Strontium as a tracer for calcium: uptake, transport and partitioning within tomato plants

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Abstract
Purpose Calcium (Ca$^{2+}$) is a major structural plant nutrient whose low mobility in the phloem causes deleterious nutritional disorders in non-transpiring organs. Since strontium (Sr$^{2+}$) and Ca$^{2+}$ share many chemical properties, Sr$^{2+}$ is frequently used as a tracer to study Ca$^{2+}$ cycles in ecosystems. However, the level of agreement between Sr$^{2+}$ and Ca$^{2+}$ distribution pattern in plants is debatable, and several studies have reported toxic effects of Sr$^{2+}$. Therefore, we investigated Sr$^{2+}$ and Ca$^{2+}$ uptake rates and distribution pattern to determine how reliably Sr$^{2+}$ can be used as a tracer of Ca$^{2+}$ in tomato plants (Solanum lycopersicum L.).

Methods We conducted six independent experiments of various duration: from a few hours to several weeks, in hydroponic and perlite substrate. We treated plants with either Ca$^{2+}$ or Sr$^{2+}$ at equivalent concentrations and monitored their accumulation in shoot and fruits.

Results Under short-term exposure (hours), Ca$^{2+}$ and Sr$^{2+}$ uptake and distribution within the plant were comparable, while the long-term exposure (days and weeks) to 4 mM Sr$^{2+}$ reduced transpiration and biomass accumulation. The toxic effect of Sr$^{2+}$ was more prominent when growth conditions were favourable. Nonetheless, Sr$^{2+}$ accumulated similarly to Ca$^{2+}$ in shoot and fruit. Surprisingly, Sr$^{2+}$ deposition in tomato fruit cell walls prevented blossom end rot (BER) to the same degree as Ca$^{2+}$.

Conclusion Sr$^{2+}$ can credibly be used as a tracer of Ca$^{2+}$ uptake and allocation in the short-term, making Sr$^{2+}$ a powerful tool to study the factors governing Ca$^{2+}$ allocation to plant organs, primarily fruit Ca$^{2+}$ delivery.

Keywords Calcium · Strontium · Tomato · Tracer · Blossom end rot (BER)
Introduction

Calcium (Ca) is an essential macronutrient for plants with vital structural, metabolic and signalling roles (Thor 2019). Ca has a role in stomatal movement, intracellular signal transduction, cell wall integrity (strength and elasticity), stress amelioration and resistance to fruit disease and disorders (White and Broadley 2003; Hocking et al. 2016; Parvin et al. 2019; Thor 2019). Ca is mainly present in the soil solution as a cation (Ca2+) originating mainly from mineral weathering release and atmospheric deposition (Drouet et al. 2005; Marschner 2011). Ca2+ enters the plant root system mostly with the water mass flow, moving via symplast or apoplast (Gilliham et al. 2011). The symplastic pathway is mainly used for short-distance Ca2+ delivery to the cells for the purpose of nutrition (metabolism s.str.) and signalling; in contrast, the apoplastic pathway (which is significantly dependent on transpiration rate) is primarily used for long-distance Ca2+ translocation into highly transpiring organs via xylem (González-Fontes et al. 2017). Transpiring organs tend to accumulate high Ca2+ levels while non-transpiring organs like fruits and tubers tend to have low Ca2+ concentration (Gilliham et al. 2011; Kumar et al. 2015; González-Fontes et al. 2017). When inside highly transpiring organs, Ca2+ is taken up by the cells and deposited inside vacuoles or sequestrated into leaf-trichomes, which imposes Ca2+ phloem immobility (White 2001; Gilliham et al. 2011; Kumar et al. 2015).

The function of Ca2+ in plants can be crudely divided into two groups: “nutritional (structural)” and “signalling”. Depending on the function, Ca2+ uptake and transport across plant biological membranes can be passive, mediated by non-selective ion channels, or active, mediated by Ca2+/ATP-ases and Ca2+/H+ exchangers (White and Broadley 2003; Demidchik et al. 2018; Thor 2019). Moreover, pathways of Ca2+ uptake and transport in plants, to the large degree, are not specific only to Ca2+; mono- and divalent cations (e.g. Mg2+, Rb+, Sr2+ and Ba2+) can also utilise these pathways (White and Broadley 2003; Moyen and Roblin 2010; Demidchik et al. 2018). Commonly used blockers of these pathways, at the root cell membrane level, are lanthanides (Gd3+ and La3+), dihy nes (Demidchik et al. 2002, 2018; Achary et al. 2013).

Ca2+ cross-links with pectin residues in the cell wall and modifies the activity and expression of various cell wall enzymes, strongly determining the physical and structural properties of fruits (de Freitas et al. 2012a; Martins et al. 2018). Unobstructed Ca2+ delivery is a prerequisite for normal fruit development and stress amelioration (Hocking et al. 2016; Parvin et al. 2019). Insufficient Ca2+ supply may cause membrane and cell wall breakdown, leading to the onset of various physiological disorders and shorter shelf life (Gerasopoulos and Drogoudi 2005; de Freitas et al. 2012a, b). The most widely recognised Ca2+ related disorders are blossom end rot (BER) in bell peppers and tomato (Hagassou et al. 2019; Mayorga-Gómez et al. 2020), bitter pit in apples (de Freitas et al. 2010) or internal rust in potato (Palta 2010). BER is a widespread disorder in tomato production, causing substantial economic damage. Symptoms typically include the development of the dark spot at the distal part of the tomato fruit (Taylor and Locascio 2004; Ho and White 2005; Hagassou et al. 2019).

