# Effect of calcium on fruit quality: A review

## Efecto del calcio en la calidad de los frutos: una revisión

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### ABSTRACT

Calcium (Ca) plays a crucial role as a nutrient influencing the ripening, post-harvest duration, and quality of fruits. Its impact on the cell wall and its function as a secondary messenger at the cellular level underscore its significance. While recently there has been an increase in studies examining the effects of Ca on fruit quality, there remains a need to consolidate and expand the literature on pre-harvest and post-harvest applications of Ca concerning the physical-chemical properties of fruits. This review aims to compile information on the mechanisms of Ca absorption by plants, as well as the interaction of Ca with the cell wall in fruit development and growth; the review also aims to synthesize literature on the effects of calcium on the physical and chemical properties of fruits that ultimately influence their quality. The review considers a comprehensive analysis of studies published in reputable scientific publishers (Elsevier, Springer, Frontiers, Wiley, MDPI, Hindawi, SciELO) over the last ten years, encompassing various relevant topics. Calcium proves effective in retarding the loss of firmness in fruits, increasing their mass, mitigating mass loss during storage, and extending postharvest life, thereby enhancing marketability. Furthermore, Ca demonstrates a role in decreasing the activity of enzymes responsible for cell wall degradation. Additionally, it reduces ethylene production in fruits, delaying the climacteric peak and reducing its intensity. Its application results in delayed color changes in fruits. For soluble solids, Ca diminishes sugar values and postpones their peak during the post-harvest period while maintaining high total acidity values. Notably, Ca applications contribute to a decreased incidence of certain physiological disorders.

**Key words:** fertilization, preharvest, postharvest, ripening, fruit development, physiopathy.

### RESUMEN

El calcio (Ca) es un nutriente muy importante en la maduración, la duración poscosecha y la calidad de los frutos, debido a su acción en la pared celular y su papel como mensajero secundario a nivel celular. En los últimos años se han incrementado los estudios sobre el efecto del Ca en la calidad de los frutos; no obstante, la literatura sobre sobre las aplicaciones precosecha y poscosecha del Ca en las propiedades físico-químicas de los frutos debe ser consolidada y ampliada. Por lo anterior, esta revisión tiene como finalidad consolidar información sobre cómo es el mecanismo de absorción del Ca por la planta y su interacción con la pared celular en el desarrollo y crecimiento del fruto, así como recopilar literatura sobre el efecto del calcio en las propiedades físicas y químicas de los frutos y su calidad. La revisión considera un análisis exhaustivo de estudios publicados en prestigiosas editoriales científicas (Elsevier, Springer, Frontiers, Wiley, MDPI, Hindawi, SciELO) en los últimos diez años, abarcando diversos temas relevantes. El calcio resulta eficaz para retardar la pérdida de firmeza de los frutos, aumentar su masa, mitigar la pérdida de masa durante el almacenamiento y prolongar la vida poscosecha, mejorando así su comercialización. Además, el Ca desempeña un papel en la disminución de la actividad de las enzimas responsables de la degradación de la pared celular. Así mismo, reduce la producción de etileno en los frutos, retrasando el pico climatérico y reduciendo su intensidad. Su aplicación también produce un retraso en los cambios de color en los frutos. En cuanto a los sólidos solubles, el Ca disminuye los valores de azúcar y retrasa su pico durante el periodo poscosecha, manteniendo altos valores de acidez total. En particular, las aplicaciones de Ca contribuyen a disminuir la incidencia de ciertos desórdenes fisiológicos.

**Palabras clave:** fertilización, precosecha, poscosecha, maduración, desarrollo de fruto, fisiopatía.

## Introduction

In recent years, Colombia has emerged as a significant producer and exporter of fruits and exotic food products. In 2021, fresh fruit production reached a volume of 12.4 million t, exhibiting an average annual growth of 3.7% since 2017 (Procolombia, 2021). This surge in production within the Colombian fruit sector is attributed to its tropical location, enabling year-round harvesting of fruits. Consequently, Colombia has solidified its position as one of the primary exporting nations of exotic fruits in Latin America (Analdex, 2023). In 2022, approximately 246 million kg of fresh fruits were consumed globally, marking a nearly 7 million kg increases from the previous year. This

trend will persist in the upcoming years, which would allow reaching over 303.5 million kg in 2028 (Statista, 2023).

According to Aune et al. (2017), a high consumption of fresh fruits as part of a healthy diet can mitigate the risk of heart disease, cancer, obesity, and diabetes. The authors suggest that a minimum daily intake of 800 g is required to reduce mortality from various causes, offering health and environmental benefits. Moreover, most fruits are low in calories, rich in fiber, contain a high concentration of micronutrients, and are enjoyable for the palate (Guyenet, 2019).

In this context, the term "nutritional density" has been introduced to describe the proportion of nutrients in foods, including vitamins, proteins, fibers, antioxidants, and carbohydrates. This depends on the concentration of nutrients accumulated per unit of mass produced by a crop, and it is directly influenced both by the fertilization practices applied to plants (Barker & Stratton, 2020) as well as by the nutrient availability in the soil, the absorption capacity of the plant, irrigation, and environmental factors (Davis, 2009).

Fertilization in fruit trees has become an indispensable tool for intensive crop production, as the soil lacks the capacity to meet the optimal nutritional requirements demanded by such commercial agricultural operations (Srivastava & Malhotra, 2017). The absence of adequate fertilization leads to nutritional imbalances in plants, resulting in physiological disorders that can impact fruit yield and quality (Kumar & Kumar, 2016).

