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Review

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Review

Effect of Boron on Fruit Quality: A Review

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Abstract

Boron is a crucial micronutrient for the initial formation, development, and final quality of fruits, as it affects their physical and chemical properties and helps prevent various functional disorders. Recently, numerous physiological disorders in fruits have been reported, which have been linked to boron deficiency. However, there is still uncertainty about whether these issues are directly related to boron, other nutrients, their combinations, or environmental conditions. This review aims to compile current and accurate information on how boron is absorbed by plants, its role in the cell wall and membrane, its impact on flowering and fruit set, and its influence on the physical and chemical properties, as well as its role in preventing physiological disorders. The review examines the latest studies on boron published in major scientific journals (Elsevier, Springer, MDPI, Frontiers, Hindawi, Wiley, SciELO). Boron is mobile in the xylem and slightly mobile in the phloem, and it plays a crucial role in pollination and fruit set. It reduces mass loss, maintains firmness, improves color, and results in larger, heavier fruits. Also, boron increases soluble solids, regulates total titratable acidity and pH, decreases respiration rate, and stabilizes ascorbic acid by delaying its breakdown. It also helps prevent disorders such as splitting, cork spots, internal rot, shotberry in grapes, blossom end rot, and segment drying in citrus. Foliar or soil application of boron enhances fruit yield and postharvest quality.

Keywords: fertilization; preharvest; postharvest; ripening; fruit development; physiopathy

1. Introduction

Improper fertilization management can lead to physiological problems in plants, resulting in disease processes that impact fruit quality [1]. In this context, boron (B) is involved in forming borate-pectin complexes that strengthen cell walls, improve chemical properties, and enhance the sensory attributes of fruits [2]. However, boron content in tropical soils is generally low because the primary source of the element is organic matter, and its deficiency in plants limits agricultural production [3].

B deficiency is linked to multiple problems in fruits, directly impacting physical and chemical properties and ultimately reducing commercial quality [4]. B has a structural role and is critical for the architecture of fruit walls and membranes. Thus, its deficiency weakens cell walls by limiting the formation of dRG-II-B complexes (rhamnogalacturonan II-borate dimers) [5], leading to cracking, deformities, reduced mechanical resistance, and faster deterioration, which decreases post-harvest storage. From a physiological standpoint, B deficiency causes conditions such as corky spots (abnormal suberization), internal rot (activation of enzymes that degrade the cell wall), blossom end rot (involvement in calcium mobility), and segment drying in citrus fruits (dehydrated vesicles) [4]. Additionally, metabolically, the absence of B reduces sugar transport, alters acidity and pH, raises respiration rates, accelerates degradation of ascorbic acid, and diminishes fruit color intensity [6]. It also results in decreased fruit mass, size, and overall yield due to its role in pollen germination and pollen tube extension [7].

Applying B significantly enhances fruit quality by reinforcing cell walls and stabilizing lipid bilayers through complexes with glycoproteins, which regulate cell permeability and signaling, consequently, it reduces fruit weight loss, prevents deformation, and increases firmness by inhibiting enzymes such as polygalacturonase (PG) and pectin methyl esterase (PME) [8]. Furthermore, it modulates the synthesis of anthocyanins and offers protection against oxidative stress, improving the fruits' color intensity [9]. B also raises soluble solids in fruits by facilitating efficient carbohydrate transport [10]. Adequate B levels decrease fruit respiration, prolonging energy reserves and limiting mass loss [11]. Studies on pear, strawberry, and avocado indicate that foliar B applications improve pollen germination and enhance fruit set and retention, leading to higher yields [7,12,13].

Applying boron shows great potential for enhancing fruit quality in various crops; however, a detailed review of its specific effects on fruit quality is still needed. Therefore, this study aims to gather information about the effects of B on fruit production and quality.

2. Plant Uptake of Boron

Boron is the most mobile micronutrient in the soil. It moves via passive diffusion without the need for protein catalysis or energy use [3], making it highly prone to leaching (pH below 5.0) and one of the most deficient elements in the soil [14]. However, the optimal concentration is 2 mg kg^{-1} [15], because higher levels are considered toxic to plants [16]. Boron in soil exists as undissociated boric acid [$B(OH)_3$] in acidic and neutral soils (pH < 7.0) and as borate anion $[B(OH)_4]^-$ in alkaline soils (pH > 8.5). Therefore, its availability depends on pH, being less available at alkaline pH levels [4].

Plants absorb boron as boric acid through plasma membrane channels, and it is then transported via specific carriers in the form of $[B(OH)_4]^-$ [5]. In this context, two types of boron transporters have been identified: one called BOR1, which is crucial for moving B through the xylem and to younger plant tissues, and another made up of a subgroup of aquaporins known as nodulin-26-like intrinsic proteins (NIPs), which act as channels for transporting boric acid, essential for plant growth and delivering B to new shoots [17] (Figure 1).

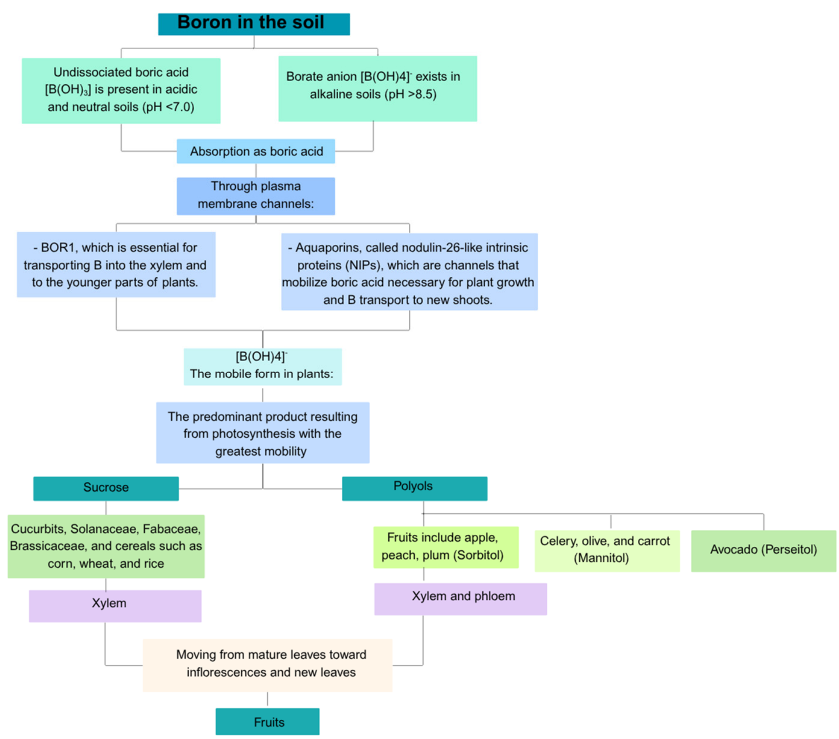

Figure 1. Boron transfer from the soil to the fruits.