Strontium (Sr) is an alkaline earth metal that is mainly found as an oxide in the Earth’s crust, released as an ion (Sr2+) during weathering of rocks or originating from anthropogenic sources. Sr2+ is typically found at low environmental concentration compared to Ca2+ (370 vs 36,500 ppm, in the soil) (Lide 2005; Burger and Lichtscheidl 2019). Four stable isotopes of Sr2+, have been identified: 84Sr, 0.56%; 86Sr, 9.87%; 87Sr, 7.04%; and 88Sr, 82.53% (Capo et al. 1998). The increased cycling of radio and stable Sr2+ isotopes through the biosphere via trophic chains in the last 50 years led to an increase in the number of scientific studies on the biological effect of Sr2+ (Gould et al. 2000). Some of these studies have shown that plants (e.g. sunflower) do not differentiate between the uptake of radioactive and stable strontium isotopes (Soudek et al. 2006).

The effect of Sr2+ on plants varies from a negative impact on the growth, photosynthesis, genetic material to a positive impact on the increase in the production of secondary metabolites and alleviation of calcium deficiency (the data varies with plant taxonomy and plant growth conditions) (Burger and Lichtscheidl 2019). Starting at low concentrations (about one mM, depending on the plant species and growing conditions), Sr2+ may exhibit a toxic effect on plants, which is reflected in the reduction of plant biomass,
chromosomal abnormalities and the destruction of the photosynthetic apparatus (Seregin and Kozhevnikova 2004; Kanter et al. 2010; Burger et al. 2019a, b).

Numerous studies have reported that Ca\(^{2+}\) and Sr\(^{2+}\) behave very similarly in the biosphere (Pett-Ridge et al. 2009) and lithosphere where Sr\(^{2+}\) can substitute Ca\(^{2+}\) in various minerals, including gypsum, calcite and dolomite (Coelho et al. 2017) due to similar physicochemical characteristics. The inability of plants to discriminate between these two elements has been shown in the soil of the forest ecosystems, inside plants organs of 138 plant families (Watanabe et al. 2007; Drouet and Herbauts 2008; Burger et al. 2019b) and in the field crop species of different families (Watanabe et al. 2016). It is interesting to note that several Arabidopsis accessions can discriminate between Ca\(^{2+}\) and Sr\(^{2+}\) in the growth medium (Kanter et al. 2010) and that Ca\(^{2+}\) concentration in the medium governs the process of discrimination.

Natural Sr\(^{2+}\) isotopes are increasingly used as tracers of Ca\(^{2+}\) in land and water ecosystems, mainly to characterise and monitor Ca\(^{2+}\) cycles in the biosphere and lithosphere (Åberg et al. 1990; Drouet et al. 2005; Drouet and Herbauts 2008; Peek and Clementz 2012). Moreover, Sr\(^{2+}\) is also used as a tracer of Ca\(^{2+}\) uptake and its symplastic and apoplastic transport to various plant organs: to fruits, fruit pedicel and leaves (Storey and Leigh 2004; Song et al. 2018; Rosen et al. 2019); to roots (McGonigle and Grant 2015) and embryos during development (Laszlo 1994). Some studies have established the direct connection between Ca\(^{2+}\) and Sr\(^{2+}\) allocation to the level of cell types (Storey and Leigh 2004), while others established an agreement in more general distribution patterns (Rosen et al. 2019). However, the level of agreement between uptake and distribution of Sr\(^{2+}\) and Ca\(^{2+}\) in plants is debatable. The physiological segregation of Sr\(^{2+}\) relative to Ca\(^{2+}\) does occur (Dasch et al. 2006; Watanabe et al. 2016), and several studies have reported toxic effects of Sr\(^{2+}\) (Burger et al. 2019a). Moreover, tissue and cellular distribution patterns of different ions can be linked to many processes, including plants’ mechanisms to withstand abiotic stresses (Pongrac et al. 2013), which possibly can be an additional source of differences between Ca\(^{2+}\) and Sr\(^{2+}\) plant uptake and distribution.