In this regard, fertilization with calcium ($Ca^{2+}$) positively influences the growth of organs and tissues and stimulates root growth by facilitating the incorporation of materials into cell walls (Prado, 2021). Initially, the $Ca^{2+}$ ion is absorbed by the plant, transported through the xylem with the transpiration flow, and is considered a slightly mobile element within the plant when transported via phloem (Thor, 2019).

Calcium is more abundant in older leaves, and a deficiency of calcium is common in fruits, young leaves, and storage organs (Prado, 2021). In fruits, a deficiency of calcium is attributed to the reduced number of stomata, impeding the transport of calcium through the xylem (Bonomelli et al., 2022). Plant absorption of $Ca^{2+}$ is faster during the initial stages of fruit growth (Casero et al., 2017), as it serves as an enzyme activator and an essential element for cell division, cell elongation, and growth (Prado, 2021).

Applications of calcium ($Ca^{2+}$) in fruits contribute to the maintenance of firmness and cell turgor, reducing the incidence of diseases, and preventing physiological disorders (Jain et al., 2019). Additionally, calcium plays a crucial role in the expression of genes influencing fruit production and quality (Wu et al., 2023), as it stabilizes cell walls and ensures their permeability, protecting them from enzymatic degradation (Zhi et al., 2017). This regulation affects ripening in some fruits and influences respiration rates and ethylene production, thereby extending the quality of fruits during storage (Michailidis et al., 2020).

Among the physiological disorders resulting from an insufficient $Ca^{2+}$ supply or alterations in the balance of Ca with other nutrients (Freitas & Mitcham, 2012), various conditions have been identified, including 'blossom end rot' in tomatoes (Karlsons et al., 2023), 'bitter pit' spots in apples (Griffith & Einhorn, 2023), cork spots in pears (Zhang & Cui, 2023), internal browning in pineapples (Zhang et al., 2022), 'tip burn' in strawberries, 'cracking' in cape gooseberries (Fischer et al., 2021), nectarines (Zhu et al., 2023), grapevines (Yu et al., 2020), and melons (López-Zaplana et al., 2020), as well as the recently identified 'crease' skin wrinkling in citrus (Huai et al., 2022), and these conditions result in significant economic losses (Yu et al., 2020).

Among the treatments widely employed for fruit conservation, foliar applications and dips of $Ca(NO_3)_2$ and $CaCl_2$ have been extensively reported. These applications occur during fruit development, at specific intervals, and during the harvest period. The uniform distribution of this solution over the fruits enhances the concentration of Ca in internal tissues, contributing to prolonged shelf life (Dorostkar et al., 2022). However, in some fruits, Ca applications have no effect since sometimes their results are reflected in leaves but not in fruits due to high leaf transpiration (Winkler & Knoche, 2019). While the application of Ca has demonstrated the potential to enhance fruit quality across various crops (Lobos, Retamales, Luengo Escobar et al., 2021), the specific impact of Ca on fruit quality has not been thoroughly studied and summarized. Therefore, the objective of this work was to conduct a comprehensive review that compiles and presents information on the effects of $Ca^{2+}$ on fruit production and quality.

## Absorption of Ca by the plants

The movement of calcium (Ca) in the soil towards the roots occurs through mass flow and subsequently it enters the apoplastic space within the apical zone of the root (Doyle *et al.*, 2021). Ca is absorbed as a divalent cation ($Ca^{2+}$) by the cells of the root endodermis (Gulbagca *et al.*, 2020), specifically through channels located in the plasma membrane that can be voltage-dependent or voltage-independent. The first are activated by depolarization or hyperpolarization and are probably encoded by annexins, while the latter are activated by cyclic nucleotides (Lemtiri-Chliel *et al.*, 2020).

After absorption, Ca is transported with water apoplastically to avoid interference with its role as a secondary messenger. This is because the concentrations of $Ca^{2+}$ in the cytosol must remain in submicromolar ranges (< 0.1 μM) to ensure the ability of cells to generate $Ca^{2+}$ signals (Prado, 2021). Thor (2019) suggests that $Ca^{2+}$ moves mostly via the apoplast from the epidermis of the cortex until it reaches the Caspary band that restricts the apoplastic movement of solutes. Even so, $Ca^{2+}$ can reach the xylem via the apoplast only in regions where the Casparian bands are absent or discontinuous (White & Broadley, 2003). In the selective symplastic pathway, $Ca^{2+}$ enters the cytosol through channel proteins and is pumped to the apoplast of the stele through $Ca^{2+}$-ATPases or the $Ca^{2+}/H^+$ antiport pathway, ultimately contributing to its upload in the xylem. From there, $Ca^{2+}$ is transported to the shoots where it is unloaded and distributed to the leaf cells through channels activated by cyclic nucleotides (Wang *et al.*, 2017). In this phase, absorption is quite rapid; and $Ca^{2+}$ supplies from the soil are of fundamental importance. Likewise, the $Ca^{2+}$ flow rate is strongly influenced by transpiration (White & Broadley, 2003).

## Calcium absorption by the fruits

In the realm of nutrition and calcium physiology, fruits pose challenges in water and nutrient supply due to their low transpiration rates and limited xylem transport networks compared to other plant organs. This limitation hinders the delivery of calcium to fruits (Hocking *et al.*, 2016). Key factors influencing the supply and distribution of calcium in aerial tissues include the mass flow rate of xylem sap (as $Ca^{2+}$ is not highly mobile in the phloem), competition among ions for binding sites in xylem vessel walls, the presence of ionic transporters (including $H^+$, influencing pH), membrane channels, and the formation of poorly soluble or insoluble complexes, such as calcium oxalate (Sotiropoulos *et al.*, 2021). Calcium concentration

in various cellular compartments can impact water transport through membrane-controlled pathways. An increase in cytosolic calcium concentration may decrease water transport through aquaporins, affecting the relative proportions of apoplastic and symplastic water flow and the magnitude of calcium supply. Symplastic pathways exhibit a lower capacity for long-distance $Ca^{2+}$ movement (Doyle *et al.*, 2021).