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Boron mobilization and distribution in both xylem and phloem depend on the dominant photosynthesis product, which has the highest mobility in each species. When sucrose is the primary carbohydrate transported—such as in cucurbits, solanaceae, fabaceae, brassicaceae, and cereals like corn, wheat, and rice—B primarily moves within the xylem, relying on the transpiratory flow because B binds to sucrose and forms insoluble complexes [18]. Conversely, B is mobile in both xylem and phloem in species that transport primary products like polyols, including apple, peach, and plum (sorbitol), as well as celery, olive, and carrot (mannitol). In these plants, B forms stable complexes with polyols, such as boropentahydroxyl sorbitol, which enables its movement through the phloem and redistribution to younger tissues [19]. For example, in avocado, Minchin et al. [20] report that B forms a complex with perseitol, the polyol form of D-mannoheptulose, and is transported via the phloem from mature leaves to inflorescences and new growth.

It has been observed that, depending on the phenological state of the plant, species vary in their polyol production, which causes changes in B mobility within the phloem. In this regard, during reproduction and fruit filling, low polyol production occurs, affecting the B transporters that supply the reproductive shoots [21].

3. Boron in the Cell Wall and Membrane

Boron in plants is mainly stored in the cell wall, where it acts as a borate bridge that links with the polysaccharide rhamnogalacturonan II (RG-II) to form the dimer RG-II bound to boron (dRG-II-B) and contributes to pectin formation [2]. Under B deficiency, the demethylation of new pectin is hindered [22], with only 10% to 20% being incorporated into the cell wall as dRG-II-B, whereas more than 80% of B remains in its dimeric form. Therefore, the ratio of dimers can serve as an indicator for diagnosing B deficiency in plants [15]. Similarly, the amount of B correlates with the development and lignification of secondary walls [23]. B is crucial for cell wall adhesion because it forms a complex with RG-II and glycosyl inositol phosphoryl ceramides (GIPC) in the cell membrane, confirming its role in the pectin matrix formed by cellulose, hemicellulose, and proteins. This helps maintain the wall's rigidity and thickness and is vital for proper assembly, ensuring the structural and functional stability of the cell wall [24].

B plays a structural role in the membrane by forming cis-diol complexes with glycoproteins, which improves the stability and function of the lipid bilayer [3]. These complexes form through boron's interaction with hydroxyl groups in the cis configuration of mobile sugar residues, such as apiose, found in glycoproteins and glycolipids, thereby stabilizing their structure and facilitating their involvement in cell signaling and adhesion. This interaction is also crucial for maintaining the integrity, fluidity, and permeability of the cell membrane [25].

Another role of B in the cell membrane is regulating electron transport [16]. In this context, Malavé [26] explains that the autoinducer AI-2 is made of a furanosyl borate diester, which not only acts as a bacterial signal but also transports B into and out of the cell. Similarly, it was observed that as water stress increases, these channels reduce their activity, limiting B transport and causing B deficiency [27]. Likewise, the activity of the B transporter (AtBOR1-1) heavily depends on the B level in the soil [3].

B deficiency impacts the membrane potential because it decreases ATPase activity in proton pumping, alters the electrochemical gradient across the membrane, and reduces the activity of enzymes like Fe-reductase, superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and antioxidants such as ascorbic acid (ASA) [15]. Additionally, under stress conditions and B deficiency, levels of phenolic compounds and other derivatives, such as quinones, increase, which can be oxidized and accelerate reactive oxygen species (ROS) production [5].

4. Effect of Boron on Flowering and Fruit Set

Boron is a vital element during flowering and fruiting in crops, and its deficiency is linked to low fruit set. This leads to underdeveloped pistils, reduced pollen viability, smaller flowers, and floral abortion. These issues are connected to decreased carbohydrate translocation and lower starch content in these structures [28,29]. In this context, Botelho et al. [30] note that boron is particularly immobile in most plant tissues of particular species and faces difficulty translocating from source organs to young buds, where it is essential for pollen production, pollen tube growth, and other reproductive processes.

The role of B in the cell wall and membrane is evident in the growth and development of the pollen tube, because the gene responsible for borate binding to RG-II is highly active in pollen tubes, influencing flower fertility and the development of reproductive tissues [29]. In this regard, it was observed that once pollen germinates, pollen tubes extend through apical growth via secretory vesicles transported to the tip by cytoplasmic flow [31]. These vesicles bind to the plasma membrane of the tube and release polysaccharides and pectins into the exterior, where they become part of the cell wall. This ongoing activity enables the elongation of the pollen tube, a structure that grows from its apex and follows a polarized pattern [32].

In this regard, the stigma or style must supply B in flowers to ensure proper pollen tube growth and is essential for the development of female reproductive organs [33]. In this sense, applying 300 mg L^{-1} of boric acid in *Pyrus pyrifolia* had a significant effect on pollen germination and pollen tube growth [34]. They also observed increased weight of the anthers and pollen, and higher boron concentration in the buds. Similarly, in strawberry, Sarıdaş et al. [35] achieved significant increases in pollen viability, up to 71.8%, with foliar (5 g per 100 L^{-1} of Tween 20) and soil (0.5 kg ha^{-1}) application of B. Likewise, Mir et al. [36] (2025) found that applying the sugar-borate complex has a greater translocation capacity than non-ionized or uncomplexed sugars, which enhances the efficiency of carbohydrate transport during pollen germination.