With this in mind, the potential of utilising Sr\(^{2+}\) as a tracer of Ca\(^{2+}\) uptake and transport is not yet well understood. The Sr\(^{2+}\) uptake and transport require more attention, especially considering the toxic effects of Sr\(^{2+}\) on plants related to the experimental conditions, duration of exposure and Sr\(^{2+}\) concentrations. Furthermore, the degree of similarity between Ca\(^{2+}\) and Sr\(^{2+}\) related to partitioning within different plant organs (e.g. fruits and leaves) of different plant species, under different environmental conditions and the possible physiological role of Sr\(^{2+}\) are not that well established (Dasch et al. 2006; Watanabe et al. 2016). The current study’s objective was to evaluate the feasibility of using a stable isotope of Sr\(^{2+}\) (\(^{88}\)Sr as SrCl\(_2\)) as a short and long-term tracer for Ca\(^{2+}\) uptake and distribution within tomato plants and to assess Sr\(^{2+}\) toxicity as affected by the duration of the exposure. The utilisation of non-radioactive Sr\(^{2+}\) isotopes to monitor Ca\(^{2+}\) transport may provide us with a simple but powerful tool for studying environmental factors determining Ca\(^{2+}\) allocation to different plant organs and, specifically, fruits.

Materials and methods

We have conducted six independent experiments on tomato plants (Solanum lycopersicum L. var. Brigade, Hishtil Nursery, Israel): four long-term experiments conducted in perlite and two short-term experiments conducted in hydroponics (Table 1). In all experiments, plants were treated with Ca\(^{2+}\) or Sr\(^{2+}\), separately, to avoid the interaction of these two elements at the plant cell membrane (Moyen and Roblin 2013).

Long-term Sr\(^{2+}\) exposure experiments

Four independent long-term experiments were conducted at various environmental conditions detailed in Table 1 (Exp 1—4). Tomato plants were grown in soilless culture using perlite substrate with a particle size of 0.075–1.5 mm (Agrikal, Israel). Plants were grown in net house or greenhouse at the Gilat Research Centre, southern Israel (31°21’N, 34°42’E). Plants were irrigated at excess three times a day with an irrigation solution containing 100 mg l\(^{-1}\) N-NO\(_3\), 10 mg l\(^{-1}\) N-NH\(_4\), 5 mg l\(^{-1}\) P, 80 mg l\(^{-1}\) K, 15 mg l\(^{-1}\) Mg, and 35 mg l\(^{-1}\) Ca. Microelements were supplied by liquid chelated solution (Koratin, Deshanim, Israel). Five to six weeks after planting,
when plants had four to five fruitlets, three treatments were applied: Ca2+ nutrition ("+Ca") and no Sr2+ and no Ca2+ and no Sr2+ ("-Ca/-Sr"), (Table 1. Exp. 1–4). The remaining nutrients and irrigation pattern remained the same for all treatments. Plants were treated for 24 to 40 days. At the end of the experiments, the plants were harvested, and shoot and fruit biomass was determined. The development of blossom end rot (BER) was quantified by visually observing and counting the dark spot symptoms developed on and inside each tomato fruit. All plant material was oven-dried on 70 °C for a minimum of 72 h, ball grounded (Mixer Mill MM 400, Retsch GmbH, Germany), digested using a microwave digestion system (MARS 6, CEM Corporation, USA) and analysed for mineral concentration using ICP-OES (ICP-OES 5100, Agilent Technologies Inc., USA). The results of the four independent long-term experiments (Exp. 1 - 4) are presented on Fig. 3, while each individual long-term experiment has been presented on supplementary Figs. S1, S2, S3 and S4.

Table 1  Description of all the Sr2+ exposure experiments conducted at Gilat

| Exp. # | Time frame of the whole experiment | Treatmentb | Length of the treatment | Temperature during the exposure | Humidity during the exposure | n |
|--------|-----------------------------------|------------|------------------------|-------------------------------|-----------------------------|---|
| 1.     | September-December 2016; greenhouse, perlite | + Ca (1 mM CaCl2) + Sr (1 mM SrCl2) -Ca/-Sr (No Ca and no Sr) | 40 days | Max: 30 °C Min: 7 °C Average: 18 °C | ND | 5 |
| 2.     | July–October 2017; greenhouse perlite | + Ca (2 mM CaCl2) + Sr (2 mM SrCl2) -Ca/-Sr (No Ca and no Sr) | 26 days | Max: 31 °C Min: 16 °C Average: 23 °C | ND | 5 |
| 3.     | June–September 2018; net-house perlite | + Ca (4 mM CaCl2) + Sr (4 mM SrCl2) -Ca/-Sr (No Ca and no Sr) | 29 days | Max: 42 °C Min: 20 °C Average: 28 °C | Max: 90% Min: 31% Average:66% | 5 |
| 4.     | October-January 2018–2019; net-house perlite | + Ca (4 mM CaCl2) + Sr (4 mM SrCl2) -Ca/-Sr (No Ca and no Sr) | 24 days | Max: 28 °C Min: 6 °C Average: 14 °C | Max: 94% Min: 30% Average:70% | 8 |
| 5.     | July 2019 greenhouse, hydroponics | + Ca (4 mM CaCl2) + Sr (4 mM CaCl2) | 20.5 h | Day: 33 °C Night: 23 °C | Max: 94% Min: 30% Average:70% | 4 |
| 6.     | July 2020, growth room, hydroponics, Night 12 h /Day 12 h | No blockers | 4 h | Day: 25 °C Night: 21 °C | Day: 65% Night: 83% | 8 |

aBackground for all treatments in the Exp. 1-4 is Ca-free fertilizer: 100 mg l⁻¹ N-NO₃, 10 mg l⁻¹ N-NH₄, 5 mg l⁻¹ P, 80 mg l⁻¹ K, 15 mg l⁻¹ Mg + liquid chelated microelement solution

bBackground for all treatments in the Exp. 5 is Ca-free fertilizer: 56 mg l⁻¹ N-NO₃; 6 mg l⁻¹ N-NH₄; 14 mg l⁻¹ P; 69 mg l⁻¹ K; 27 mg l⁻¹ S; 19 mg l⁻¹ Mg; 76 mg l⁻¹ Cl; 50 mg l⁻¹ Na; 1.2 mg l⁻¹ Fe; pH = 7.2-7.8, EC = 660-731 μS