In the early stages of fruit development and before the formation of Casparian bands in the root and the suberization of the tissues when the fruit is small, over 50% of the total calcium is contained within it. Therefore, the quantity of calcium fertilization applied to the soil before this stage is of principal importance, as well as the moisture content in the soil, and the presence of many idioblast cells in the root that serve as a Ca sink. Once the Casparian bands are formed, the idioblast cells provide Ca for cell elongation and differentiation (Storey *et al.*, 2003). However, as the fruits expand in later stages, most $Ca^{2+}$ is transported to the leaves, where it cannot be redistributed to the fruits; this results in the dilution of Ca amounts in fruits (Doyle *et al.*, 2021). During this phase, foliar applications of calcium must be implemented through spraying to meet additional nutrient needs and prevent potential physiopathy related to calcium deficiency.

Casero *et al.* (2017) report that in apple (*Malus domestica* Borkh.) cv. 'Golden Smoothee' calcium is absorbed by fruits during the initial stages of development, accumulating until 80 d after full bloom (DAFB). The absorption peaks at 38 DAFB and may be antagonistic with nutrients such as potassium ($K^+$), ammonium ($NH_4^+$), and magnesium ($Mg^{2+}$) at the early stage of fruit development. Similarly, Bonomelli *et al.* (2022) find significant differences in calcium distribution in orange (*Citrus sinensis*) fruits cv. 'Fukumoto' with applications at various stages of development (30 DAFB, 44 DAFB, 66 DAFB, and 99 DAFB). The application at 30 DAFB resulted in the accumulation of 61% of calcium in the peel and 39% of calcium in the fruit pulp. This suggests that calcium mobility to the fruit pulp varies with phenological stages and fruit morphology and is more substantial at the early stages of development.

Doyle *et al.* (2021) note an inverse correlation between fruit growth rate and calcium content in fruits. In blueberry fruits, calcium content increases during early fruit development, with higher levels observed in peel and seed tissues compared to a fruit pulp (Doyle *et al.*, 2021). Calcium deficiency symptoms may manifest a few weeks after anthesis, primarily in the distal zone of the fruits.

## Functions of calcium in the fruits

Adequate supply and transport of calcium are crucial for fruit development, as only a small portion of the absorbed calcium is transported to the fruits. Its accumulation relies on xylem flow due to the low mobility of calcium in the phloem (Gao *et al.*, 2019). Calcium accumulation in the fruits primarily occurs during the initial stages of fruit development, where calcium absorption is linked to cell division and metabolism, particularly during the initial fruit expansion. In the later stages of fruit growth, calcium absorption predominantly influences cell-to-cell adhesion (Hocking *et al.*, 2016).

## Interactions between Ca and the cell wall during fruit development

Calcium combines with pectic acid in the cell wall to form calcium pectate, constituting the structural skeleton of the cell wall. This structure prevents the disintegration of the gel layer in the cell wall, enhancing the structural strength of the cell wall (Zhang & Wang, 2019). A sufficient calcium supply inhibits the entry of hydrolases and reduces changes in the pectic composition of the cell wall, thereby maintaining fruit firmness. Additionally, being a structural component of the cell membrane, calcium forms bridges connecting phospholipids and proteins within the plasma membrane. This interaction affects phase transition and fluidity, preserving membrane integrity (Xu *et al.*, 2022).

The cell wall comprises various polysaccharides forming a network of cellulose microfibrils linked to a matrix of pectins through α-1,4-glycosidic bonds and hemicelluloses (Hocking *et al.*, 2016). Additionally, it contains minor structural components such as proteins, lignins, and phenolic compounds (Polko & Kieber, 2019). Pectins stand out as the primary polysaccharide of the cell wall in most fruits, and calcium-pectin bonds significantly influence their physical, structural, and resistance properties (Cui *et al.*, 2021).

The prevalence of either ionic or ester bonds among pectins plays a crucial role in the physical properties of fruit cell walls, impacting the solubility of pectins (Hocking *et al.*, 2016). Homogalacturonan, the primary pectic polysaccharide, constitutes 60% of all pectins in the cell wall (Gawkowska *et al.*, 2018), interconnected with $Ca^{2+}$ ions to form pectates, collectively known as the egg-box (Huang *et al.*, 2023).

During cell growth and expansion, acidification of the cell wall takes place, displacing calcium bound to pectin through the protonation of carboxyl groups (Hocking *et al.*, 2016). This phenomenon is triggered by changes in pectin concentration, leading to the release of apoplastic $Ca^{2+}$ [$Ca^{2+}$]. These changes induce secretion and modification of pectins, crucial for fruit growth (Gao *et al.*, 2019). According to Hocking *et al.* (2016), apoplast pH is influenced by xylem sap pH under conditions of ample water supply, potentially resulting in significant alterations in cell wall dynamics and composition.