Similarly, in avocado flower styles, the concentration of B has a strong positive correlation with initial fruit set [7]. These authors [7] also state that adding B improves fruit set after self-pollination because self-pollination tubes generally grow more slowly than cross-pollination tubes, which reduces the chances of self-fertilization and fruit set. Furthermore, B is transported in small amounts to flowers and fruits [7]. They mention that in the 'Hass' variety, applying 30 g per tree resulted in higher boron levels in the flowers compared to the control. In this regard, it was suggested that the higher demand for B in reproductive tissues is due to the limited number of vascular bundles that facilitate B movement through transpiration [31]. This necessitates the application of additional foliar boron (B) to the developing reproductive tissues, which promotes the crop's reproductive success even when soil B levels are adequate.

Similarly, foliar application of B has been shown to increase boron levels in flower buds, which enhances initial fruit set, retention, and final fruit set. This has been documented in species such as *Persea americana* [37] and *Punica granatum* [38]. In this context, in *Macadamia integrifolia*, applying 15 g of B before flowering improved fruit set three weeks after peak anthesis. Likewise, a dose of 30 g of B elevated foliar B levels during peak anthesis, contributing to an increase in total yield [39]. Additionally, foliar B applications in gulupa (*Pasiflora edulis* f. edulis Sims) increased flower bud emission, the number of fruits, and the percentage of fruit set with the application of 0.6 kg ha^{-1} of B [28]. They also note that B requirements are higher in reproductive tissues than in vegetative tissues. In sweet cherry (*Prunus avium* L.), boron applications nine days before flowering increased endogenous B content and fruit set [40]. Similarly, in mango, B application reduces the time to fruit set, which is linked to B's role in regulating RNA synthesis, an essential factor in enhancing physiological activity and enabling earlier flowering [41]. Likewise, applying 1% B to pomegranate fruits increased fruit set and retention while decreasing fruit drop compared to the control [42].

With B deficiency, pollen tube secretory activity is impaired due to abnormal swelling or rupture of the apical region. The latter occurs because of cell wall weakness caused by B deficiency, which explains the slow pollen tube growth [43]. Additionally, boron deficiency can disrupt key processes, such as microsporogenesis, leading to decreased pollen production, size, and viability. On the other hand, adequate or high levels of boron in the pistils can promote pollen germination and pollen tube growth, which benefits pollination, fertilization, and, ultimately, fruit setting and yield [7]. However,

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in a study with apple pollen (*Malus domestica*), high boron concentration (0.02%) inhibited both pollen germination and pollen tube growth, accompanied by morphological abnormalities such as short pollen tubes with swollen ends and larger-than-usual diameters [32]. Higher doses (0.2%) significantly decreased pollen germination, reducing the percentage by up to 12.87%.

5. Effect of B on the Physical Properties of the Fruit

Boron is a micronutrient that significantly influences the physical properties of the fruit, as it improves fruit firmness, size, and uniformity, which promotes the development of strong and well-organized cellular structures (Figure 2). Likewise, B is involved in cell wall synthesis, which directly affects fruit quality [5]. In this sense, boron deficiency causes deformation, cracking, and reduced mechanical strength, which limits the marketability and post-harvest life of the fruit [10,23].

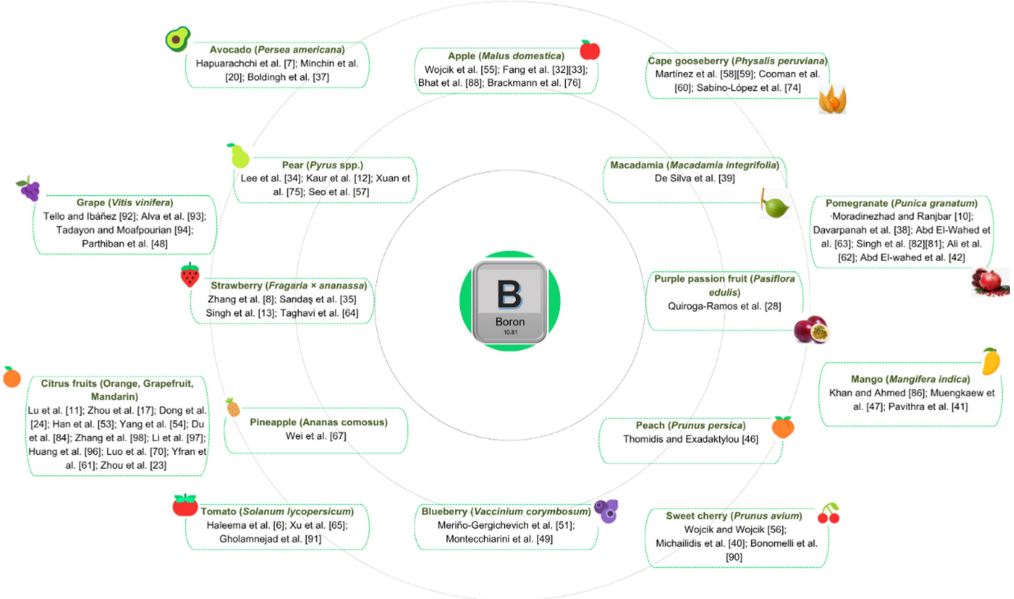

Figure 2. Authors who have reported the effect of boron on different fruits.

5.1. Mass Loss

B plays a vital role in maintaining cell wall integrity, and a deficiency can weaken cell structure and reduce tissue cohesion, making fruits more prone to dehydration and mass loss during storage [4]. In this context, B deficiency often causes abnormal, thick, and fragile cell walls with altered porosity and mechanical strength [44]. It is also noted that boron forms a complex that acts as a bridge with both the RG-II in the cell wall and glycosyl inositol phosphoryl ceramides (GIPC) in the cell membrane [45], which helps explain why B significantly influences the mechanical strength of fruits. Additionally, B deficiency can inhibit the activity of oxidoreductase, an enzyme bound to the plasma membrane involved in increasing the output of potassium and organic compounds, leading to faster water loss in deficient fruits [44]. Adequate boron supply is essential for minimizing fruit mass loss, as observed in a study on peaches where immersing fruits in 6 μg mL^{-1} of Power B reduced mass loss to only 6%, compared to 18% in the control [46]. Similarly, an application of 3% boric acid to pear fruits caused a significant reduction in mass loss, with only 3.2% compared to 5.4% in control fruits, demonstrating the effectiveness of B in decreasing post-harvest dehydration and preserving fruit quality during storage [12]. Moreover, spraying mangoes with 1 mL L^{-1} of Ca-B delayed mass loss, while also increasing cell wall thickness and decreasing intercellular space in the exocarp [47]. Likewise, a 10.18% reduction in mass loss with the application of 0.1% boric acid combined with 0.2% calcium [48].