Gas exchange measurement

In Exp. 3 and Exp. 4, the stomatal conductance to H₂O (gₛ) and photosynthetic rate (A) of fully expanded leaves were measured using the CIRAS-III.
portable photosynthesis system (PP Systems, USA) on the first, second and ninth day after starting the treatment. The CIRAS-III system was equipped with a modular LED chamber head, set to the photosynthetic photon flux density of 1,000 μmol photons m$^{-2}$ s$^{-1}$, with the reference CO$_2$ concentration of 400 μmol mol$^{-1}$, and leaf temperature of 25 °C. Measurements were taken on the morning of a clear day (between 8:00 h and 10:00 h).

Scanning electron microscopy of the fruits

Intact tomato fruits from Exp. 4 (Table 1) were kept at 4°C in 70% ethanol until further processing. Before the scanning, freehand sections of the outer pericarp containing epidermis and vascular bundles were made using a razor blade, six sections per treatment. The sections were rehydrated two times for 10 min in double-distilled water and placed inside the microscope’s low vacuum chamber. A scanning electron microscope (SEM, VEGA3, Tescan, Czech Republic) equipped with EDS (Energy-dispersive X-ray spectroscopy) detector (model X-act, Oxford Instruments, UK) and AZTec Software (AZtec—Nanoanalysis, Oxford Instruments) was used for scanning as described in Tan et al. (2020). Briefly, the SEM’s acceleration potential was set to 30 kV, working distance to 15 mm, beam intensity to 15 units (20 units is the highest setting in our software), chamber pressure to 10 Pa (low vacuum), the spot size was 280 nm and the emission current was 47 μA. On the EDS, the following elements were selected for scanning: C, O, Na, Mg, P, K, Ca and Sr, while the processing time was set to level 5 (out of 6 levels offered in the software), number of frames to 1, pixel dwell time to 15 μs, frame time was 15.72 s and resolution was 1024×1024 pixels. Scan time per spot was approximately 42 s while the total scanning time per sample was approximately 180 s. A representative fruit tissue scan is presented in Fig. 1. Ca and Sr results were averaged for four separate scanning points and expressed as weight percentages of total analysed elements.

Short-term Sr$^{2+}$ exposure experiments

Two short-term Sr$^{2+}$ exposure experiments (Table 1, Exp. 5—6) were conducted on tomato plants in a hydroponics system. Plants were grown in a 1:1,000 solution of the commercial 5–3-8 NPK fertiliser (Shefer+, Deshanim, Israel) for two weeks (first flowers).

Diurnal nutrients uptake

Exp. 5 was conducted in a greenhouse to describe the diurnal uptake rate of Ca$^{2+}$ and Sr$^{2+}$. Plants were washed in distilled water and separated into two groups (n=4) and exposed to either: 4 mM Ca$^{2+}$ or Sr$^{2+}$ dissolved in Ca-free fertilizer (56 mg l$^{-1}$ N-NO$_3$; 6 mg l$^{-1}$ N-NH$_4$; 14 mg l$^{-1}$ P; 69 mg l$^{-1}$ K; 27 mg l$^{-1}$ S; 19 mg l$^{-1}$ Mg; 76 mg l$^{-1}$ Cl; 50 mg l$^{-1}$ Na; 1.2 mg l$^{-1}$ Fe; pH=7.2–7.8, EC=660–731 μS).

The exposure lasted for 20.5 h (8.5 h of the night and 12 h of daylight). The “nutrient depletion” method was used to determine the diurnal uptake rate of Sr$^{2+}$ and Ca$^{2+}$, using the elements’ mass in the solution (at the beginning and the end of the exposure), the element’s molar weight and the duration of the uptake. The nutrient solution sampling was done every three hours. The “nutrient depletion” method was verified by conducting destructive tissue analysis (Fig. 2).
C₁—element’s concentration at the beginning of the exposure (mg L⁻¹).

C₂—element’s concentration at the end of the exposure (mg L⁻¹).

V₁—the volume of the solution at the beginning of the exposure (L).

V₂—the volume of the solution at the end of the exposure. (L).