During fruit growth, pectins undergo de-esterification, catalyzed by pectin methylesterases (PMEs), releasing carboxylic residues linked to calcium (Hocking *et al.*, 2016). The level of PME activity and the availability of $Ca^{2+}$ within the apoplast significantly impact the strength of the cell wall, its expansion, as well as the disassembly and remodeling of pectin (Khan *et al.*, 2019). In the ripening phase, calcium inhibits polygalacturonase (PG) activity, and a reduction in calcium concentration favors increased PG activity (Hocking *et al.*, 2016). PG exhibits its maximum expression at 100 d after anthesis (DAA) in grapes, indicating a programmed role in cell wall disassembly at maturity (Khan *et al.*, 2019). At the initial stages of fruit growth, low activity of PG and pectate lyases (PL) is regulated by specific isoforms of these enzymes (Hocking *et al.*, 2016). However, as the fruit matures, extensive depolymerization of pectins occurs, resulting in shorter subunits that are more soluble, indicating a decrease in the xyloglucan and cellulose networks in the cell wall. This is attributed to the action of PG and PL in tomato fruits. In this context, Nie *et al.* (2022) tested targeted mutations of the SIPG gene and found that it was possible to delay the loss of firmness and water in tomato fruits.

The strength of the bonds forming Ca pectates is dependent on pH, with apoplastic values between 6 and 7 enhancing these bonds. Furthermore, the formation and dissolution of pectate gels by Ca bonds depend on the level of de-esterification, specifically the concentration of free carboxyl groups and free calcium ions (Frempong *et al.*, 2022). As the dissolution and hydration of pectic gels occur, the breaking of calcium bonds with pectins increases, resulting in a reduction in cell wall rigidity evident in small deformations. This process occurs at a pH of 3, where the resistance of the links is minimal (Lara-Espinoza *et al.*, 2018).

According to Gao *et al.* (2019), an adequate calcium concentration in the fruits delays and decreases the climacteric peak and ethylene production. This is largely dependent on the phosphorylation of calcium-dependent proteins, inhibiting the activity of 1-aminocyclopropane-1-carboxylic

acid oxidase (ACO) and ethylene-forming enzyme (EFE), subsequently reducing the contents of 1-aminocyclopropane-1-carboxylic acid (ACC).

Moreover, calcium treatments also diminish microbial growth and susceptibility to pathogens, delaying fruit ripening and extending postharvest life (Gao *et al.*, 2019). However, an excessive calcium supply can elevate cytosolic calcium concentration, potentially causing membrane damage and increase respiratory intensity.

Calcium exerts an inhibitory effect on enzymes and co-enzymes during fruit ripening and softening (Huai *et al.*, 2022). It significantly suppresses the expression of genes that encode cell wall-degrading enzymes such as cellulase, pectinesterase, polygalacturonase, β-galactosidase, and pectate lyase. However, when pectin degradation occurs, there is an increase in free $Ca^{2+}$, resulting in the loss of cell-to-cell polymerization and fruit softening (Gao *et al.*, 2019). Additionally, in the cell membrane, calcium inhibits lipid peroxidation initiated by the activation of the enzyme lipoxygenase. Calcium also enhances the activity of enzymes neutralizing reactive oxygen species, including superoxide dismutase, peroxidase, catalase, and the enzymes of ascorbate-glutathione cycle (Xu *et al.*, 2022).

According to Saure (2005), the concentration of calcium varies according to the different growth rates of each part of the fruit. Calcium in the fruit can be found as water-soluble Ca or exchangeable Ca; the latter increases during fruit development until reaching 84% of the total Ca that indicates that as the fruit matures, Ca is found in more available forms. Likewise, Ca can be redistributed, since, in ripe fruits, the concentration of Ca is higher in the peel and lower in the pulp section just below the peel.

As a secondary messenger calcium elevates the level of phosphorylation in fruits, inducing the activation of MAKP (mitogen-activated protein kinases) cascades. These cascades control protein stability and regulate the expression of genes that inhibit ethylene synthesis, ultimately prolonging the post-harvest life of the fruits (Yu *et al.*, 2018).

## Effect of calcium on the physical properties of the fruits

The physical transformations within fruits play a pivotal role in determining their postharvest handling. These changes primarily manifest in the cell walls of the fruits and are associated with the modification and continuous solubilization of pectins. Generally, controlled depolymerization of the cell wall structure occurs, leading to the loss of cell adhesion, which results in the associated reduction of fruit firmness and the leakage of internal juices during the ripening process. Consequently, this leads to mass loss and a decline in overall quality (Fig. 1).

### Mass loss

Calcium mitigates mass loss in fruits by reducing the phosphorylation of phosphatidylinositol bisphosphate. This reduction diminishes the activity of aquaporins, thereby likely decreasing the movement of water from the cytoplasm to the apoplast. This, in turn, limits evaporation and helps maintain fruit weight for an extended period (Xu *et al.*, 2022).

In support of this, Sinha *et al.* (2019) observed that a pre-harvest application of 2% $Ca(NO_3)_2$ by spraying on plum trees resulted in approximately 1% less mass loss in fruits compared to the control during all post-harvest measurements. Similarly, Ali *et al.* (2021) sprayed pre-harvest peach fruits with 1% $CaCl_2$ and found lower mass losses (ranging from 21.6% to 26.9%) compared to other treatments and the control (ranging between 34.66% and 35.16%). Additionally, Thakur *et al.* (2019) applied $CaCl_2$ at the time of harvest in melon (*Cucumis melo*) and papaya, reducing the loss of fruit mass after 20 d after harvest (DAH). In lemon, at 42 DAH, mass loss was 28.7% for control fruits and 23.2% for those treated with 0.18 M $CaCl_2$ (Frempong *et al.*, 2022). Xu *et al.* (2022) immersed apple fruits at harvest in doses of 2% $CaCl_2$ for 30 min resulting in mass losses ranging between 4.7% and 5.6% for treated and control fruits. Similarly, calcium application is known to decrease mass loss in grapes (Shi *et al.*, 2023) and blueberries (Lobos, Retamales, Luengo Escobar *et al.*, 2021).