5.2. Firmness

Boron affects pectin synthesis, which is crucial for maintaining fruit firmness, as it is distributed within various cell wall components that can induce changes in the parenchyma and the fruit's mechanical strength by impacting the cell wall structure and key chemical elements [49]. In this context, applying B delays fruit softening and improves firmness during postharvest because it reduces the activity of enzymes that break down the cell wall, such as cellulose, polygalacturonase (PG), pectin methylesterase (PME), β-galactosidase (β-Gal), pectate lyase (PL), and α-L-arabinofuranosidase (AFase) [8]. Additionally, these authors [8] found that applying B to strawberry fruits significantly lowered the activity of PG (20.2%) and PL (38.1%), while increasing PME activity by 18.9%. This process reduces pectin breakdown, promotes pectin demethylation, and facilitates B binding to the cell walls, thereby stabilizing the structure and slowing fruit softening [47]. Moreover, during fruit softening and ripening, B bound to the cell wall is transferred to the protoplast and the apoplast, leading to fruit decomposition. However, with B application, this transfer is decreased, which further helps keep the cell wall firm and extends the fruit's postharvest life [8].

The effect of B application on fruit firmness has been documented by various researchers (Figure 3). For example, strawberries harvested from plants treated with B showed 11% greater firmness than control fruits [50]. In strawberries, foliar spraying with 0.1% H_3BO_3 resulted in 45.7% higher yields and fruits that were 25.6% firmer than the control [8]. Similarly, peach fruits of the 'Andross' cultivar immersed in 6 μg mL^{-1} of powdered B exhibited 36.9% more firmness than control fruits [46]. Additionally, applying a 1 mL L^{-1} calcium and boron solution to mangoes significantly delayed fruit pulp softening for up to 21 days after harvest, which was linked to lower activity of PME and PG [47]. Likewise, in the blueberry variety 'Brigitta,' spraying plants with 400 mg L^{-1} B increased fruit firmness by 25%, whereas in the 'Legacy' variety, a dose of 200 mg L^{-1} increased firmness by 48%. However, higher doses than those mentioned decreased firmness values [51].

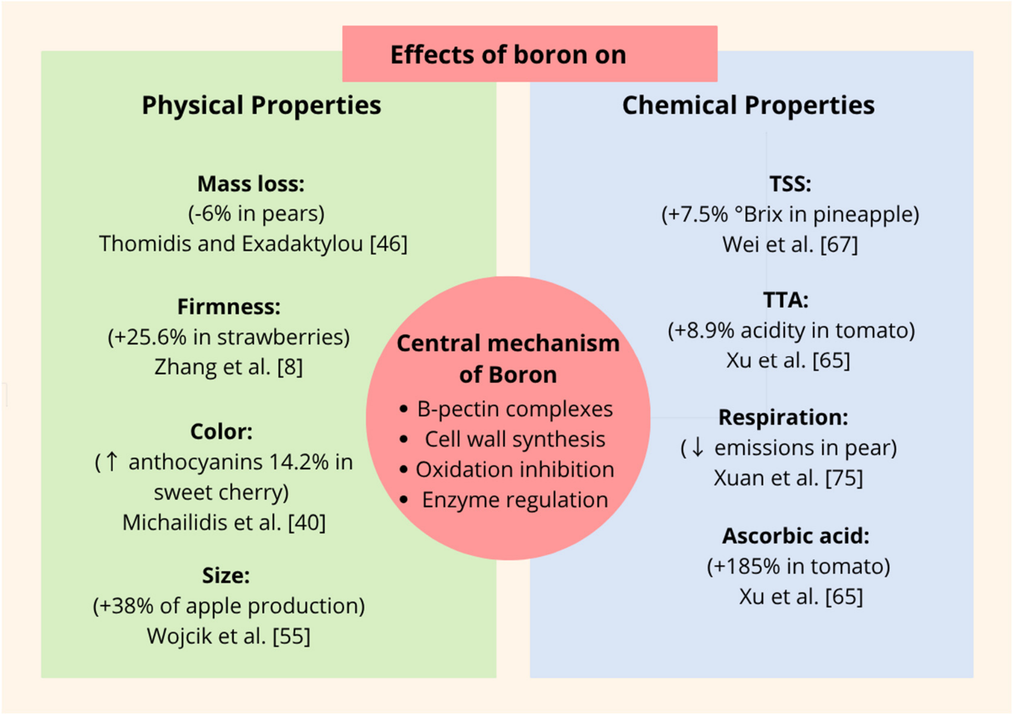

Figure 3. Effects of Boron on the physicochemical properties of fruits.

5.3. Color

Boron is crucial for the structural and functional integrity of cell walls by forming borate-pectin complexes, which prevent the leakage of phenols into the apoplast and their oxidation by polyphenol oxidases (PPOs), thereby reducing browning [52,5]. Similarly, B influences the activity of phenylalanine ammonia-lyase (PAL), and its deficiency suppresses PAL expression, limiting the production of lignin precursors, flavonoids, and anthocyanins, the latter of which are responsible for red, purple, and blue colors [9]. B deficiency is linked to decreased photosynthetic efficiency, which hampers the production and transport of sugars needed for pigment formation [53] and compromises cell membrane stability, leading to increased reactive oxygen species (ROS), lipid peroxidation, and electrolyte leakage. These effects accelerate the degradation of chlorophylls and carotenoids [54] and cause fruit discoloration [48].

In this regard, it was found that soil boron fertilization in apple trees improved fruit color intensity compared to the control, which is attributed to increased photosynthesis and enhanced transport of photoassimilates from leaves to fruits [55]. Likewise, postharvest application of boric acid on pear fruits maintained more negative values in the green-red direction (a*) for longer, indicating greater retention of green color. At the same time, luminosity (L*) and variation along the blue-yellow axis (b*) increased to a lesser extent in treated fruits, indicating that B application preserves chlorophyll pigments and delays carotenoid synthesis [12]. However, pre-harvest boron application did not significantly affect the external color of strawberry fruits; nevertheless, when combined with calcium, fruits showed higher luminosity, a*, and b* values, suggesting that B, in combination with Ca, contributes to the external appearance of the strawberry [13]. Additionally, in 'Buttner's Red' sweet cherry trees, B fertilization increased anthocyanin content, which improved color intensity [40]). In pomegranate fruits, coloration increased with B application [42]. This is attributed to the role of B in the metabolism of phenolic compounds, which promotes the synthesis of pigments that enhance skin color and improve its commercial appeal [56].