MW—the molar weight of the element (g mol⁻¹).

\[
Uptake\ (\text{mmol h}^{-1}) = \frac{\left[ (C_1 \times V_1) - (C_2 \times V_2) \right]}{MW} \times 1000 \times \frac{\text{Duration of the uptake (hr)}}{1000}
\]

Ca²⁺ / Sr²⁺ blockers

Exp. 6 was conducted in a 3.7 by 6.1 m growth room equipped with a ventilator, AC, humidifier and dehumidifier connected to a controller. Photosynthetic light (Solar system 550, California lightworks, US) conditions were: 12 h light / dark and light intensity of 680 μE m⁻² s⁻¹. Following two weeks of growth, roots were washed in distilled water and plants were divided into three groups (“No blockers”, “Lanthanum” and “Gadolinium”, n=8), each with two sub-groups (“Ca” and “Sr”, n=4), and treated for four hours (distilled water; 4 mM LaCl₃ and 4 mM GdCl₃; 4 mM CaCl₂ and 4 mM SrCl₂, respectively).

The “nutrient depletion” method was used to determine the uptake rate of Sr²⁺ and Ca²⁺, using the elements’ mass in the solution (at the beginning and the end), duration of the uptake, and roots’ surface area. The elemental analysis of the solution and the plant material was done using ICP-OES (ICP-OES 5100, Agilent Technologies Inc., USA). Root surface area was measured by digital images on a flat-bed scanner (Expression 11000XL, Epson, Japan) and analysed using WinRhizo software (WinRhizo 2016a, Regent Instruments Inc. Canada). Water uptake was measured by recording the solution’s mass at the beginning and the end of the experiment.

Statistical analyses

All experiments’ setup was a complete randomisation design; the number of replicates is indicated next to each experiment in Table 1. Statistical analysis was done by JMP 14 software (JMP, SAS Institute, USA). The linear regression was fitted and tested to the correlation between Sr²⁺ uptake by “solution depletion” versus tissue analysis. The results of the remaining experiments were averaged, tested by ANOVA. To test the long-term effect of Ca versus Sr across four independent experiments (experiments 1 to 4, Table 1), we combined the experiments using the ANCOVA model testing the treatments effect as an independent variable (3 levels) and the experiment # as covariant (4 levels). Results are expressed as least square means (adjusted according to the covariant, n=23) rather than the simple arithmetic mean. If the treatment effect was significant, groups were compared using Tukey’s HSD-test. Results were plotted on graphs together with standard errors, generated using GraphPad Prism 6 (GraphPad Software, Inc. USA).

Results

Long-term response to strontium

In Fig. 3, we present the combination of the four long-term experiments. The data of each individual experiment is presented in the supplementary file (Figs. S1, S2, S3 and S4). Following long-term exposure to CaCl₂, SrCl₂ or Ca-free fertiliser (labelled as “+Ca”, “+Sr” and “-Ca/-Sr” respectively, Fig. 3), plant biomass (shoot + fruit)
was significantly higher in the “+Ca” compared to the “+Sr” treatment (Fig. 3a). The percentage of fruit with visual external and internal symptoms of BER was markedly high in “-Ca/-Sr” plants (47%), lower in “+Ca” (17%) and lowest in the “+Sr” (13%) (Fig. 3b). The concentration of Ca$^{2+}$ in the shoot and fruit was the highest in the “+Ca” group, while there was no difference between the two other groups (“-Ca/-Sr” and “+Sr”). Sr$^{2+}$ was only detectable in the group treated with SrCl$_2$. Moreover, the combined Ca$^{2+}$ and Sr$^{2+}$ concentration in the group “+Sr” was at a similar level as Ca$^{2+}$ concentration in the group “+Ca” (e.g. fruits: Ca$^{2+}$+Sr$^{2+}$ = 0.078 mol kg$^{-1}$ while Ca$^{2+}$ = 0.071 mol kg$^{-1}$) (Fig. 3c, d).

In the Exp. 4, stomatal conductance and net photosynthesis were measured on the second and the ninth day after the treatments’ initiation. After two days, Ca$^{2+}$/Sr$^{2+}$ treatments did not affect stomatal conductance and net photosynthesis (Fig. 4a, b). On the ninth day, a significant reduction of both parameters was observed only in the group “+Sr” but not in the “-Ca/-Sr” (Fig. 4a, b). Moreover, a similar response was observed in Exp. 3 (Table 1.) while the decrease of both parameters during the ninth day was observed in the “-Ca/-Sr” group also (Fig. S5).

The data obtained using the SEM coupled with EDS showed that the relative cell wall concentration of Ca$^{2+}$ (in the groups not supplied with Ca$^{2+}$) were 0.1—0.085%, (Fig. 5), less than half of the concentration of the group supplied with Ca
In groups that were not supplied with Sr²⁺, no Sr²⁺ was detected. In the group "+Sr", the relative Sr²+ concentration was not significantly different from the Ca²+ concentration in the group "+Ca". ("+Sr": Ca²+ + Sr²+ = 0.212% while "+Ca": Ca²+ = 0.252%).

Diurnal uptake of Ca²+ and Sr²+

In Exp. 5, water and nutrients uptake were measured every three hours. The diurnal pattern of water uptake was similar for both treatments ("+Ca" and "+Sr") except for the midday peak that was moderately and significantly higher in the "+Ca" group (Fig. 6a). The diurnal uptake rates of Ca²+ and Sr²+ were comparable, except at the beginning of the exposure, at 21:30 h, when the Sr²+ uptake rate was significantly higher (Fig. 6b) (refer to Discussion, “The uptake rate and translocation pattern of Ca²+ and Sr²+ in tomato”).