### Firmness

Firmness is a critical quality parameter in fruit marketing (Huang *et al.*, 2023). Calcium enhances fruit firmness by strengthening the cell wall structure, reinforcing cell adhesion, and forming Ca pectate when combined with pectic acid (Zhang & Wang, 2019). Additionally, exogenous calcium application causes the accumulation of homogalacturonans and an increased number of pectin networks (Huang *et al.*, 2023).

Calcium applications are typically done pre-harvest alongside fertilization, while in other instances, they are directly administered to fruits during the final stages of development or post-harvest. These applications have demonstrated positive outcomes in enhancing or sustaining fruit firmness over an extended period. However, according to
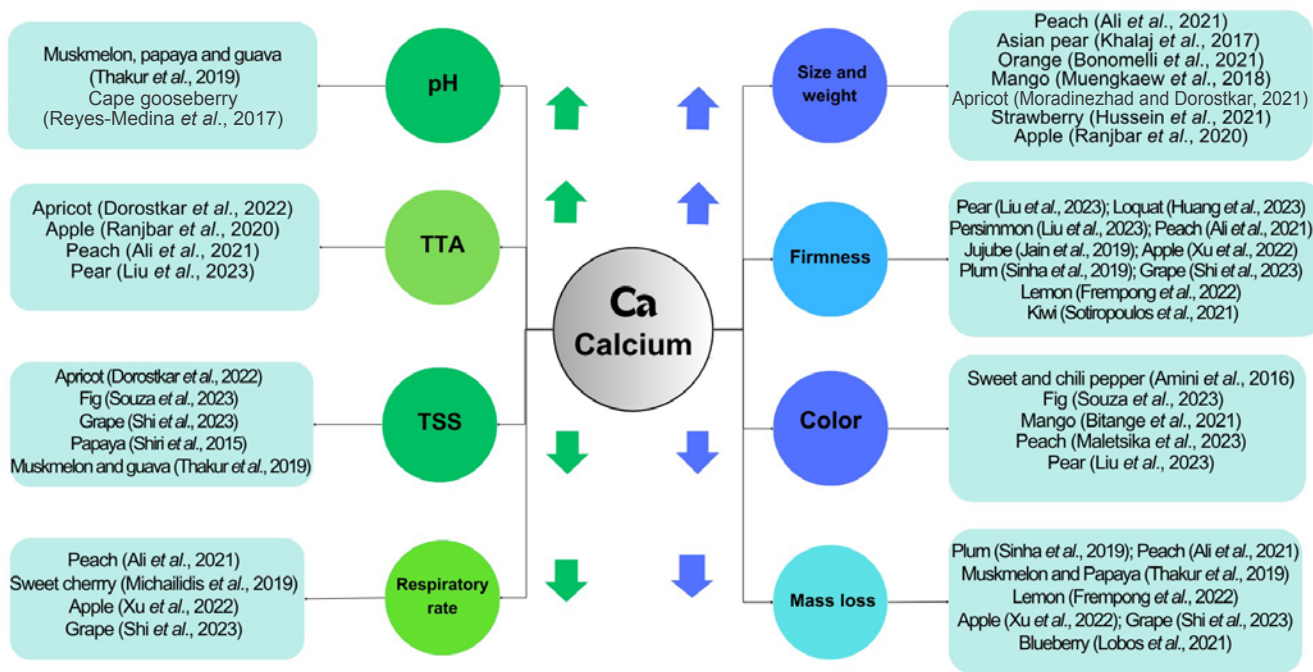
**FIGURE 1.** Effect of calcium on the physical and chemical properties of fruits. TTA – total titratable acidity, TSS – total soluble solids.

Sena *et al.* (2024), foliar Ca fertilizations prove to be more effective than soil applications in augmenting Ca levels within the fruits. In this context, Khakpour *et al.* (2022) observe that the soil application of 150 g of $Ca(NO_3)_2$ per apple tree results in fruits exhibiting increased firmness compared to the control group. Conversely, Álvarez-Herrera *et al.* (2022) found no significant disparities in fruit firmness when employing fertilizations ranging from 0 to 100 kg ha$^{-1}$ of Ca.

Liu *et al.* (2023) further notes that $CaCl_2$ application reduces the amount of water-soluble pectins, indicating prolonged firmness in persimmon (*Diospyros kaki*) fruits. Ali *et al.* (2021) applied $CaCl_2$ through pre-harvest sprays (1%, 2%, and 3%) and significantly increased peach fruit firmness by 28%, 13%, and 24%, compared to the control. Overall, calcium applications have successfully maintained fruit firmness for longer durations in various fruits such as jujube (*Ziziphus mauritiana* Lamk.) (Jain *et al.*, 2019), papaya, melon, guava (Thakur *et al.*, 2019), apple (Xu *et al.*, 2022), plum (Sinha *et al.*, 2019), grapevine (Shi *et al.*, 2023), blueberry (Lobos, Retamales, Luengo Escobar *et al.*, 2021), lemon (Frempong *et al.*, 2022), and kiwi (Sotiropoulos *et al.*, 2021). Also, Melo *et al.* (2022) find that two weekly applications of 0.3 g L$^{-1}$ of $CaCl_2$ increase the calcium content and firmness in tomato fruits. During postharvest, Liu *et al.* (2023) immersed freshly harvested pear fruits in 5 g L$^{-1}$ of Ca lactate for 10 min, resulting in fruits with greater firmness at 8 DAH (28.8 N) compared to the control (27.3 N). A similar

effect was observed in loquat (*Eriobotrya japonica* Lindl), where Ca lactate increased fruit firmness from 4.1 to 4.6 N at 30 DAH.