5.4. Fruit Size and Mass

Boron is essential for determining fruit size and weight because it stabilizes pectin through dRG-II-B complexes. Therefore, a deficiency reduces tissue elasticity and extensibility, limiting cell expansion during growth, which results in smaller and misshapen fruits [5]. Additionally, boron helps regulate sugar transport via the phloem and plays a role in synthesizing auxins, which are vital for cell division. As a result, a deficiency in this element decreases energy supply and inhibits mitosis in meristems and ovaries [48]. This affects pollination and protein synthesis, reduces dry matter accumulation, and produces fruits with lower weight and insufficient size for marketability. In this context, under limited B conditions, B application helps stimulate new cell wall synthesis and promotes optimal fruit growth by maintaining physical pressure inside and outside the fruit [57].

Boron deficiency reduced the diameter and mass of cape gooseberry fruits by 56% and 86% at harvest [58]. This occurs because the lack of B disrupts the translocation of photosynthates to the fruits, affecting their development and dry mass accumulation. Furthermore, B deficiency in fruits causes reduced size, deformities, and severe tissue damage from rot in the stem insertion area, as well as calyx deformities [59]. Similarly, it was observed that foliar application of a B nano-fertilizer before flowering increased yield in *Punica granatum*, likely due to high boron absorption by flowers, which enhanced metabolic processes like carbohydrate transport [10]. These authors also state that the yield increase may be due to the role of B in pollen germination, pollen tube elongation, and fruit formation, similar to findings in apples, where production per tree increased by 38% and 119% with soil and foliar B applications, respectively [55]. Likewise, both foliar and soil B applications increased fruit size in avocado trees, noting that fruits with higher boron levels have better post-harvest quality and less browning [7].

The effects of B have also been seen in the 'Chandler' strawberry variety, where combining it with calcium increased yield per plant by 20%. This was due to less fruit loss caused by poor quality. However, individual fruit weight was not affected by separate applications [13], similar to findings

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for cape gooseberry fruit [60]. Likewise, in mandarin, a reduction in dropped fruits was observed when a 0.6% Ca-B mixture was applied, which helped to increase the production [61].

6. Effect of B on the Chemical Properties of the Fruit

Adequate B availability improves sugar transport, which increases total soluble solids (TSS) content, and is associated with fruits that exhibit greater sweetness and better organoleptic quality. Furthermore, B plays a role in balancing organic acids, which can alter pH and ATT, enhancing flavor perception and the chemical stability of the fruit. Additionally, this micronutrient is essential in regulating enzymes involved in ripening and cellular metabolism, such as polyphenol oxidase and peroxidase. A deficiency can disrupt these processes, reducing the nutritional and commercial quality of the fruit.

6.1. Total Soluble Solids

The effects of boron on TSS are closely linked to the phloem translocation of sugars and carbohydrate metabolism [10]. Similarly, B stabilizes borate-polysaccharide complexes in membranes and cell walls, which facilitates the transport of photoassimilates from leaves to fruits [5]. Additionally, B regulates enzymes such as invertases and sucrose synthases, which are essential for the hydrolysis and accumulation of sugars in vacuoles [62]. Moreover, a deficiency of this element reduces photosynthetic activity in leaves (resulting in fewer photoassimilates for fruit filling). It increases cellular respiration in fruits, indicating a loss of accumulated substrates [11]. At the same time, B influences pectin synthesis, decreasing osmotic potential and causing water imbalances that dilute TSS, resulting in fruits with lower °Brix and imbalances in the maturity ratio (MR), which affect their organoleptic quality.

In this regard, Moradinezhad & Ranjbar [10] found that foliar application of B significantly increased leaf chlorophyll, soluble carbohydrates, relative water content, and proline in *Punica granatum* fruits [63]. Likewise, the absence of B fertilization decreased the °Brix concentration in cape gooseberry fruits by 40% compared to the control, which received all nutrients [58], similar to findings that B deficiency results in fruits with poor TSS and ascorbic acid accumulation [64]. Similarly, pear fruits treated with 3% boric acid during the first 60 days of storage (DSS) had a delayed increase in TSS, while at the end of postharvest, fruits with B application had higher TSS content and maintained eating quality longer [12]

Moreover, the TSS of strawberry fruits from plants treated with B during storage for 5 days at 10 °C showed 8.2 ° Brix, while the control had higher values (8.5 ° Brix) [13]. This difference is attributed to the effect of B, which reduces respiration rate and helps maintain post-harvest fruit quality by modulating TSS content, delaying softening, and lowering the incidence of pathogens and physiological disorders. Additionally, Xu et al. [65] found that tomato fruits treated with 5.7 mg L^{-1} of H_3BO_3 achieved greater TSS accumulation (5.13 ° Brix) compared to the control (4.63 ° Brix). Likewise, in paprika, increases in TSS were observed with doses of 2 g L^{-1} applied to both soil and foliage [66]. Moreover, the application of 1 and 2 mL L^{-1} of Ca-B resulted in slower growth of RM values, enhanced post-harvest stability, and better preservation of vitamin C, indicating fruits with higher nutritional and antioxidant value [47]. Additionally, apple fruits from trees fertilized with foliar and soil B contained 7.5% higher TSS than the control [56]. On the other hand, the application of B at doses of 0.5 and 1 mg kg^{-1} increased TSS by 6.3 and 7.5%, respectively [67]. Still, doses of 4 mg kg^{-1} reduced TSS and negatively affected pineapple quality [67]. Similarly, in blueberries, applying 200 mg L^{-1} of B increased TSS, while higher doses decreased it [51].