The average uptake during the day was moderately and significantly higher in the "+Ca" compared to the "+Sr", while during the night, uptake rates were similar (Fig. 6c). Moreover, the day uptake rates of both Ca²+ and Sr²+ were twice as high as the night uptake rates (Day: Ca²+ 0.042 mmol h⁻¹, Sr²+ 0.036 mmol h⁻¹; Night: Ca²+ 0.020 mmol h⁻¹, Sr²+ 0.019 mmol h⁻¹ excluding the first data point at 21:30 h) (Fig. 6c).

The effect of Ca²⁺ channel blockers on the uptake of Ca²⁺ and Sr²⁺

In Exp. 6, when no blockers were applied, the uptake of Ca²⁺ and Sr²⁺ was similar (Fig. 7 “No blockers”). In the two groups treated with blockers (Fig. 7, “Lanthanum” and “Gadolinium”), the uptake of Ca²⁺ and Sr²⁺ was significantly lowered, showing a statistical difference compared to not treated plants (the Ca²⁺ and Sr²⁺ uptake halved).
Moreover, in both groups treated with blockers, the uptake of Ca\(^{2+}\) was somewhat lower than Sr\(^{2+}\) but not significantly.

**Discussion**

Ca\(^{2+}\) is a major structural and regulatory plant nutrient whose function strongly determines and regulates the structural properties of plant cell walls (de Freitas et al. 2012a; Martins et al. 2018). The low mobility of Ca\(^{2+}\) in the phloem can lead to several nutritional disorders such as BER in tomato and pepper, internal rust in potato and bitter pit in apples (de Freitas et al. 2010; Palta 2010; de Freitas and Mitcham 2012; Hagassou et al. 2019; Mayorga-Gómez et al. 2020). Therefore, it is crucial to monitor and understand the factors governing the Ca\(^{2+}\) allocation within the plant, for which Ca\(^{2+}\) or Sr\(^{2+}\) stable isotopes are the most common tracer tool (Kalcsits et al. 2017; Song et al. 2018). Stable (\(^{44}\)Ca) and radioactive (\(^{45}\)Ca) Ca\(^{2+}\) isotopes have been extensively used as tracers of plant Ca\(^{2+}\) distribution (Shear and Faust 1970; van der Heijden et al. 2014; Kalcsits et al. 2017). Nevertheless, the use of isotopes requires expensive and not readily available equipment and is subject to special safety
and health regulation in the case of radioisotopes. Moreover, radioisotopes, in general, are currently used mostly in live plant imaging of nutrient uptake and distribution and new and advanced imaging techniques are being developed (Sugita et al. 2016). Compared to Ca\textsuperscript{2+} stable and radioisotopes, the stable Sr\textsuperscript{2+} isotope (\textsuperscript{88}Sr) has many advantages: it is accessible, cheap, safe and simple to analyze. Here we demonstrated that in tomatoes, Ca\textsuperscript{2+} and Sr\textsuperscript{2+} uptake and allocation within the plant are comparable in the short-term (on a time scale between two to twenty hours), while in the long-term, nutrition with Sr\textsuperscript{2+} has detrimental effects starting from decreased transpiration to impaired biomass production. Nonetheless, we show that Sr\textsuperscript{2+} accumulates in a manner similar to Ca\textsuperscript{2+} in tomato plant tissues, specifically in tomato fruit cell walls, helping to prevent BER.

The uptake rate and translocation pattern of Ca\textsuperscript{2+} and Sr\textsuperscript{2+} in tomato

Previous studies demonstrated that Ca\textsuperscript{2+} and Sr\textsuperscript{2+} behave similarly in the biosphere and that most plants cannot discriminate between them at their biospheric concentrations (Watanabe et al. 2007, 2016; Drouet and Herbauts 2008; Burger et al. 2019b). Therefore, Sr\textsuperscript{2+} has been used as a long- and short-term tracer of Ca\textsuperscript{2+} uptake and transport to all plant organs (Laszlo 1994; Storey and Leigh 2004; McGonigle and Grant 2015; Song et al. 2018; Rosen et al. 2019). However, data on comparing Ca\textsuperscript{2+} and Sr\textsuperscript{2+} uptake and translocation in tomato plants are scarce (Bowen and Dymond 1956; Seligmann et al. 2009), and to our knowledge, studies on using Sr\textsuperscript{2+} as a specific tracer of Ca\textsuperscript{2+} in tomato plants have not been done.

Our current study found that the diurnal uptake rate of Sr\textsuperscript{2+} and Ca\textsuperscript{2+} in the short-term experiments was comparable (Fig. 6b, c) and that tomato plants do not distinguish between Ca\textsuperscript{2+} and Sr\textsuperscript{2+} in the short-term. The results agree with an early hydroponic study which showed that tomato plants do not distinguish between Ca\textsuperscript{2+} and Sr\textsuperscript{2+} (Bowen and Dymond 1956).