## Color

Color significantly influences the physical appearance and market acceptability of fruits, making it a crucial quality parameter (Sinha *et al.*, 2019). Calcium is known to delay changes in fruit color by retaining chlorophyll content. The application of Ca reduces respiratory intensity and ethylene production, thereby slowing down the ripening phase (Souza *et al.*, 2023). This retention of green pigments is attributed to the inhibition of enzymes, such as chlorophyllase, by Ca, which is the initial enzyme involved in chlorophyll degradation (Nassarawa *et al.*, 2024). In this context, Bitange *et al.* (2021) notes that the application of Ca slows chlorophyll degradation and pigment synthesis, aligning with Amini *et al.* (2016), who observed a reduction in carotenoid content in sweet pepper fruits treated with nano-calcium.

Souza *et al.* (2023) reported that spraying the plants with 1% $CaCl_2$ maintained high chromaticity and hue values in fig fruits. Similarly, Bitange *et al.* (2021) observed higher hue values in mango fruits treated with $CaCl_2$ compared to the control throughout the postharvest period. Additionally, in peaches, the epidermis of the fruits exhibited a greener color after treatment with $CaCl_2$ (Maletsika *et al.*, 2023). Liu *et al.* (2023) found that the values of L*, a*, and b* in

pear fruits increased to a lesser extent with the application of Ca lactate compared to the control, indicating that postharvest fruits subjected to Ca treatments experience a delay in color development, making them less perishable.

## Fruit size and mass

Calcium plays a pivotal role in the growth and development of fruits, particularly during the cell division stage; it impacts the size and mass of the fruits, as observed in peaches (Ali *et al.*, 2021). Foliar application of 1% $CaCl_2$ in peach trees improved the fresh mass, size, and pulp-to-stone ratio, resulting in larger-diameter fruits and a higher economic return. Khalaj *et al.* (2017) demonstrated that foliar application of Ca increased pectic substances in the cell walls, leading to an increase in pericarp tissue thickness and overall fresh mass of the fruits. Additionally, the influence of Ca on the contents of endogenous growth substances, especially cytokinins, has been reported (Ali *et al.*, 2021). In this context, Bonomelli *et al.* (2022) found that early applications of Ca were more effective in increasing the dry mass of orange fruits.

Similar results have been reported for the improvement of physical traits in various horticultural products through the use of $CaCl_2$. In mango fruits, applications of $CaCl_2$ increase length, width, thickness, and average fresh mass (Muengkaew *et al.*, 2018). In apricot, these increase the diameter and fresh mass of the fruits (Moradinezhad & Dorostkar, 2021). In strawberries, the diameter increases (Hussein & Al-Doori, 2021), and in apples, the fresh mass and diameter increases following by applications of $CaCl_2$ (Ranjbar *et al.*, 2020). In contrast, Hirzel (2023) found that, for Ca applications ranging between 0 and 4 kg ha$^{-1}$, the size and mass of blueberry fruits are not affected; similarly, Yu *et al.* (2020) show that the application of Ca did not significantly affect the diameter of grapefruits.

## Effect of Ca on the chemical properties of the fruits

Among the chemical changes during fruit development are depolymerization and modifications in the side chains of pectin, degradation of xyloglucan, increasing activity of non-catalytic proteins (arabinogalactan proteins, AGP), and processes related to ripening such as the accumulation of solutes and acid degradation, some of which are detailed below.

## Total soluble solids (TSS)

One of the most impactful characteristics of fruits on the market is flavor, primarily determined by the amount of TSS. During ripening and storage, the starch in fruits slowly converts into sugars. However, calcium slows down respiration and metabolism, thereby delaying processes like the hydrolysis of polysaccharides to monosaccharides, which, in turn, delays ripening and reduces the TSS of fruits during postharvest (Dorostkar *et al.*, 2022). Similarly, Souza *et al.* (2023) mention that the application of $CaCl_2$ decreases the concentration of TSS and reduces the content of reducing sugars in figs, attributed to the greater stabilization of pectin structures provided by calcium. Shi *et al.* (2023) find that the application of Ca in grapevine fruits delayed the maximum TSS peak from 14 DAH in the control to 28 DAH for the treated fruits. Shiri *et al.* (2015) report that TSS decreases in papaya fruits with increasing calcium concentration. Furthermore, Thakur *et al.* (2019) mention that the application of $CaCl_2$ decreases the amount of TSS by 20%, 12.6%, and 9.34% compared to the control in papaya, melon, and guava fruits, respectively, after 20 d of storage. However, in some fruits, the application of calcium does not affect the TSS concentration, such as apples (Fallahi & Mahdavi, 2020), blueberries (Lobos, Retamales *et al.*, 2021), and cape gooseberry (Álvarez-Herrera *et al.*, 2022).

## Total titratable acidity (TTA)

The effects of Ca application on TTA in fruits vary depending on the application period, storage time, concentration, and species evaluated (Souza *et al.*, 2023). Ali *et al.* (2021) mention that the application of calcium decreases the activity of oxidative enzymes, such as ascorbate oxidase, peroxidase, oxidase, catalase, and polyphenol oxidase, which, during storage, decrease the amount of organic acids (Shi *et al.*, 2023). This indicates that the treatment of fruits with Ca maintains high TTA values (Dorostkar *et al.*, 2022).