6.2. Total Titratable Acidity (TTA)

Boron influences the synthesis, storage, and breakdown of organic acids. By stabilizing cell walls with borate-pectin, it encourages vacuolar compartmentalization, which prevents acids like malic and citric from leaking into the cytosol [68]. In this context, B deficiency blocks PEP carboxylase activity, thereby decreasing malate production and overactivating NADP-malate dehydrogenase, which accelerates acid breakdown and acid loss through respiration [11]. B deficiency also impacts processes like photosynthesis, limiting the supply of carboxylic precursors and causing oxidative stress that triggers fermentative pathways [60]. This results in unstable TTA, with lower TTA levels in unripe fruits and abnormally high TTA levels in ripe fruits, which impacts taste and reduces shelf life.

In this regard, applying B to pear fruits increased TTA retention by 22.8% to 40% compared to the control [12]. Similarly, foliar and soil fertilization with B in apple trees increased fruit TTA values by 14.2% and 3.1%, respectively, compared to the control, which is attributed to the effect of B on a higher photosynthetic rate and, possibly, greater accumulation of organic acids [55]. Also, the application of foliar and soil B at doses ranging from 1.9 to 5.7 mg L^{-1} of H_3BO_3 resulted in average increases in the TTA of tomato fruits of up to 8.9% [65]. Likewise, increases in TTA were observed in bell pepper fruits with the application of 2 g L^{-1} of both foliar and soil [66]. Similarly, the foliar application of boron in strawberries increased TTA by 3% compared to the control [13]. In contrast, no significant differences in the TTA of pineapple fruits with varying doses of B, ranging between 0.5 and 4 mg kg^{-1}, were found [67]. Conversely, applying B at toxic levels (Borax: 100 g per plant of $Na_2B_4O_7{\cdot}10H_2O$) showed a significant increase in TTA in *Citrus grandis* fruits [70].

6.3. pH

B deficiency affects the synthesis of malic and citric acids and weakens cell membrane and wall integrity, which allows protons (H^+) to leak from vacuoles into the cytosol. This leads to an increased pH during the early stages of fruit growth [71]. However, during ripening, low B levels cause metabolic dysfunction that accelerates the oxidative breakdown of sugars and nitrogenous compounds [72], resulting in the production of acetic and succinic acids, as well as amines, which lower the pH by acidifying the medium [73]. Simultaneously, the inhibition of proton pumps (H^+-ATPases) and changes in tissue buffering capacity [71] result in abnormal pH fluctuations, affecting the fruit's sensory qualities and biochemical stability. It has also been reported that B does not significantly influence the pH values of cape gooseberry fruits [58,74]. Conversely, applying borax at 100 g per plant significantly lowers pH values in *Citrus grandis* fruits [70].

6.4. Respiration Rate (RR)

Boron plays a vital role in the structure of cellular and mitochondrial membranes, affecting their permeability and the efficiency of the electron transport chain [43]. B deficiency increases O_2 consumption and promotes uncontrolled substrate oxidation, which raises respiratory activity in fruits. Likewise, B deficiency influences the activity of citrate synthase and pyruvate dehydrogenase, limiting efficient ATP production [11]. This results in the rapid depletion of fruit acids and carbohydrate reserves, thereby accelerating the senescence process.

In this regard, foliar application of 0.2% boric acid to cherry trees (*Prunus avium* L.) decreased the fruit respiration rate during growth stages from day 12 to 46 after full bloom, compared to the control [40]; however, after this period, no differences were observed between treatments. Similarly, 'Conference' pear fruits treated with B showed lower CO_2 emissions during five months of refrigerated storage [75]. Furthermore, after applying 1.5 kg ha^{-1} of B to apple trees via leaves, the fruits exhibited a lower respiration rate during the first two days of storage; subsequently, the control treatment showed the highest values [76]. In this context, Dar [77] mentions that applying B slightly decreases respiratory activity and affects the activity of enzymes involved in respiration.

6.5. Ascorbic Acid (AsA)

Although B does not directly influence the synthesis of ascorbic acid (AsA), adequate levels of the element are essential to prevent its breakdown and maintain a balanced redox potential [15]. However, B presence affects the activity of L-galactono-1,4-lactone dehydrogenase, a key enzyme in AsA biosynthesis, by limiting the conversion of sugar precursors into vitamin C [78]. Similarly, B

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deficiency causes oxidative damage to cell membranes due to the excessive accumulation of reactive oxygen species [72], which exposes AsA to enzymes like ascorbate oxidase and catalytic metals (Fe^{2+}/Cu^{+}), thereby accelerating its conversion to dehydroascorbic acid. This lowers AsA levels and reduces the nutritional quality and antioxidant defense of the fruits [15].

In this context, applying 3% boric acid to fruits before storage kept 48% higher AsA levels in 'Patharnakh' pears compared to the control [12]. This is due to the role of B in suppressing PPO, thereby delaying oxidative deterioration by reducing the oxidation of phenolic compounds and ascorbate. Similarly, cape gooseberry fruits from plants that received foliar spraying of 3 mg L^{-1} of B showed 21.2% more AsA compared to the control treatment [74]. Likewise, Wei et al. [67] demonstrated that applying B to pineapple fruits had a positive effect on vitamin C content. In tomato, the soil application of B increased AsA content by 185.2% compared to the control [65]. In harrow fruits, it was observed that applying B increased vitamin C and anthocyanin levels [42]. However, treating strawberry fruits with boron did not significantly affect the AsA content [13].

7. Boron in Fruit Functional Disorders

Fruit production and quality depend on proper plant nutrition. Since boron is relatively immobile within the plant, its deficiency first appears in the youngest tissues, impacting crop yields [44]. This mainly occurs in arid or water-scarce areas where sandy soils contain soluble B levels below 0.5 mg kg^{-1} [4]. In such cases, B-deficient plants show reduced activity of the enzyme indoleacetic acid (IAA) oxidase due to increased accumulation of auxin [79] and IAA [80], leading to short, thick stems and rosette formation. This also results in wrinkled leaves and slower leaf growth, ultimately causing fruit issues and a decline in quality.

7.1. Fruit Deformation and Cracking

Fruit deformation and cracking occur due to impaired cell division, among others, caused by boron deficiency (Figure 4a,b,c) [1]. Boron directly contributes to cell wall expansion through the production of pectin, which helps maintain structural integrity [81]. It also plays a role in regulating indole-3-acetic acid (IAA) and enhancing water absorption, both of which support fruit structure and reduce susceptibility to cracking [10]. Foliar application of boron reduces cracking symptoms by improving carbohydrate transport, overall metabolism, and ascorbic acid levels, thereby enhancing fruit quality and postharvest shelf life [4]. In this context, B deficiency causes flower and fruit deformation, resulting in a decrease in their size and quantity [64]. Fertilizing plants with B results in fewer deformed fruits, which correlates with a higher concentration of B in fruits and leaves [64].