Notably, at the first measuring point of the diurnal uptake dynamic (Fig. 6b, at 21:30 h), the uptake rates of Ca\textsuperscript{2+} and Sr\textsuperscript{2+} were transiently significantly different, with the uptake rate of Sr\textsuperscript{2+} being much higher. This transient uptake increase might be because of the i) immediate and concentration-dependent effect of Sr\textsuperscript{2+} on the depolarisation of the root cell membrane (lasting for up to two hours and probably mediated by the voltage-dependent ion channels); ii) adsorption of Sr\textsuperscript{2+} onto root cell walls (Seligmann et al. 2009; Moyen and Roblin 2010; Moyen et al. 2011). The Sr\textsuperscript{2+} concentrations used (1–4 mM) in all our experiments falls in the range of concentrations known to cause these effects (1–10 mM). Nevertheless, in long-term Sr\textsuperscript{2+} exposure experiments, tomato plants accumulated Ca\textsuperscript{2+} and Sr\textsuperscript{2+} at comparable rates (Fig. 3, S1, S2, S3 and S4), indicating that the differences in the uptake rates are transient.

The Ca\textsuperscript{2+} and Sr\textsuperscript{2+} accumulation in tomato fruit cell wall

The inability of many plants to distinguish between Ca\textsuperscript{2+} and Sr\textsuperscript{2+} has been shown in the literature (Watanabe et al. 2007, 2016; Drouet and Herbauts 2008), yet their transport and allocation within plant organs are not well described. In the current study, we showed that Sr\textsuperscript{2+} allocation to tomato fruit is comparable to Ca\textsuperscript{2+}. Using EDS detector on fruit pericarp sections (Fig. 1), we showed that Ca\textsuperscript{2+} and Sr\textsuperscript{2+} accumulated in the same weight percentages in the fruit’s cell walls, strongly suggesting that Ca\textsuperscript{2+} and Sr\textsuperscript{2+} share uptake and translocation pathways in tomato. The EDS results are congruent with the destructive mineral analysis (Fig. 3d). Moreover, previous studies support our observation on cell wall Ca\textsuperscript{2+} and Sr\textsuperscript{2+} allocation (Brambilla et al. 2002; Von Fircks et al. 2002; Burger and Lichtscheidl 2019). Specific co-localisation and comparable sink capacity of Ca\textsuperscript{2+} and Sr\textsuperscript{2+} in the “cell wall sac” of idioblasts in Morus alba L. has been shown by Katayama et al. (2013). The comparable uptake and allocation of Sr\textsuperscript{2+} and Ca\textsuperscript{2+} do not necessarily mean that Sr\textsuperscript{2+} can replace Ca\textsuperscript{2+} in its physiological roles. Here we report (to our knowledge, for the first time) that the application of Sr\textsuperscript{2+} strongly mitigated the development of BER to a level identical to Ca\textsuperscript{2+} (Figs. 3b, S1b, S2b, S3b and S4b).

The development of BER in tomato is multivariable but is always related to the fruit Ca\textsuperscript{2+} concentration, partitioning and distribution (Ho and White 2005; Hagassou et al. 2019), which in turn is strongly connected with the class of enzymes called “Pectin methylesterases” (PMEs). PMEs create Ca\textsuperscript{2+} binding sites in the cell wall and directly modify cell wall properties. De Freitas et al. (2012a, b) have shown
that the reduction in the activity of PMEs can directly determine \( \text{Ca}^{2+} \) partitioning and distribution in tomato fruits by reducing the amount of \( \text{Ca}^{2+} \) bound to the cell wall and decreasing BER development in tomato (more water-soluble apoplastic \( \text{Ca}^{2+} \)—less BER). Moreover, the work of Wu et al. (2018) and Anthon and Barrett (2006) supports the idea that stress (particularly heat stress) activates the PMEs, additionally depleting water-soluble apoplastic \( \text{Ca}^{2+} \), consequently leading to more pronounced stress symptoms. Our supposition is that \( \text{Sr}^{2+} \) can partly replace \( \text{Ca}^{2+} \) in the cell wall, competing with \( \text{Ca}^{2+} \) for \( \text{Ca}^{2+} \)-binding sites, particularly during stress, slowing down the depletion of the water-soluble apoplastic \( \\text{Ca}^{2+} \), which in turn mitigates the development of BER. This hypothesis needs to be verified by further study.