Ranjbar *et al.* (2020) applied $CaCl_2$ and nano-calcium to pre-harvest apple fruits and found that TTA increased at the time of harvest, attributed to the decrease in respiratory activity, leading to a decrease in the hydrolysis of organic acids. Ali *et al.* (2021) mention that fruits treated with 1% $CaCl_2$ maintain high TTA values during storage due to a decrease in respiratory intensity, preventing the decrease in acids used as a respiratory substrate (Saltveit *et al.*, 2019). Similarly, Liu *et al.* (2023) achieve higher TTA values throughout the postharvest in pear fruits with the application of Ca, consistent with that reported in apricot (Dorostkar *et al.*, 2022). In contrast, Maletsika *et al.* (2023) find that the application of calcium in peach fruits decreases TTA as well as the concentration of citric and quinic acid. However, these authors mention that the lower values of organic acids found are not related to the ripening of the fruits. Nevertheless, they obtain higher contents

of succinic acid in fruits. Ribeiro *et al.* (2020) report that the preharvest application of 4% $CaCl_2$ decreases TTA in guava fruits. In other studies, the application of Ca through fertilization does not affect TTA values in gooseberry fruits (Álvarez-Herrera *et al.*, 2022) and blueberries (Lobos, Retamales *et al.*, 2021).

## pH

During ripening, fruit filling occurs mainly by symport, in which $H^+$ plays an important role, as they are part of substrates such as glucose and sucrose. Consequently, the concentration of $H^+$ at the vacuolar level decreases, and the pH increases slightly. Therefore, it is likely that the application of Ca slows down the decrease in pH by decreasing respiratory and fruit metabolism, minimizing the oxidation processes of organic acids (Álvarez-Herrera *et al.*, 2022). Thakur *et al.* (2019) mention that the application of 2% $CaCl_2$ in papaya, melon, and guava maintain higher pH values in fruits (4.15, 4.48, and 3.85, respectively) at the end of storage (20 DAH) compared to the control (3.80, 4.05, and 2.30, respectively). Similarly, Reyes-Medina *et al.* (2017) obtained higher pH values in cape gooseberry fruits at 35 DAH with the application of 0.5% $CaCl_2$.

## Respiration

The respiratory intensity of the fruits is affected by the concentration of Ca (Michailidis *et al.*, 2019). According to Khlopkov *et al.* (2021), sudden changes in respiration are associated with a drastic change in the concentration of some ions. Ca has a significant effect on the activity of a series of enzymes and membrane complexes involved in respiration, including alternative NADPH-dehydrogenases or complex IV. Once the concentration of Ca increases at the cytoplasmic level during the generation of electrical signals, it leads to an increase in Ca in the mitochondrial matrix, where Ca is likely involved in the formation of the respiratory response (Sweetman *et al.*, 2020). Similarly, Gao *et al.* (2019) mention that the application of Ca can delay and reduce the intensity of the climacteric peak. Ali *et al.* (2021) applied Ca at preharvest and managed to reduce the climacteric values in peach fruits by 1.4 times on average. Michailidis *et al.* (2019) find a reduction in respiratory activity with calcium applications in cherry fruits (*Prunus avium* L., cv. 'Tsolakeika'), while Xu *et al.* (2022) demonstrate that the application of 2% $CaCl_2$ in apples managed to reduce respiration by 17.5% during all measurements over 20 d of storage. Furthermore, as the preharvest application of Ca increases, ethylene production decreases in peach fruits (Ali *et al.*, 2021) and grapevines (Shi *et al.*, 2023).

# Ca in physiological fruit disorders

Calcium deficiencies usually appear in fruits at the initial stages, and although sometimes they are not noticeable to the naked eye, they can cause disorders that affect the development and quality of fruits and, consequently, the postharvest behavior. In this regard, low levels of $Ca^{2+}$ in fruits cause bitter spots, blossom end rot, cracking, and watery fruits, among other physiological disorders (Gao *et al.*, 2019). On the other hand, if high concentrations of calcium occur, it can cause cellular toxicity, cell walls that are too rigid, and abnormalities in the growth and development of the fruits (Hocking *et al.*, 2016).

## Bitter pit

Bitter pit manifests as concentrated depressions at the end of the calyx of apple fruit caused by the physiological degradation of cells under the epidermis. This phenomenon is associated with localized calcium deficiency, occurring between the fourth and sixth week after anthesis during the stage of cell division and elongation (Griffith & Einhorn, 2023). The decrease in Ca levels leads to an increase in the concentration of potassium and magnesium, affecting membrane permeability and potentially resulting in cell death (Yahia *et al.*, 2019). Similarly, Ranjbar *et al.* (2020) note that apple fruits treated with nano-calcium exhibit reduced sensitivity to bitter spots, as measured by the K/Ca ratio. Additionally, Griffith and Einhorn (2023) suggest that abscisic acid, as a gibberellic acid antagonist, mitigates bitter pit stains by reducing transpiration, improving xylem function, and facilitating calcium transport to the fruits.

## Blossom end rot (BER)

Blossom end rot occurs at the apical end, specifically in the section of the fruit opposite the stem. It is associated with low absorption and distribution of calcium during stages of it's high demand, leading to a lack of union between the cell wall and pectins, resulting in reduced cellular resistance. The lesion begins as a dark-colored depression that oxidizes as it grows. Gao *et al.* (2019) mention that increased PME activity raises the $Ca^{2+}$ contents bound to the cell wall, decreasing the availability of $Ca^{2+}$ for other functions and generating susceptibility to blossom-end rot.

Moreover, Watanabe *et al.* (2021) find that the lowest incidences of BER in tomatoes occur with less fruit growth and high concentrations of Ca during the initial stages of growth, particularly when Ca distribution is preferentially directed towards the fruits instead of the leaves.