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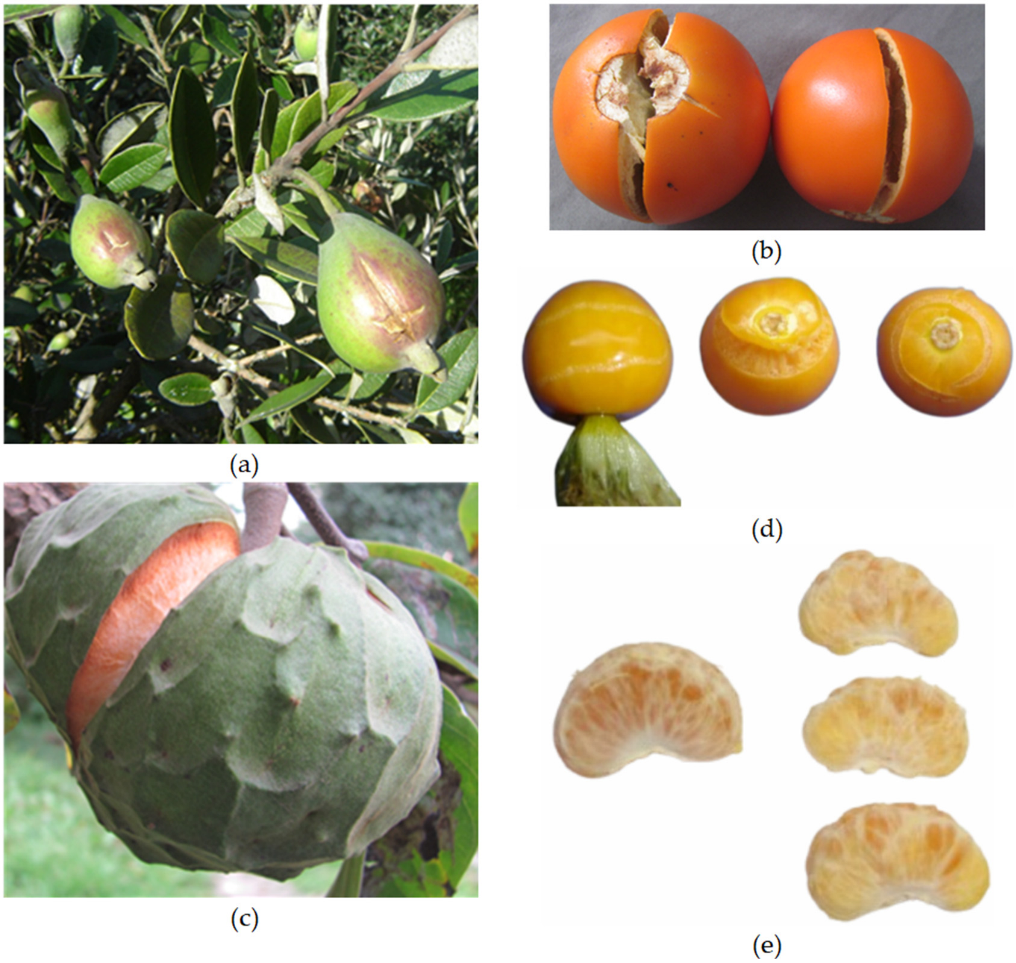

Figure 3. Possible Boron deficiencies in fruits (**a**), cracking in feijoa, (**b**) cracking in *Passiflora edulis*, (**c**) cracking in chirimoya, (**d**) fruit deformation and cracking in cape gooseberry, and (**e**) segment drying in tangerine 'Arrayana'.

The absence of B in the nutrient solution of cape gooseberry plants resulted in a 5.5% to 13% increase in the incidence of cracked fruits [60] (Figure 4d). Therefore, B is essential for maintaining the integrity of the epidermis [60]. These authors also state that during the early growth stage of cape gooseberry fruit, the leaf area proportion exceeds that of the fruit, which could lead to competition for assimilates, causing B deficiency and contributing to cracking [60]. In this regard, applying 0.4% borax to pomegranate fruit reduced cracking by 12% to 20.4% [82]. Also, it was found that pre-harvest foliar application of borax reduced cracking and increased resistance to salt stress in pomegranate fruit [10]. Likewise, borax application decreased fruit cracking and increased sugar, anthocyanin, and vitamin C content [63], consistent with the findings that borax treatment reduced cracking and sunburn in the same fruit [42].

Similarly, the application of 0.1% boric acid + 0.2% calcium reduced grapefruit cracking and fruit drop by 3.46% and 2.42%, respectively [48], while B + putrescine decreased cracking in Asian pears (*Pyrus pyrifolia*), and it was noted that B applied before flowering and after harvest extended the fruit's shelf life [57]. In *Aegle marmelos* (Rutaceae), ripe fruits exhibit cracks due to B deficiency [83]. In grapefruit, applying B decreased the percentage of fruit cracking; however, adding Ca and Ca + B further reduced cracking, indicating that combined applications significantly improve crack prevention [84].

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7.2. External Corking

Boron promotes the formation of borate-pectin complexes in the middle lamella. Therefore, a deficiency in this element weakens cell adhesion and causes micro-tears in the hypodermis [5]. These lesions trigger a repair process in which damaged cells accumulate phenolic compounds and activate an overexpression of enzymes such as polyphenol oxidase, which generates quinones that cause oxidation [85]. This stimulates uncontrolled lignification and suberization, resulting in rigid, rough patches (corky spots) that ultimately lead to depressed, necrotic areas, reducing fruit quality.

In this regard, Khan and Ahmed [86] mention that inadequate B supply causes corky spots both internally and externally in mango fruits. They also state that foliar application of B is more effective than soil application and that it improves fruit quality. Similarly, it was noted that B deficiency causes hardening of the fruit's internal tissue, giving it a dry, corky appearance [87]. They report that the incidence of bitter spots averaged 13% across different varieties [87]. They also found that native Indian cultivars are more susceptible to physiological disorders than exotic cultivars, and that fruits with these disorders have lower concentrations of B and Ca [87]. At the same time, other nutrients remained at similar levels compared to healthy fruits.