\( \text{Sr}^{2+} \) uptake pathway in tomato

No specific \( \text{Sr}^{2+} \) transporters in plants have been reported to the best of our knowledge. Nevertheless, non-selective cation channels, which are pathways of \( \text{Ca}^{2+} \) and \( \text{K}^{+} \) uptake, can also be utilised by other cations, including \( \text{Sr}^{2+} \) (White and Broadley 2003; Kanter et al. 2010; Moyen and Roblin 2010; Demidchik et al. 2018). Lanthanum (\( \text{La}^{3+} \)) and gadolinium (\( \text{Gd}^{3+} \)) influence the \( \text{Ca}^{2+} \) uptake, at the level of the root cell membrane, by physically blocking the pore of non-selective cation channels and by competing with \( \text{Ca}^{2+} \) for the \( \text{Ca}^{2+} \)-binding sites (Demidchik et al. 2002, 2018; Demidchik and Maathuis 2007; De Vriese et al. 2018). Using these blockers, we showed a comparable decrease in the uptake rate of both the \( \text{Ca}^{2+} \) and the \( \text{Sr}^{2+} \) (Fig. 7), indicating that \( \text{Ca}^{2+} \) and \( \text{Sr}^{2+} \) share a part of the channel pathway in tomato plants. The uptake of elements was not completely suppressed, and a certain amount of \( \text{Ca}^{2+} \) and \( \text{Sr}^{2+} \) was uptaken by the plant (removed from the solution) (Fig. 7). There has been much debate in the last 20 years about the specific pathways of \( \text{Ca}^{2+} \) uptake into the roots and how it is transported into the xylem. A certain amount of evidence suggests that direct apoplastic uptake might play a substantial role in the process (White 2001; Thor 2019). Considering that \( \text{Ca}^{2+} \) and \( \text{Sr}^{2+} \) have been uptaken at the same rate, even in the presence of the blockers, it might be feasible that these two elements also share a possible root apoplastic uptake pathway; this hypothesis needs to be investigated further.

\( \text{Sr}^{2+} \) toxicity in tomato, related to the duration of exposure

Strontium toxicity to plants is well established (Burger and Lichtscheidl 2019), with toxic symptoms likely depending on the duration of the exposure and the concentration of \( \text{Sr}^{2+} \). This fact raises the following question, under which conditions can we utilise “\( \text{Sr}^{2+} \) as a tracer for \( \text{Ca}^{2+} \)” without experiencing the adverse, toxic effects? In a study on tomato seedling grown in agar medium for two weeks, \( \text{Sr}^{2+} \) toxicity leads to a significant reduction in shoot and root biomass at \( \text{Sr}^{2+} \) concentration of 4 mM and above (Nagata 2019). Accordingly, in our current study, the addition of \( \text{Sr}^{2+} \) led to decreased stomatal conductance and net photosynthesis nine days after initiation of the treatments but not in the first 48 h of the application (Fig. 4 and S5). Minor, but a significant decrease in ET of \( \text{Sr}^{2+} \) treated plants was measured in mid-day only of the short-term hydroponic trial (Fig. 6a). These results indicate that in short-term trials, at concentrations of 1–4 mM, \( \text{Sr}^{2+} \) toxicity effects are minor and that \( \text{Sr}^{2+} \) is a reasonably reliable tracer. That does not hold for longer trials (over a few days). In the long-term experiments, the addition of \( \text{Sr}^{2+} \) had a significant adverse effect on the shoot biomass only in the experiments conducted in the summer (Exp. 2 and 3; Fig. S2 and S3), indicating that the acceleration of \( \text{Sr}^{2+} \) accumulation with high illumination and temperature had probably led to a faster expression of the toxic effects (Kondo et al. 2003). These results are in accordance with Burger and Lichtscheidl (2019), which concluded that an increase in light intensity and temperature would drive the acceleration in \( \text{Sr}^{2+} \) uptake, while the \( \text{Sr}^{2+} \) accumulation itself will lead to phytotoxicity.

Conclusion

Our results indicate that in tomato plants, \( \text{Sr}^{2+} \) is comparable to \( \text{Ca}^{2+} \) in terms of uptake rate and, more importantly, in its distribution within plant organs, most notably tomato fruits. Using acknowledged \( \text{Ca}^{2+} \) blockers, we have shown that \( \text{Ca}^{2+} \) and \( \text{Sr}^{2+} \) most probably share similar molecular uptake pathway.
Additionally, when Sr\(^{2+}\) is deposited in the fruit cell wall, it can partly substitute for Ca\(^{2+}\) and prevent BER formation. Therefore, we conclude that Sr\(^{2+}\) can act as a reliable tracer for Ca\(^{2+}\) in short-term experiments conducted on different tomato organs. However, in the long-term studies, Sr\(^{2+}\) toxicity impairs photosynthesis and overall plant performance, slightly hindering its use as the reliable Ca\(^{2+}\) tracer. Furthermore, under conditions that stimulate growth, the establishment and manifestation of Sr\(^{2+}\) toxicity is expected to be faster.

The utilisation of Sr\(^{2+}\) as a tracer to study Ca\(^{2+}\) uptake and allocation can be used as an essential tool for understanding the environmental factors governing Ca\(^{2+}\) delivery to different plant organs, notably, fruit Ca\(^{2+}\) delivery. Such tools may support the development of new strategies aimed at mitigating fruit physiological disorders related to limited Ca\(^{2+}\) supply, affecting many fleshy fruit producers worldwide.

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**Declarations**

**Ethics approval** All authors declare that this article does not contain any studies with human participants or animals.

**Consent to participate** Not relevant to the study.

**Consent for publication** All authors also declare that they have read the manuscript in full and approved the manuscript submission.

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