-linking between two rhamnogalacturonan-II (RG-II) domains, forming borate diester bridges within pectic polysaccharides of the primary cell wall (Sechet et al., 2018). Under sufficient boron supply, most RG-II molecules can form dimer structures. Although RG-II represents only a minor fraction of total pectin, its cross-linking status has a substantial influence on cell wall mechanical properties and porosity. The absence of boron-mediated RG-II cross-links results in abnormal cell wall properties, reduced structural stability, and impaired plant growth. In contrast, the combined action of calcium and boron can partially alleviate defects in cell wall integrity caused by impaired pectin cross-linking (Feng et al., 2018; Sechet et al., 2018). Begum and Fry (2023) further demonstrated that boron-mediated RG-II cross-linking affects not only local cell wall architecture but also broader pectin organization by enhancing homogalacturonan-calcium interactions and reducing cell wall porosity.

The effects of boron on fruit development extend beyond pectin cross-linking and also involve the regulation of cell expansion and normal tissue growth (Funakawa and Miwa, 2015; Begum and Fry, 2023). When RG-II dimerization is disrupted, plants commonly exhibit reduced growth, restricted cell expansion, and abnormal cell wall permeability, indicating that boron-dependent cell wall organization is essential for maintaining normal cellular expansion and development. Begum and Fry (2022) reported that borate cross-linking primarily occurs within the endomembrane system during pectin biosynthesis, while some dimerization processes may continue after pectin secretion into the cell wall. This suggests that boron availability during active growth stages may influence cell wall assembly both before and after pectin deposition. In blueberry production, boron has also received considerable attention due to its close association with reproductive growth and young fruit development