The application of 1.5 g L^{-1} of B resulted in a 65% reduction in bitter spots (bitter pit in apples) and increased yield by 60.8% [88]. However, they note that applying 2.5 g L^{-1} of Ca plus 2 g L^{-1} of B successfully reduced bitter spots by 90.4% and increased yield by 107% [88]. Thus, they conclude that the individual use of B and Ca has positive effects, but combining these two elements further enhances the benefits to the fruits [88].

7.3. Internal Rot (Brown Rot)

Boron enhances the structural integrity and biochemical resistance of tissues. Therefore, a deficiency of this element causes cell walls to weaken [5]. This facilitates the rupture of parenchymal cells, creating cavities that fill with sugars and nutrients. Along with damage to cell membranes, this releases enzymes such as polygalacturonase that break down the pectic matrix, resulting in watery, brown, and foul-smelling areas. This promotes the growth of endophytic fungi (*Fusarium*, *Botrytis*, *Rhizopus*) and bacteria, which accelerate tissue decay [89].

Similarly, B deficiency decreases the synthesis of phytoalexins and polyphenols involved in plant defense by disrupting the phenylpropanoid pathway and inhibits lignification in vascular tissues, which allows pathogens to grow and cause internal fruit decay. In this context, applying B to peach fruit reduced internal rot from 53.2% to 5.2% [46]. Likewise, in mango fruits, internal rot is linked to B deficiencies and excess nitrogen, and it is noted that applying 500 g of Borax to the soil and 1% foliar B significantly reduces internal necrosis [83]. Additionally, in amla (*Indian gooseberry*), internal necrosis in fruits has been reported, and biweekly foliar application of 0.6% Borax resulted in a notable increase in B levels in leaves and fruits, along with a reduction in internal browning [83].

7.4. Blossom End Rot (BER)

Boron plays a crucial role in the disease known as Blossom End Rot (BER), as it facilitates efficient calcium mobilization and promotes cell wall integrity [6]. Boron deficiency disrupts calcium pectate formation, which weakens cell cohesion at the fruit apex [90]. Similarly, boron regulates the expression of ATPases, so its deficiency reduces the flow of Ca^{2+} into the phloem, limiting its role in membrane stability and cell signaling [6]. This triggers a loss of turgor and selective permeability, resulting in watery, sunken, and brown lesions characteristic of BER in tomatoes or bell peppers. In this regard, the application of B to tomato fruit increases symplast Ca levels and firmness, while decreasing PME activity and the incidence of BER in the fruit [91].

7.5. Shotberry

Shotberry is also known as Millerandage disease. In this disease, grapes in the same bunch are found that are significantly smaller and less ripe than the other berries. This disease is attributed to a

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boron deficiency and results in loss of quality and an appearance that affects the marketability of the product [92].

In this regard, the concentration of B in floral tissues affects the formation of parthenocarpic fruits in grapevines, which shows a high correlation with the amount of abnormal pollen, where defective grains do not germinate or develop pollen tubes, leading to the presence of shot berries [93]. Likewise, the exogenous application of gibberellins increased the incidence of shot berries and reduced both the B content in flowers and the expression of the VvBOR3 and VvBOR4 genes, which are responsible for transporting B to reproductive tissues, limiting their mobility and increasing the occurrence of parthenocarpic fruits [93]. Additionally, it was found that foliar application of 0.5 g L^{-1} of B reduced the number of berries with shot berries compared to the control, with a much greater decrease when B was combined with zinc and epibrassinolide [94]. These treatments reduced the number of seedless berries, attributed to the effect of B on pollen germination and pollen tube growth, which promotes successful fertilization. Likewise, the application of 0.05% boric acid decreased the incidence of shot berries in grapes; however, its effect was more pronounced when combined with glutamic acid, reducing shot berries by 6.5% and increasing berry weight, size, and overall quality.

Furthermore, the incidence of shotberry has been reported in olive trees. It is reported that foliar application of different doses of B improved fruit set. However, it did not affect the proportion of parthenocarpic fruits, and shotberry production was similar to that of the control. These factors are attributed to inadequate fertilization management rather than boron deficiencies [95].

7.6. Segment Drying

Segment drying is a physiological disorder that affects citrus fruits during the pre- and post-harvest stages. This condition leads to dehydration, flavor loss, and a hardened texture, impacting the fruit's organoleptic quality [96] (Figure 4e). In some regions, it is called "fruit hardening" or "vesicle thickening," while in China, it is known as "kushui," as the fruits appear dull and dry, with a grayish color, dry vesicles, a bland flavor, a grainy texture, and a juice content reduction of up to 70% in mandarin, grapefruit, and orange [97]. In citrus fruits, it was found that B deficiency causes low sugar levels and thickening of the peel, due to the role of B in sugar translocation, indicating a strong link between boron fertilization and grapefruit granulation [98]. Also, dry juice vesicles in citrus were attributed to low B and P levels, high temperatures, and high relative humidity [83].

7.7. Bumpy Fruit

Bumpy fruit is a disease that affects papaya fruits and is caused by a B deficiency [83]. The deformation begins in young fruits, worsens during ripening, and is marked by the exudation of milky latex from the fruit surface. The infection spreads, forming a ball-shaped bump at the ends of the tissue. Its incidence has been reduced by applying 0.25% borax to the leaves and 1 to 3 kg ha^{-1} of boron (B) to the soil, which has increased B concentrations in the petioles and decreased the occurrence of this defect.

8. Conclusions

Adequate levels of B are crucial for good fruit quality because it serves multiple functions. Its role in forming borate-pectin complexes helps maintain cellular integrity, which reduces fruit mass loss. B also aids in the efficient transport of sugars and the compartmentalization of organic acids, while preventing the degradation of antioxidants like ascorbic acid. Additionally, B shortens anthesis time in fruit trees, increases the number of flowers per shoot, reduces flower drop, and boosts fruit set. It also decreases cork spots and deformed fruits while increasing overall production and yield. Fruits from plants treated with B have a lower respiration rate, which helps preserve postharvest quality by maintaining soluble solids content, delaying softening, and reducing the incidence of pathogens and physiological issues such as cracking, cork spots, internal rot, blossom end rot, and segment drying. Foliar application of B is more effective than soil application.

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