BER prevention involves pre-harvest Ca application. In this regard, BER is lower in plants treated with calcium (Coulibaly *et al.*, 2023). Similarly, Reitz *et al.* (2021) applied $CaCl_2$ to tomato fruits, reducing BER severity with a 10 mg $L^{-1}$ dose.

### Cracking

Cracking involves the fissuring of the fruit peel and outer pulp during cell expansion (Yahia *et al.*, 2019), occurring in the final stage of fruit growth where the layer of newly enlarged cells exhibits weak elasticity, in addition to the biochemical changes that the exocarp undergoes, leading to cracking (Santos *et al.*, 2023). This phenomenon occurs in fruits of the crops such as cape gooseberry (Fischer *et al.*, 2021), nectarines (Zhu *et al.*, 2023), grapevines (Yu *et al.*, 2020), pears (Seo *et al.*, 2022), melons (López-Zaplana *et al.*, 2020), and others. Choi *et al.* (2020) suggest that cracking arises from rapid cell division, non-uniform arrangement of epidermal cells, and intense rain periods (Seo *et al.*, 2022). In that sense, excessive water contents in soil increase turgor pressure at the cellular level, rapidly increasing the volume of the fruits, which exceeds the extensibility of the peel and causes cracking (Santos *et al.*, 2023).

Numerous studies link fruit cracking to cell wall metabolism, affirming that $Ca^{2+}$ can inhibit cell wall softening, thereby increasing the structural strength of fruit peel (Fan *et al.*, 2023). Zhu *et al.* (2023) report that nano-calcium application decreases cracking in nectarines by up to 20%. Ca applications have also decrease fruit cracking incidence in cherries (Matteo *et al.*, 2022), grapevines (Shi *et al.*, 2022), and cape gooseberry (Álvarez-Herrera *et al.*, 2012). Additionally, Cooman *et al.* (2005) found, in cape gooseberry, that fruit cracking is influenced by the presence of Ca or B in the fertilizers applied, with this physiopathy increasing between 5.5% to 13.0% when either of these two elements was absent from the nutrient solution.

### Cork spot

Cork spot, primarily occurring in pears and apples, are attributed to calcium deficiencies. The main symptoms involve the appearance of round, sunken spots on the fruit peel, followed by subsequent browning and lignification of the pulp beneath the damaged area (Zhang & Cui, 2023). In apples, the spots acquire a bitter taste and impact the fruit size, with their occurrence being more frequent in larger fruits (Yahia *et al.*, 2019). Cui *et al.* (2021), inducing Ca deficiency with nitrendipine in pear fruits, find a 12% higher incidence of cork spots than in the control.

However, they mention that $Ca^{2+}$ concentration is not the sole biochemical indicator of cork spot.

### Spongy tissue

Spongy tissue, a physiological disorder associated with calcium deficiency, results in poor quality and an unpleasant flavor in mango fruits (Ma *et al.*, 2023). External symptoms are not evident, and the physiopathy becomes apparent only upon cutting the fruits (Yahia *et al.*, 2019). Alterations develop in the pulp closest to the seed, acquiring a spreading brown color over time, leading to a decrease in nutritional properties and affecting marketing (Yahia *et al.*, 2019). Positive regulation of specific genes increases Ca accumulation in the cell wall and vacuoles of the pulp, reducing available Ca for other metabolic functions, thus, altering cellular Ca homeostasis and causing localized Ca deficiency, resulting in the development of spongy tissue (Ma *et al.*, 2023).

### Watery fruits

This physiopathy, reported by Gao *et al.* (2019), primarily occurs in Passifloraceae, such as passion fruit, banana passion fruit, and purple passion fruit. It involves the alteration of textural and ultrastructure properties of the peel, causing softening and giving the impression of a watery fruit with low quality (Xu *et al.*, 2023). Applying $CaCl_2$, as mentioned by Xu *et al.* (2023), maintains the structural integrity of the passion fruit peel, reduces enzymatic activity, and preserves postharvest quality, delaying peel wrinkling and fruit senescence.

### Sunburn

Sunburn is damage occurring in the epidermis of fruits caused by a combination of events such as water deficit, salinity, high temperature, and intense solar radiation, expected to be more common due to climate change (Park *et al.*, 2022). This disorder is primarily observed in high tropic areas, and a strategy to mitigate its effects is the application of calcium carbonate nanoparticles (Teixeira *et al.*, 2022), which act as a suppressor and reduce sunburn in pineapple (Fischer *et al.*, 2022).

## Conclusions

Foliar applications of calcium have a more significant impact on fruits when carried out in the initial stages of development. Calcium positively influences fruit mass and reduces fresh mass loss during storage. The softening of fruits is delayed due to calcium inhibitory action on enzymes degrading the cell wall, maintaining firmness for an

extended period, and favoring fruit storage. Calcium applications maintain high total acidity values while generating low total soluble solids (TSS) values, delaying TSS peaks during postharvest. Calcium decreases ethylene production, delays the climacteric peak, and reduces its intensity, along with delaying color changes in fruits. Calcium also reduces the appearance of physiological disorders related to deficiencies, playing a crucial role in preventing disorders that affect fruit quality. It's noteworthy that the deficiency of this nutrient causes specific symptoms in each species.

## Conflict of interest statement

The authors declare that there is no conflict of interests regarding the publication of this article.

## Author's contributions

MJG wrote the initial draft and carried out the final revision of the manuscript. JAH wrote, carried out the revision of the manuscript, and translated the initial draft. GF revised and complemented the manuscript. All authors reviewed the final version of the manuscript.

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